Lat. Am. J. Aquat. Res., 42(3): 401-417, 2014
DOI: 103856/vol42-issue3-fulltext-2

Research Article

Diel variation in the vertical distribution of fish larvae forced by upwelling filaments off Punta Angamos (northern Chile)

Pablo M. Rojas[1]
[1]División de Investigación en Acuicultura, Instituto de Fomento Pesquero (IFOP)
Balmaceda 252, Puerto Montt, Chile

ABSTRACT. The role of daily vertical migration (DVM) of ichthyoplanktonic associations off Punta Angamos, in northern Chile, was examined. In September 1998 and January 1999, two oceanographic surveys were conducted during coastal upwelling events. Fish larvae were collected during the day/night in three depth strata (0-20, 20-80 and 80-200 m) and inside/outside of upwelling filaments. The study area was dominated by a southward flow along 200 m depth; meanwhile, the Ekman layer did not exceed 20 m depth. The greatest accumulation of larvae was found in the middle layer (20-80 m), where the current velocity was low and did not interact with the circulation associated with upwelling the filament formation. Most fish larvae were found in non-upwelling waters in the middle stratum. Independent of the origin of water (upwelling/non-upwelling), larvae of *Dioge-nichthys laternatus* (Myctophidae), *Engraulis ringens* (Engraulidae) and *Bathylagus nigrigenys* (Bathylagidae) showed a deeper vertical distribution during the day, suggesting a daily vertical migration. This behavior can potentially increase retention of larvae near the coast in productive areas through vertical evasion of the Ekman layer during upwelling events.

Keywords: fish larvae assemblages, vertical migratory behaviour, upwelling filament, northern Chile.

Variación diaria en la distribución vertical de larvas de peces forzada por filamentos de surgencia frente a Punta Angamos (norte de Chile)

RESUMEN. Se analizó el papel de la migración vertical diaria (DVM) en las asociaciones ictioplanctónicas frente a Punta Angamos (23°29'S, 70°59'W) norte de Chile. En septiembre de 1998 y enero de 1999 se realizaron dos campañas oceanográficas durante eventos de surgencia costera. Las larvas de peces fueron recolectadas durante el día/noche en tres estratos de profundidad (0-20, 20-80 y 80-200 m) y dentro/fuera de filamentos de surgencia. El área de estudio estuvo dominada por un flujo hacia el sur a lo largo de 200 m de profundidad, mientras que la capa de Ekman no excedió los 20 m. La mayor acumulación de larvas se encontró en el estrato medio (20-80 m), donde la velocidad de las corrientes fue baja y no interactuó con la circulación asociada a la formación de filamentos de surgencia. La mayoría de las larvas de peces fueron encontradas en aguas de no-surgencia en el estrato medio. Independiente del origen del agua (surgencia/no-surgencia), las larvas de *Diogenichthys laternatus* (Myctophidae), *Engraulis ringens* (Engraulidae) y *Bathylagus nigrigenys* (Bathylagidae) mostraron una distribución vertical más profunda durante el día que por la noche, lo que sugiere una migración vertical diaria. Este comportamiento de las larvas puede potencialmente aumentar la retención cerca de la costa en áreas productivas mediante la evasión vertical de la capa de Ekman durante eventos de surgencia.

Palabras clave: asociaciones ictioplantónicas, comportamiento migratorio vertical, filamentos de surgencia, norte de Chile.

INTRODUCTION

The interaction between vertical distribution, migration and hydrodynamic processes is of special importance to the horizontal distribution of fish larvae in coastal upwelling regions and adjacent areas (Parrish *et al*., 1981; Norcross & Shaw, 1984; Olivar, 1990; Smith & Suthers, 1999). Recent studies in the Gulf of California have shown the importance of the thermocline and the mixed layer for the vertical distribution of fish larvae (Danell-Jiménez *et al*., 2009; Inda-Díaz *et al*., 2010). Fish eggs and larvae with near-surface distribution are more susceptible to the offshore transport in the Ekman layer associated with coastal upwelling (John & Re,

---

Corresponding author: Pablo M. Rojas (pablo.rojas@ifop.cl)

1995; Smith & Suthers, 1999; Rojas *et al*., 2002). In the vertical plane, current speed is of a magnitude that allows fish larvae and other planktonic organisms to conduct vertical migrations through the water column (Munk *et al*., 1989; Pringle, 2007). As the intensity of currents can vary along the water column, the vertical distribution may affect the horizontal dispersal of fish larvae and thus the drift of larval cohorts to their nursery areas.

Fish larvae migrate vertically at two temporal scales: they accompany most of zooplankton in its diel or subdiel (*e.g.*, tidal) migration and their mean preferred depth also seems to change as they develop (Fortier & Harris, 1989; Paris & Cowen, 2004; Leis *et al*., 2005). The most common pattern of larval migration is the movement toward the top of the water column during the night, and the descent toward deeper waters during daytime (Tsukamoto *et al*., 2001). However, the reverse pattern has also been seen (Brodeur & Rugen, 1994), as well as fish larval disperse during the night and aggregate in daytime (Brewer & Kleppel, 1986; Munk *et al*., 1989).

The vertical distribution of zooplanktonic organisms has been observed to correlate with many environmental factors, such as light intensity (Job & Bellwood, 2000; Guizien *et al*., 2006), temperature (Annis, 2005), or the depth of pycnocline (Munk *et al*., 1989), thermocline (Boehlert *et al*., 1992; Annis, 2005) and chlorophyll maximum (Lampert *et al*., 2003). In most cases, these correlations relate to diel or subdiel movements and presumably result from a trade-off among reaching high concentrations of food near the surface or around the clines (Munk *et al*., 1989) and avoiding surface-dwelling visual predators (Fiksen & Giske, 1995), and cold water at depth which slows down growth (Lampert *et al*., 2003). The advantages of the vertical migration are generally proposed to be light-related predator avoidance (Yamashita *et al*., 1985), the pursuit of zooplankton prey (Fortier & Leggett, 1983; Munk *et al*., 1989), facilitation of larval transport in varying tidal currents (Hare & Govoni, 2005), optimization of the energetic advantage gained by larvae at certain depths in thermally stratified water (Neilson & Perry, 1990), pursuit of optimum light conditions for larval survival (Hurst *et al*., 2009), rhythms of swim bladder inflation (Stenevik *et al*., 2007), and a strategy to guarantee their retention in shallow waters, the latter of crucial importance in upwelling regions. In upwelling areas, the diel vertical position of fish larvae determines if they are retained in shallow and productive waters or advected offshore, and larvae with near-surface distributions are more susceptible to offshore transport associated with coastal upwelling than deeper distributions that render larvae to shoreward transport (Rodriguez, 1990; Hernández-León *et al*., 2007).

Eggs and fish larvae may be subjected to intense alongshore and cross-shelf flow in upwelling ecosystems, such that the ability to develop or adopt retention mechanisms near the upwelling centres may play a relevant role to maintain local populations (Wing *et al*., 1998; Pringle, 2007) and hence successful recruitment. Among proposed retention mechanisms, diel vertical migration (DVM) through the use of reversing vertical flows (Peterson, 1998; Morgan & Fisher, 2010) has been hypothesized. At the coastal zone of the Peninsula de Mejillones and Bahía Mejillones (23°05'S), it is usual the presence of coastal upwelling of cold-waters rich in nutrients (Marín *et al*., 1993, 2001). However, this upwelled nutrient-rich cold waters also produces dispersal of herbivorous planktivore populations, increasing the fish larval transport offshore to areas with reduced food availability. Associated to northern Chile upwelling system, a shallow oxygen minimum layer (<0.5 mL L^{-1}) within the euphotic zone might impose a strict physiological limit for vertical movement (Morales *et al*., 1996; Giesecke & González, 2004), forcing aggregation of planktonic organisms in the upper 50 m layer (Escribano & Hidalgo, 2000).

The local upwelling focus off Peninsula de Mejillones generates changes in the circulation patterns that modify the advective environment, inducing the mixing and transport of mero- and holoplanktonic organisms (Olivares, 2001; Rojas *et al*., 2002). Thus, the development of an upwelling plume also induces abrupt changes on physical conditions of the water column. Along with a deepening of the mixed layer, surface waters are subjected to an abrupt cooling, which is accompanied by low oxygen concentration. These changes, taking place mostly inside the upwelling plume, might also influence larval vertical distribution. However, the inherent characteristics of each species may show inter-specific and ontogenic larval differences. The objective of this article is to evaluate the role of diel vertical distributions and ontogenetic migrations of fish larvae as behaviours responsible of nearshore retention during cold water filaments development off Punta Angamos, northern Chile.

MATERIALS AND METHODS

Sampling design and procedures

Oceanographic data and plankton samples were collected during September 1998 and January 1999 off Punta Angamos (23º29'S, 70º59'W) (Fig. 1). A grid of 23 stations was quasi-synoptically sampled (26 h) on

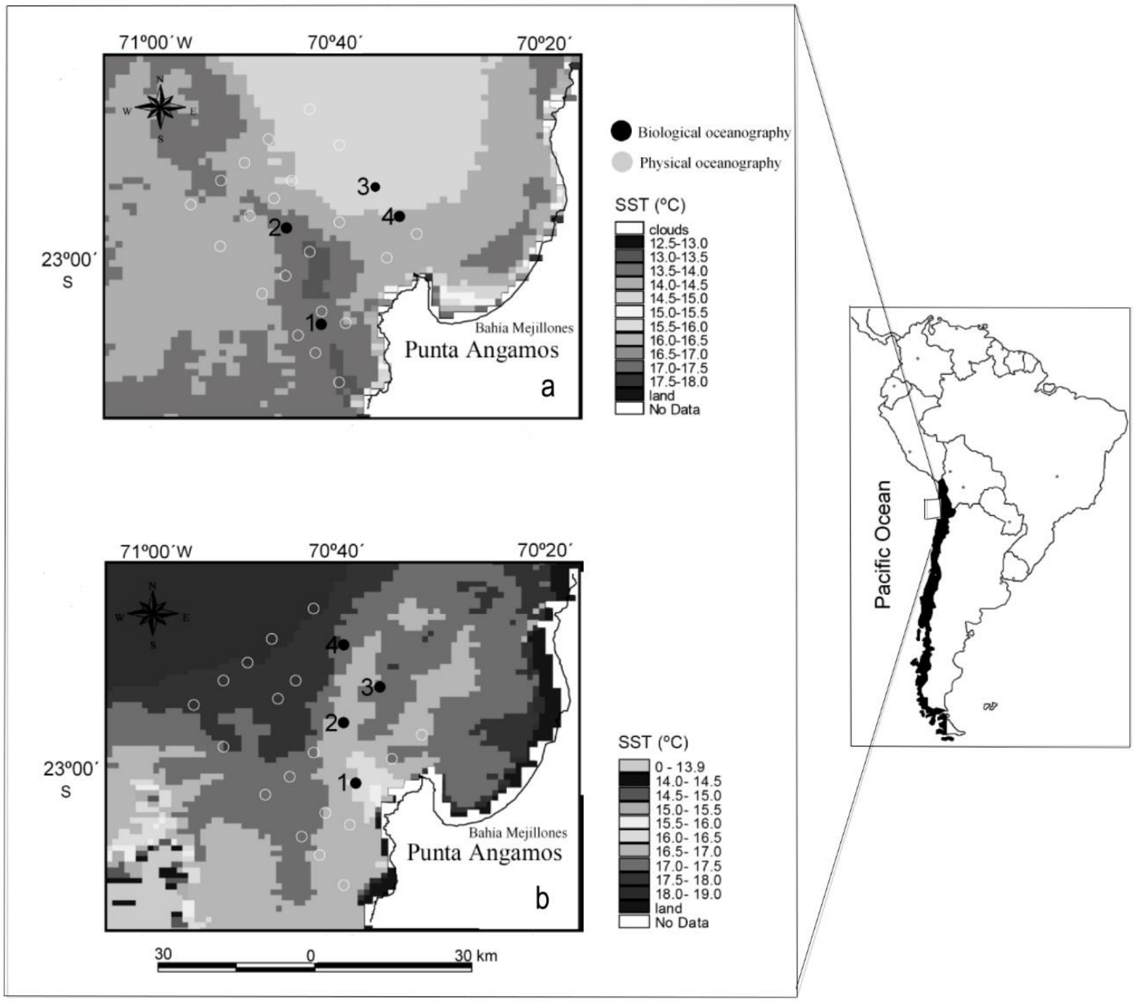


Figure 1. AVHRR images of sea surface temperature illustrating the cold upwelling plumes and location of oceanographic stations (physical/biological) on cruises from a) 9 September 1998, b) 11 January 1999 off Punta Angamos.

board the R/V Purihaalar from the Universidad de Antofagasta. At each station, vertical profiles of temperature (ºC), salinity and dissolved oxygen (mL L^{-1}) were carried out from surface to 200 m depth with a SeaBird SBE-19 conductivity temperature depth (CTD), equipped with a calibrated YSI Beckman oxygen sensor. Current profiles were measured with the vessel anchored at each station using a Doppler sensor current meter (Aanderaa RCM-9). In addition, fluorescence profiles were obtained from 100 m to surface, using a Wetstar fluorometer attached to an Ocean Sensor CTD. Fluorescence units were converted to Chl-*a* concentration by a linear algorithm derived from an *in situ* calibration (Escribano & McLaren, 1999). Four fixed stations were used for ichthyoplankton sampling: two inside and two outside the upwelling plume, in accordance with a satellite NOAA image of sea surface temperature (SST) obtained one day before the start of the sampling, on September 9 (1998) and January 11 (1999), respectively (Fig. 1). Detailed information on satellite-derived SST is described in Marín *et al*. (2001). The following two days after the oceanographic grid was finished, fish larvae were sampled again at four stations during two daytime and two night-time periods. This design considered upwelling/non-upwelling conditions as the main treatment (*i.e.*, inside/outside the cold plume) and variability introduced by daytime/night-time effect, as well as temporal changes after 24 h. Diel changes in vertical distribution of fish larvae 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.

Ichthyoplankton sampling and analysis

Ichthyoplankton was captured 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. Samples were preserved in 4% buffered formalin. To detect changes in the water column during the ichthyoplankton sampling, the CTD and fluorometer were also deployed as described above at each of the four stations in the next two days. In the laboratory, all fish larvae were removed for counting and identified to the lowest taxonomic level using descriptions by Fahay (1983), Moser (1996), and Neira *et al.* (1998). Larvae were separated into two ontogenetic groups according to the bending of the notochord, preflexion and postflexion larvae (larvae in flexion stage were included in postflexion larvae). The number of individuals collected in the different sampling strata was standardized to number unit^{-1} of volume of filtered water (densities): 1000 m^3 for fish larvae (densities). Average vertical distributions were calculated using all the stations. Fish larvae caught in the different sampling strata were also integrated to obtain the number of individuals 10 m^{-2} of sea surface (abundances).

Data analysis

The effect of diel distribution of selected taxa of larval fish was analyzed through weighted mean depth (WMD) as the density centre according (Heath *et al.*, 1991; Gronkjaer & Wieland, 1997):

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

where p_i and C_i are, respectively, the proportion and the concentration fish larvae (number 1000 m^{-3}) in the i^{th} stratum, and Z_i is the mid-depth of the i^{th} stratum.

The non-parametric Kruskal–Wallis test (Sokal & Rohlf, 1985; Siegel & Castellón, 1988) was used to assess the effects of upwelling *vs* non-upwelling locations (inside and outside the upwelling plume), the statistical significance of differences in total larval abundance between daytime and nighttime, and among the different depth strata. Because of low occurrence for many species, Kruskal-Wallis test was not used for each separated taxa. To assess short-term variability, we analysed changes in oceanographic conditions and total larval abundance at stations separated by 12 h intervals.

A nonparametric multivariate procedure (BIO-ENV) was used to analyze the relationship between select environmental variables and larval community. The details of the BIO-ENV algorithm and its suitability for use in analyzing the interactions of biological and environmental data are described by Clarke & Gorley (2001) and Clarke & Warwick (2001). A similarity matrix of depth-stratified samples by larval taxa (61 samples×15 taxa) was also performed. This matrix was analyzed in association with three environmental variables: mean depth (m), mean temperature (°C), and mean dissolved oxygen (mL L^{-1}) of each depth-stratified sample. The BIO-ENV analyses were performed by using the Spearman rank correlation method on the normalized Euclidean distance similarity matrices of the log (n+0.1)-transformed, nonstandardized environmental variables by depth-stratified samples (Clarke & Gorley, 2001). All diversity, cluster and BIO-ENV analyses were performed by using PRIMER statistical software.

RESULTS

Mesoscale features off Punta Angamos during austral spring and summer

The NOAA satellite images showed, in September 1998, a well-developed upwelling filament with cold surface waters below 14°C (Fig. 1a). Conversely, in January 1999 a weak upwelling filament was seen with surface temperatures near 15°C (Fig. 1b). Chlorophyll-*a* showed spatial heterogeneity off Punta Angamos. In September 1998, high concentrations of Chl-*a* (>2.0 mg m^{-3}) were recorded southward of Punta Angamos. In January 1999, high chlorophyll levels (>5.0 mg m^{-3}) were found northward from upwelled focus. In September 1998, the average values of SST showed significant differences ($F_{[1,6]} = 40.39$; $P < 0.01$) between upwelled and non-upwelled zones (inside and outside the filament). Similarly, significant effects ($F_{[1,6]} = 9.60$; $P < 0.05$) were seen in surface chlorophyll values in both locations. Contrary, the average values of SST in January 1999 showed non significant differences ($F_{[1,6]} = 0.346$; $P > 0.05$) between both sites (inside/outside), nor in the average surface chlorophyll values ($F_{[1,6]} = 0.089$; $P > 0.05$).

In September 1998, velocity profiles showed a southward flow throughout the water column, and a typical structure across shore of an upwelling event composed by three layers, a westward surface layer (Ekman layer, 0-25 m depth), a subsurface eastward layer (25-50 m) and a deep layer (50-200 m) flowing westward (Fig. 2a). In January 1999 the water column showed the predominance of a southward and westward flow throughout the water column (Fig. 2b). In both cruises low speeds (<0.2 m s^{-1}) were measured between surface and 20 m depth, increasing to values of ~0.3 m s^{-1} below that depth.

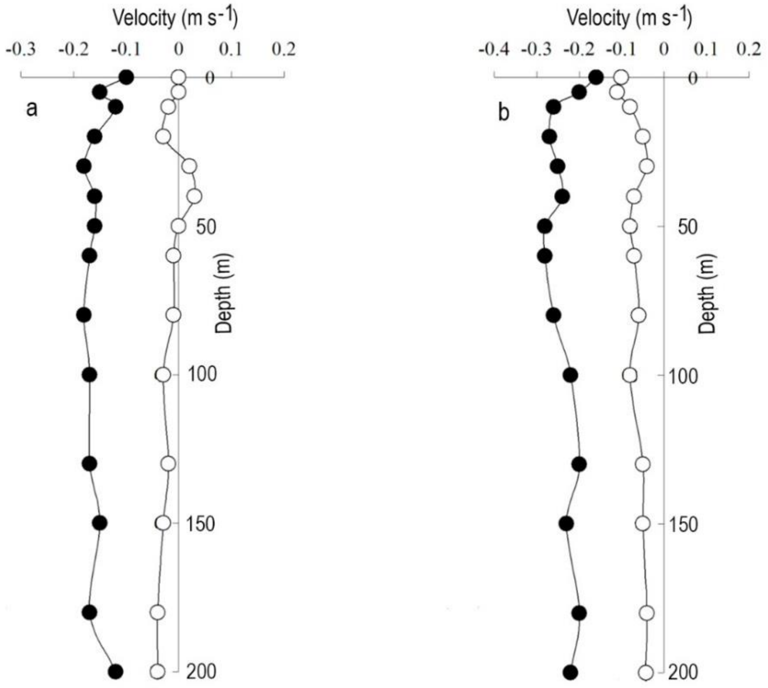


Figure 2. Velocity profiles from stations sampled (inside/outside) upwelling filament off Punta Angamos during a) September 1998, and b) January 1999. Dark circles correspond to alongshore component, open circles to the across-shore component. Values (-) southward flow; values (+) northward flow.

In September 1998 differences of ~4°C were seen in SST maps inside and outside the upwelling filament (Fig. 3a). Temperature profile at upwelled waters showed smooth vertical gradients in surface waters (0.1°C m^{-1} in the first 10 m of the water column), while outside the filament (non-upwelling) thermocline creates strong stratification in the first 50 m depth. Differences in the concentration of dissolved oxygen in surface waters were also evident inside and outside the upwelling filament (<1.5 mL L^{-1} *vs* 2.0-6.0 mL L^{-1}, respectively, Fig. 3b). From the 50 m depth oxygen values decreased below ~0.2-0.4 mL L^{-1} in non-upwelling waters. Inside the filament, subsurface waters (50-100 m) showed an increase in its dissolved oxygen concentration (~2.0 mL L^{-1}) (Fig. 3b). Chlorophyll-*a* profiles showed differences of ~2.0 mg m^{-3} at the surface layer inside and outside the upwelling filament; a subsurface chlorophyll peak (>3.0 mg m^{-3}) was detected in the filament; however, in the mixed layer the concentration of Chl-*a* was larger out the filament (3.0-5.2 mg m^{-3}). Below 50 m depth chlorophyll concentration decreased to ~2.0 mg m^{-3} in both water types (Fig. 3c).

In January 1999, SST maps showed differences less than 2ºC inside and outside the upwelling filament, and temperature profiles were similar in the vertical structure but with higher temperatures in non-upwelling surface waters (Fig. 3a). Water column outside the upwelling filament showed higher amount of dissolved oxygen in the top 75 m (Fig. 3b) and chlorophyll in the top 25 m, compared with values obtained inside the filament during austral summer (Fig. 3c).

Taxonomic composition of ichthyoplankton

During the oceanographic survey in September 1998, 42 positive samples (from a total of 48) of fish larvae were collected which represent an occurrence frequency of 93.3%. A total of 189 larvae were separated, 13 taxa identified, representing 68.9% of total larvae (Table 1). Dominant species were *Diogenichthys laternatus* (28.6%), *Bathylagus nigrigenys* (21.8%), *Engraulis ringens* (17%) and *Diogenichthys atlanticus* (6.9%). In January 1999, only 30 positive samples of fish larvae were collected out of a total of 48 samples, representing an occurrence frequency of 62.5%. A total of 350 larvae were separated, and 11 taxa identified, representing 34.5% of total larvae (Table 1). Again, larval taxa collected correspond to *D. laternatus* (28.5%), *E. ringens* (21.7%), *B. nigrigenys* (11.2%), *S. sagax* (9.6%) and *D. atlanticus* (3.8%).

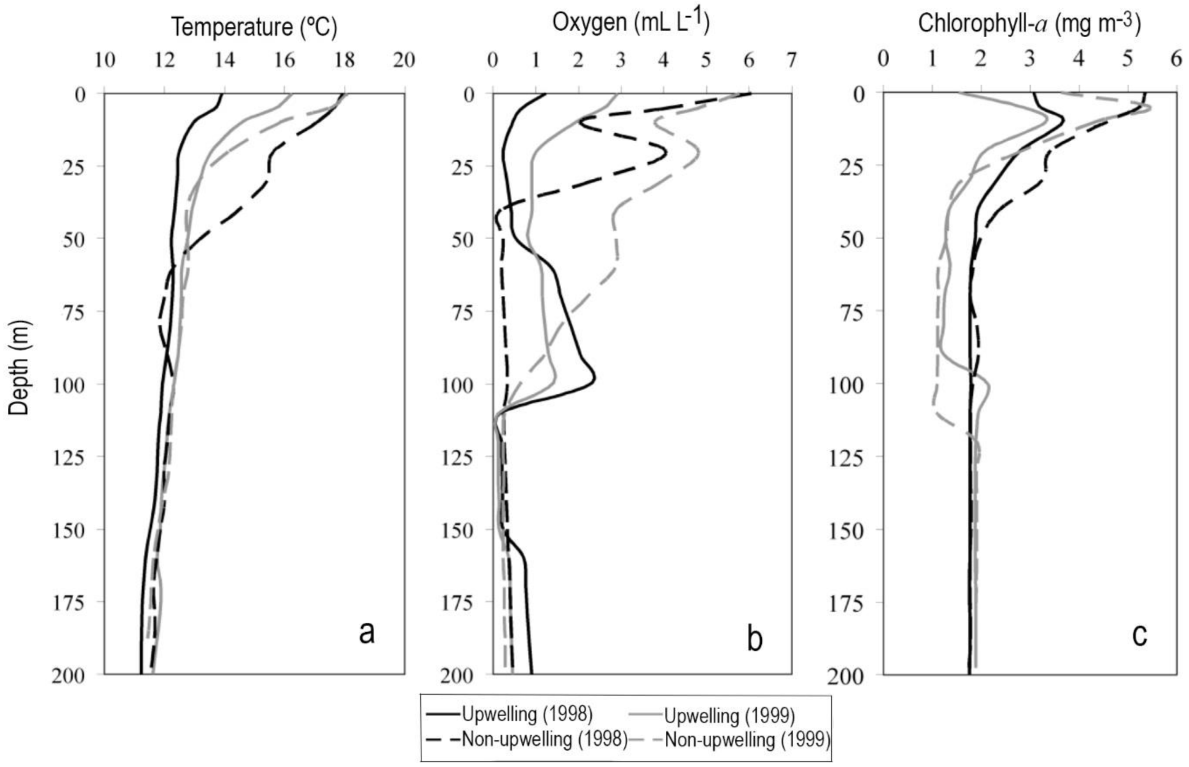


Figure 3. a) Temperature, dissolved oxygen, b) and chlorophyll-*a* c) water column profiles from stations sampled (inside/outside) upwelling filament off Punta Angamos during September 1998 and January 1999.

Larval distribution

Fish larval abundance showed differences at both locations. In September 1998, higher larval fish abundance was collected in stations located outside the upwelling filament (*i.e.*, mean ± SD: E3 = 74 ± 101 larvae 10 m^{-2}; E4 = 47 ± 47 larvae 10 m^{-2}) (Fig. 4). In January 1999, higher larval concentrations were found outside the filament (Fig. 4), and in a station near of it (*i.e.*, E2 = 210 ± 356 larvae 10 m^{-2}; E3 = 162 ± 303 larvae 10 m^{-2} and E4 = 62 ± 47 larvae 10 m^{-2}).

Kruskal-Wallis test only showed significant effects ($F_{[1,116]} = 8.05$; $P < 0.01$) for larval abundance during day and night, as well as among depth strata during September 1998 ($F_{[1,116]} = 4.64$; $P < 0.05$), this difference in abundance is explained by the high variability observed in the deep layer (80-200 m) ($P = 0.005$; Tukey *post-hoc*). In January 1999, significant effects were found inside and outside the upwelling filament as well as among strata ($P < 0.05$) and significant effects were observed in the interactions between factors (upwelling*strata) ($F_{[2,107]}= 4.02$; $P < 0.05$) and (strata*h) ($F_{[2,107]} = 3.22$; $P < 0.05$) on larval fish abundance. Interactions suggest that the location of the sampling station together with the effect of day-night explains a significant percentage of the observed variability.

Vertical distribution of fish larvae

In September 1998, higher fish larvae abundance was found during the night in the mid (20-80 m) and deep stratum (80-200 m) outside the upwelling filament (Fig. 5). In January 1999, the highest larval abundance was collected during the night in the 20-80 m stratum in both zones, and in deeper waters inside the filament larvae were collected only during dayligth (Fig. 5). Low fish larvae abundance (~200 larvae 1000 m^{-3}) was observed in the upper and middle strata (0-20 and 20-80 m) in upwelled and non-upwelled waters during daytime sampling.

In September 1998, the mid-depth layer (20-80 m) showed higher number of taxa (12), mainly associated with non-upwelling waters (Table 2). Larval *D. laternatus*, *B. nigrigenys* and *Diogenichthys* sp. were collected in all strata. However, only *D. laternatus* was found throughout the sampled water column inside and outside the upwelling plume. Myctophids *Hygophum reinhardti* and *Protomyctophum crockeri* were scarcely collected and found in mid-depth of non-upwelling waters. Larval mote sculpin *Normanichthys crockeri* were also collected in mid-depth of the upwelled waters. In January 1999, myctophids *D. laternatus*, *D. atlanticus*, *Diogenichthys* sp., *Diaphus theta*, *Lampa-*

Table 1. Total fish larvae collected (inside/outside) for upwelling filaments off Punta Angamos in September 1998 and January 1999. The number corresponds to larvae per 10 m^2. Occurrence corresponds to number of positive samples (total samples = 48) in which the species was present.

		September 1998				January 1999			
		Upwelling		Non-upwelling		Upwelling		Non-upwelling	
Family	Taxa	Maximum abundance	Occurrence	Maximum abundance	Occurrence	Maximum abundance	Occurrence	Maximum abundance	Occurrence
Myctophidae	*Diogenichthys atlanticus*	54	13	70	22	19	4	135	35
	Diogenichthys laternatus	76	39	545	44	123	13	269	30
	Triphoturus oculeus	-	-	28	4	27	4	79	13
	Diaphus theta	-	-	-	-	72	17	101	13
	Lampanyctus sp.	-	-	84	22	19	4	158	39
	Diogenichthys sp.	36	4	88	32	-	-	-	-
	Protomyctophum crockeri	-	-	84	4	-	-	-	-
	Hygophum reinhardti	-	-	28	4	-	-	-	-
	Myctophum nitidulum	-	-	35	13	-	-	25	4
	Ceratoscopelus townsendi	-	-	-	-	-	-	26	4
	Unidentified sp. 1	82	20	-	-	49	17	-	-
	Unidentified sp. 2	-	-	195	40	-	-	173	39
Engraulidae	*Engraulis ringens*	28	4	38	4	1119	39	1364	39
Clupeidae	*Sardinops sagax*	28	9	92	26	93	35	148	43
Bathylagidae	*Bathylagus nigrigenys*	54	17	397	40	34	9	48	13
Normanichthyidae	*Normanichthys crockeri*	41	13	-	-	47	9	-	-
Merlucciidae	*Merluccius gayi*	27	4	38	9	-	-	27	4
Macrouridae	Unidentified sp.	76	4	16	4	-	-	42	4

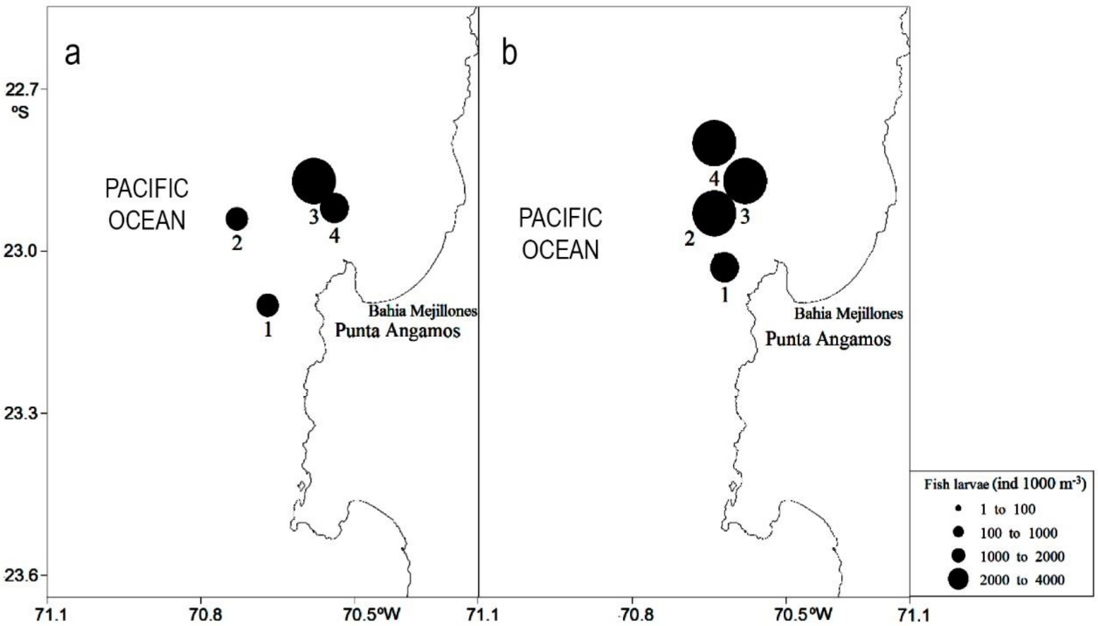


Figure 4. Spatial distribution and abundance of fish larvae in upwelling filaments, during September 1998 and January 1999 cruises off Punta Angamos.

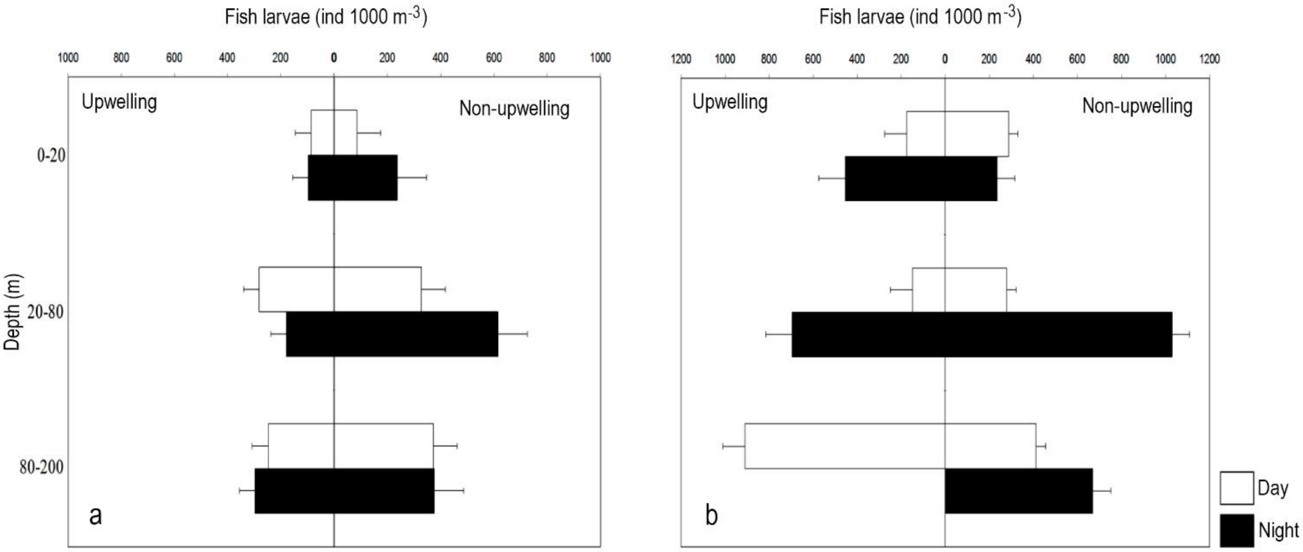


Figure 5. Vertical distribution of fish larvae (inside/outside) in the cold water filament, during diurnal *versus* nocturnal collection in a) September 1998 and b) January 1999. Bars indicate values of one standard error.

nyctus sp. and small pelagic *E. ringens* and *S. sagax* were collected in all three strata. However, only *S. sagax* was found in all three layers both inside and outside of the upwelling plume (Table 2). *N. crockeri* larvae was found only in the upper (0-20 m) and mid-depth strata of upwelled waters, while *Myctophum nitidulum*, *Merluccius gayi* and *Ceratoscopelus townsendi* were poorly represented in this cruise.

Daily changes in the vertical distribution of fish larvae

The three most abundant species were collected on surface waters (WMD was located between 10 and 72 m (range = 62 m) at night and deeper (WMD was located between 14 and 139 m (range = 125 m) during daylight. Late stage larval (postflexion) showed wider amplitude in vertical distribution during day and night

(WMD was located between 10 and 96 m (range = 86 m). Small pelagic larvae (*E. ringens*) during spring showed significant differences ($F_{[1,48]} = 58.85$; $P < 0.05$) among depth during day/night sampling as well as differences at depth for early and late-stage larvae ($F_{[1,48]} = 5.80$; $P < 0.05$) (Fig. 6). In summer larval *E. ringens* showed significant differences ($F_{[1,48]} = 89.61$; $P < 0.05$) among depth strata only during day/night catch. Larval myctophid *D. laternatus* showed significant differences among depth during sampling hours (day/night) (K-W test; $P < 0.05$), and inside/outside upwelled plume at this cruise (Fig. 6). Larval *B. nigrigenys* collected at spring showed significant differences ($F_{[1,49]} = 78.11$; $P < 0.05$) over depth during day/night sampling. Finally, *B. nigrigenys* larvae collected during summer showed significant differences ($F_{[1,36]} = 17.55$; $P < 0.05$) at vertical distribution, being found at shallower waters at day and deeper at nighttime (Fig. 6).

Environmental relationships

The similarity dendrogram (~82 %) shows three groups of fish larvae of different habitats in the adult stage (Fig. 7a). Group 1 was represented by two coastal pelagic species (*Engraulis ringens* and *Sardinops sagax*). Additionally, this group included myctophid *Diaphus theta* of epi-mesopelagic origin. All these species were found at stations under the influence of upwelling filament and coastal front. Group 2 was represented mostly by myctophids epi-mesopelagic, as well as some species of meso-bathypelagic habits (*Bathylagus nigrigenys*) and bathydemersal (*Merluccius gayi*). These species were found exclusively associated with upwelling front warm waters. Finally, Group 3 was represented by a single demersal species *N. crockeri* present in a zone influenced by cold water from upwelling filament. Cluster analyses also indicated the presence of two larval depth assemblages: <100 m and >100 m (Fig. 7b).

BIO-ENV and correlation analyses revealed significant relationships among several environmental factors and larval average concentrations. A depth-stratified BIO-ENV analysis, which included mean temperature (°C), mean dissolved oxygen (mL L^{-1}) and chlorophyll (mg m^{-3}) of each depth-stratified sample (*i.e.*, 0-20; 20-80 and 80-200), showed that depth alone explained 44% in mean larval concentrations. No multiple factor combination explained more variability in larval concentration data. Pairwise correlation analyses revealed significant negative correlations between temperature and mean concentrations of small pelagic *E. ringens* (three strata), *S. sagax* (only upper water) and Myctophid *D. atlanticus* (upper/midwater). Significant negative correlations ($P < 0.05$) were seen between *B. nigrigenys* (midwater) and *S. sagax* (deepwater) with dissolved oxygen and chlorophyll (Table 3). Average concentrations of *N. crockeri* (three strata) and *D. laternatus* (upper/midwater) larvae, were also positively correlated with temperature and negatively correlated with chlorophyll, although the correlations were not significant ($P > 0.05$).

DISCUSSION

Physical conditions

The distinctive feature of the Humboldt Current System in northern Chile is the strong oceano-graphic mesoscale activity in the region, registered from satellite images during the plankton samples collection (Marin *et al.*, 2001), and from changes in hydrographic conditions during upwelling process. Normally, an increase wind stress about sea surface layer favors the cold filament formation, as extends until 60 km offshore, clearly visible from sea surface temperature satellite images. This structures type, as well as meanders of cyclonic eddies and upwelling shadows have been described previously (Escribano & Hidalgo, 2000; Rojas *et al.*, 2002; Marin *et al.*, 2003).

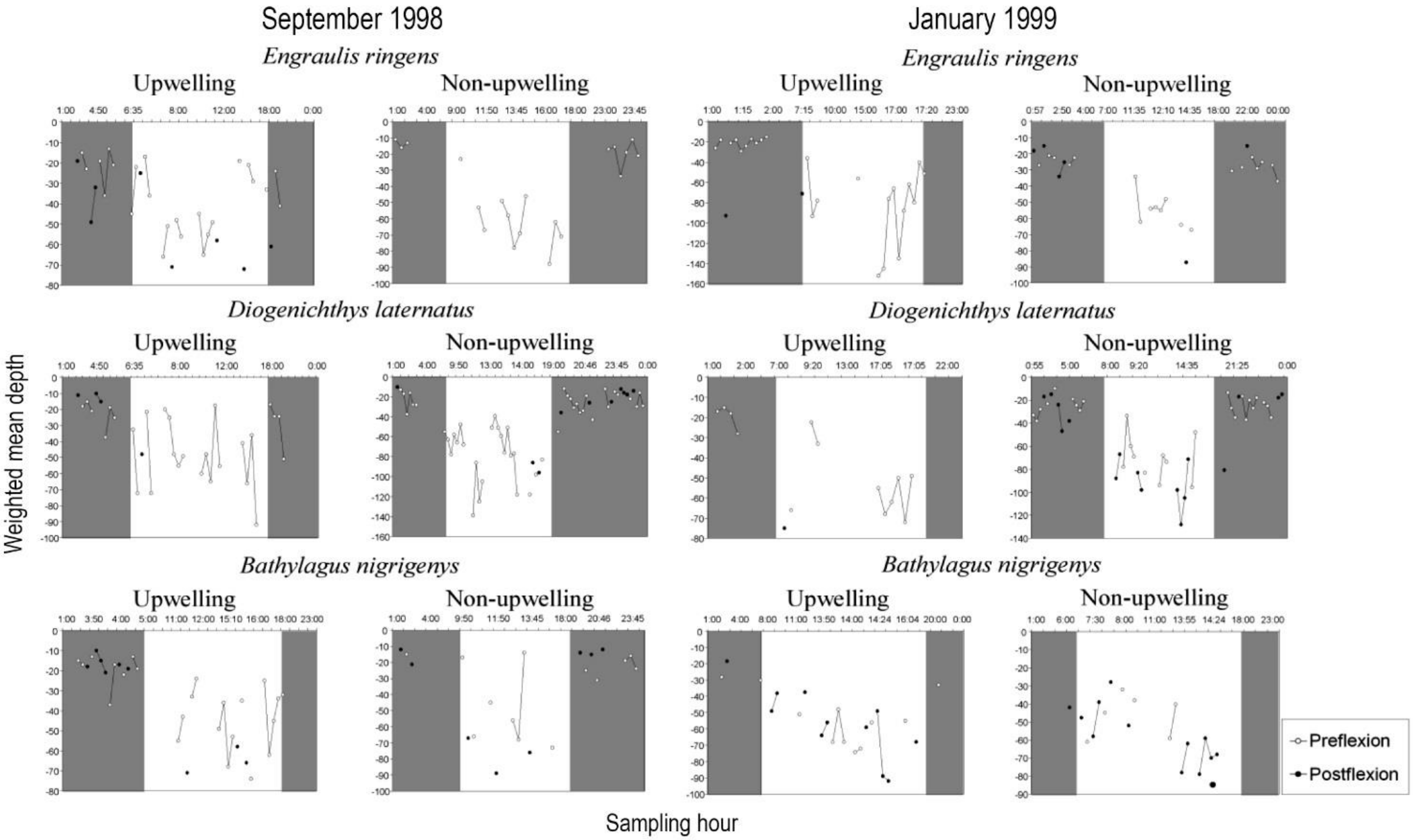
Community structure in the upwelled filaments

The highest fish larval density (96%) was found in the first 100 m of the water column, a feature documented by other studies (Auth & Brodeur, 2006; Landaeta *et al.*, 2008). The ichthyoplanktonic taxocenosis found off Punta Angamos (Peninsula de Mejillones) showed a mixture of coastal and oceanic species (epipelagic, epi-mesopelagic and mesopelagic). However, it is not possible to see a spatial gradient distribution, due to presence of epi-mesopelagic oceanic species nearshore (*i.e.*, *D. laternatus* and *D. atlanticus*) and some coastal species (*i.e.*, *E. ringens* and *S. sagax*). A dense aggregation of phytoplankton and zooplankton associated to the upwelling filament formation suggests that areas near it are suitable habitat for fish larvae feeding, increasing their survival probability (Escribano & Hidalgo, 2000). However, results do not show a clear relationship among larval abundance with high chlorophyll concentrations, because coastal fronts may modify the chlorophyll spatial distribution toward Bahia Mejillones. This suggests that the relationship between coastal species with high primary productivity areas would be too fragile if fish larval have not developed tactics and/or mechanisms that avoid or reduce offshore horizontal transport, facilitating their retention in shallow areas nearshore (Pringle, 2007; Morgan & Fisher, 2010). Usually, *E. ringens* is found in shallow areas nearshore (Castro *et al.*, 2000), however the low abundance of anchoveta larvae in the study area, suggests that a large number have been

Table 2. Location of different taxonomic groups, per strata depth, in September 1998 and January 1999 (inside/outside upwelling filament). The abundance corresponds to (N = number per 1.000 m^3) and occurrence (%) represents the number of cases (samples = 48) in which the species was present.

		September 1998				January 1999			
		Upwelling		Non-upwelling		Upwelling		Non-upwelling	
Stratum (m)	Taxa	N	%	N	%	N	%	N	%
0-20	*Diogenichthys laternatus*	195	9	65	9	162	9	-	-
	Diogenichthys atlanticus	-	-	-	-	-	-	32	4
	Diogenichthys sp.	-	-	27	4	-	-	-	-
	Lampanyctus sp.	-	-	-	-	-	-	32	4
	Diaphus theta	-	-	-	-	121	9	101	4
	Mictophum nitidulum	-	-	34	4	-	-	-	-
	Engraulis ringens	-	-	-	-	82	4	32	4
	Sardinops sagax	-	-	-	-	227	18	217	18
	Bathylagus nigrigenys	-	-	478	13	-	-	-	-
	Normanichthys crockeri	41	4	-	-	47	4	-	-
	Myctophidae Unidentified	332	30	198	13	134	13	50	4
20-80	*Diogenichthys laternatus*	114	17	1179	30	19	4	675	17
	Diogenichthys atlanticus	78	9	198	13	19	4	237	17
	Triphoturus oculeus	-	-	28	4	27	4	27	4
	Myctophum nitidulum	-	-	64	9	-	-	25	4
	Hygophum reinhardti	-	-	28	4	-	-	-	-
	Diaphus theta	-	-	-	-	50	9	27	4
	Diogenichthys sp.	36	4	201	17	-	-	-	-
	Protomyctophum crockeri	-	-	84	4	-	-	-	-
	Lampanyctus sp.	-	-	189	17	19	4	162	17
	Engraulis ringens	28	4	38	4	64	9	39	4
	Sardinops sagax	-	-	38	4	236	22	290	9
	Bathylagus nigrigenys	54	4	641	22	-	-	354	18
	Normanichthys crockeri	25	4	-	-	19	4	-	-
	Merluccius gayi	27	4	38	4	-	-	27	4
	Myctophidae Unidentified	199	17	650	22	19	4	282	13
	Macrouridae Unidentified	76	4	-	-	-	-	-	-
80-200	*Diogenichthys laternatus*	98	17	250	22	-	-	391	13
	Diogenichthys atlanticus	24	4	81	9	-	-	114	13
	Triphoturus oculeus	-	-	-	-	-	-	101	9
	Diaphus theta	-	-	-	-	-	-	22	4
	Diogenichthys sp.	-	-	49	9	-	-	-	-
	Ceratoscopelus townsendi	-	-	-	-	-	-	26	4
	Lampanyctus sp.	-	-	55	4	-	-	252	17
	Engraulis ringens	-	-	-	-	91	4	-	-
	Sardinops sagax	-	-	41	9	54	9	26	4
	Bathylagus nigrigenys	92	17	152	17	-	-	-	-
	Normanichthys crockeri	19	4	-	-	-	-	-	-
	Merluccius gayi	-	-	16	4	-	-	-	-
	Myctophidae Unidentified	106	22	165	17	-	-	158	22
	Macrouridae Unidentified	-	-	16	4	-	-	42	4

Figure 6. Weighted mean depth (WMD) of three larval species during day/night sampling in September 1998 and January 1999. The dark areas indicated sampling during night hours. Open and dark circles, respectively, correspond to pre- and postflexion larval stage.



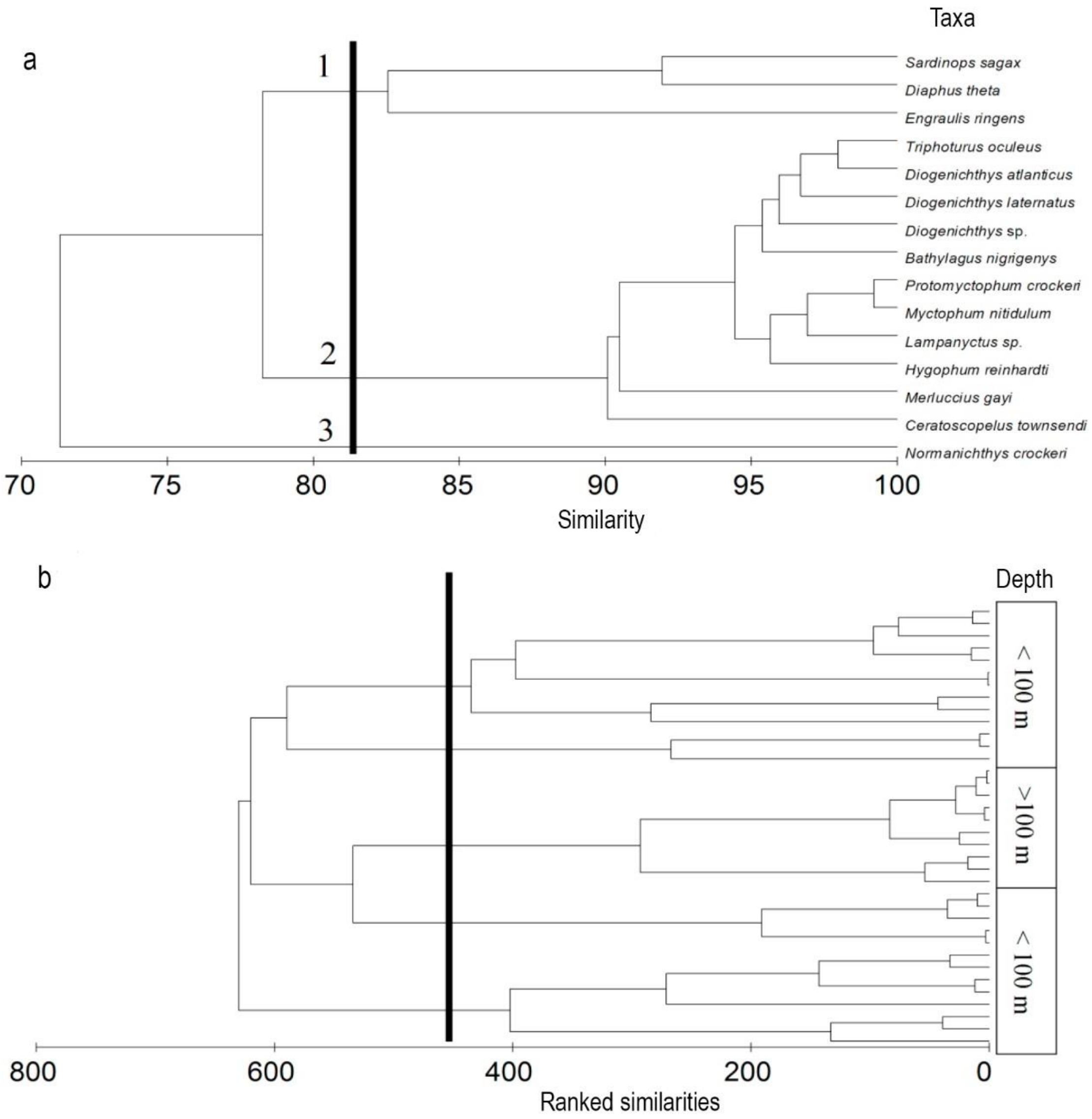


Figure 7. Bray-Curtis dendrograms of a) fish larval taxa, and b) larval depth. Clusters were performed on fish larvae collected from four stations (inside/outside) upwelling plume off Punta Angamos in September 1998 and January 1999. Taxon a) and depth b) cluster identifications are indicated on each figure.

transported from inshore to adjacent zones of the upwelling filament, condition which was also seen in fish larvae in the Canary Upwelling System (Brochier *et al*., 2011).

In both cruises the highest larval densities were found in non-upwelling waters (middle/deep strata) below the Ekman layer (>20 m), habitat continually affected by short-term variations as well oceanographic conditions changes due to circulation in the area (Marín *et al*., 2001). Myctophids *D. laternatus*, *D. atlanticus*, *Triphoturus oculeus*, *D. theta*, among others, have been previously reported by several authors in the area (Rojas *et al*., 2002; Rodríguez-Graña & Castro, 2003) and are associated with warm-water increasing their abundance. The significant presence of myctophid fish larvae found in the warm epipelagic layer (Sassa, 2001; Sassa *et al*., 2002a, 2004b; Moku *et al*., 2003), likely coincide with spawning periods during most of the year (Gjösaeter & Kawaguchi, 1980; Olivar & Beckley, 1994). Small pelagics (*E. ringens* and *S. sagax*) generally associated with cold upwelled water (Loeb & Rojas, 1988; Bécognée *et al*., 2009) were seen preferentially at warm waters, probably because of the mechanical effect exercised by cold water upwelling which facilitates larval transport nearshore (Rodríguez *et al*., 1999).

From an ecological perspective, the occurrence of *D. laternatus* and *D. atlanticus* larvae in upwelling/

Table 3. Correlation coefficients for the fish larvae collected in stratified sample with three oceanographic variables during the day and night (inside/outside) in upwelling plume off Punta Angamos in September 1998 and January 1999: water temperature (°C), dissolved oxygen (mL L^{-1}) and chlorophyll-*a* (mg m^{-3}), and log-transformed densities (number per 1000 m^3) of fish larvae present in all three strata. *$P < 0.05$.

Stratum (m)	Taxa	Temperature	Dissolved oxygen	Chlorophyll-*a*
0-20	*Diogenichthys laternatus*	0.10	0.06	-0.11
	Diogenichthys atlanticus	-0.66*	0.11	-0.17
	Engraulis ringens	-0.85*	-0.52	0.41
	Sardinops sagax	-0.70*	0.01	-0.16
	Bathylagus nigrigenys	-0.78*	-0.30	0.37
	Normanichthys crockeri	0.52	0.06	-0.06
20-80	*Diogenichthys laternatus*	0.23	0.07	-0.40
	Diogenichthys atlanticus	-0.51	-0.39	-0.54*
	Engraulis ringens	-0.83*	-0.83*	-0.60*
	Sardinops sagax	-0.45	-0.45	0.47
	Bathylagus nigrigenys	-0.65*	-0.54*	-0.61*
	Normanichthys crockeri	0.45	-0.45	-0.47
80-200	*Diogenichthys laternatus*	-0.29	0.20	-0.40
	Diogenichthys atlanticus	-0.78*	-0.81*	0.68
	Engraulis ringens	-0.70*	-0.80*	0.53
	Sardinops sagax	-0.68	-0.78*	-0.52*
	Bathylagus nigrigenys	0.17	-0.10	0.32
	Normanichthys crockeri	0.48	-0.48	-0.39

non-upwelling conditions might be the result of successive adaptations to this environment. *B. nigrigenys* and *M. nitidulum* larvae showed preferences for warmer waters due to larval abundance in non-upwelling water. On the contrary, *N. crockeri* was found exclusively in cold upwelled water. Effects of ontogeny, temperature, and ligh might explain partially the changes in migration patterns of fish larvae (Hurst *et al*., 2009). However, the distribution patterns in adult species vary according to eating habits and life history (Watanabe *et al*., 1999).

Diel variation and ontogenetic migration

Early stages of fish in presence of cold water upwelled showed a minimum difference in the average depth during night. Fish larvae were found in shallow layers (~40 m) where the drift effects would be less intense. However, during daylight only some late-stage larvae (postflexion) were found in deeper layers (~70-80 m) that match with compensatory flow coastward. Our hypothetical approach suggests that larvae with a morphological advanced development are located deepwater during daytime that facilitate eventually the return of fish larval to inshore zones using a compensatory deep flow. Thus, results obtained from cruises on 9 September (1998) and 11 January (1999) showed a trend towards a diel vertical migration and/or ontogenetic migration; this behavior would be independent of condition type (upwelling/non-upwelling) as well as from hydrographic conditions observed during active upwelling events off Punta Angamos. However, in another regions with long periods of active upwelling the traditional migratory model (down at day, up during the night) would be partially affected, as evidenced the change in the migratory behavior (down at night, up during the day) seen in some myctophids larvae (Rodriguez *et al*., 2006; Auth *et al*., 2007). In general, it is well documented that a large number of fish larvae are visual predators concentrating its feeding rhythms during the daylight hours or during dusk and dawn hours (Hunter, 1984). Thus, behavior migratory of some myctophid larvae collected for both periods off Punta Angamos seems given by daily feeding cycles, with higher ingestion of food during daylight hours (Rodríguez-Graña & Castro, 2003; Rodríguez-Graña *et al*., 2005; Sassa & Kawaguchi, 2005).

The cross-shelf currents derived from the upwelling process may cause significant offshore transport of fish larvae as well as mortality due to low food availability (Pizarro *et al*., 1998). Off Punta Angamos, especially during the active upwelling phase in September (1998), the mechanical effect generated for cold-water upwelling and the current velocity (~0.1 m s^{-1}) of the surface layer (~0-20 m) may transport offshore large numbers of larvae, decreasing their survival probability. On the contrary, a significant number of fish larvae could remain there either by staying deep in the water column or by undertaking diel vertical migrations between surface and bottom currents (Roughan *et al*., 2005). This evidence may partially explain the presence of fish larvae in the focus of the upwelling during both periods. We believe that ichthyoplankton sampling should be conducted primarily at night if at all possible to eliminate any potential bias due to net avoidance. Net avoidance should at least be factored into any model estimating abundances and depth distributions of larvae collected during both day and night. Although this study was not designed to determine the underlying causes of the DVM of larval fish, it does provide some evidence for type-I DVM (up at night, down during the day) for *E. rigens*, *D. laternatus* and *B. nigrigenys* larvae during active events of upwelling off Punta Angamos, despite not finding evidence for either type of DVM for larval *E. ringens* in previous studies (Rojas *et al*., 2002; Rodríguez-Graña & Castro, 2003). This type-I DVM could help to partially explain the retention of larval fish assemblages, in particular E ringens larvae, close to recruitment areas along and inshore from the shelf due to the ability of larvae to regulate their position in the water column and to take advantage of selective Ekman transport (Sakuma & Larson, 1995; Stenevik *et al*., 2007; Morgan *et al*., 2009; Morgan & Fisher, 2010) related to water flows generated during active and/or relaxation phase (*i.e*., spin-up/spin-down phases) of upwelling events (Send *et al*., 1987) off Punta Angamos.

CONCLUSIONS

In this study the vertical distribution of fish larvae during coastal upwelling in September 1998 and January 1999 off Punta Angamos showed changes during day/night suggesting diel vertical migration as a strategy to avoidance of the offshore Ekman layer during upwelling events; this migratory behavior would be independent of the condition type (upwelling/non-upwelling) as well as from hydrographic conditions registered at both oceanographic surveys. Early stages of fish larvae during daylight were found at an average depth which coincides with the zone boundary among the Ekman layer and the polar flow that dominates the circulation, while some late-stage larval were found at an average depth that coincide with the Ekman layer. The mixed coastal and oceanic species of fish larvae found off Punta Angamos indicated the importance of this local upwelling focus for the development of larval fish assemblages in northern Chile.

ACKNOWLEDGEMENTS

The author acknowledges the cooperation and logistical support provided by crew the R/V Purihaalar. Special thanks to Dr. Mauricio Landaeta for their valuable contributions and comments on earlier drafts of the manuscript. This work has been funded by FONDECYT-Chile, Grant 198-0366 adjudicated to R. Escribano and V. Marín.

REFERENCES

Annis, E.R. 2005. Temperature effects on the vertical distribution of lobster postlarvae (*Homarus americanus*). Limnol. Oceanogr., 50: 1972-1982.

Auth, T.D. & R.D. Brodeur. 2006. Distribution and community structure of ichthyoplankton off the Oregon Coast in 2000 and 2002. Mar. Ecol. Prog. Ser., 319: 199-213.

Auth, T.D., R.D. Brodeur & K.M. Fisher. 2007. Diel variation in vertical distribution of an offshore ichthyoplankton community off the Oregon coast. Fish. Bull., 105: 313-326.

Bécognée, P., M. Moyano, C. Almeida., J.M. Rodríguez, E. Fraile-Nuez, A. Hernández-Guerra & S. Hernández-León. 2009. Mesoscale distribution of clupeoid larvae in an upwelling filament trapped by a quasi-permanent cyclonic eddy off Northwest Africa. Deep-Sea Res., 56(3): 330-343.

Boehlert, G.W., W. Watson & L.C. Sun. 1992. Horizontal and vertical distributions of larval fishes around an isolated oceanic island in the tropical Pacific. Deep-Sea Res., 39: 436-466.

Brewer, G.D & G.S. Kleppel. 1986. Diel vertical distribution of fish larvae and their prey in nearshore waters of southern California. Mar. Ecol. Prog. Ser., 27: 217-226.

Brochier, T., E. Mason, M. Moyano, A. Berraho, F. Colas, P. Sangra, S. Hernandez-Leon, O. Ettahiri & C. Lett. 2011. Ichthyoplankton transport from the African coast to the Canary Islands. J. Mar. Syst., 87(2): 109-122.

Brodeur, R.D. & W.C. Rugen. 1994. Diel vertical distribution of ichthyoplankton in the northern Gulf of Alaska. Fish. Bull., 92: 223-235.

Castro, L.R., G.R. Salinas & E.H. Hernández. 2000. Environmental influences on winter spawning of the anchoveta, *Engraulis rigens*, off Central Chile. Mar. Ecol. Prog. Ser., 197: 247-258.

Clarke, K.R. & R.N. Gorley. 2001. Primer v5: user manual/tutorial, PRIMER-E Ltd., Plymouth, 91 pp.

Clarke, K.R & R.M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation, PRIMER-E Ltd., Plymouth, 172 pp.

Danell-Jiménez, A., L. Sánchez-Velasco, M.F. Lavín. 2009. Three-dimensional distribution of larval fish assemblages across a surface thermal/chlorophyll front in a semienclosed sea. Estuar. Coast. Shelf Sci., 85: 487-496.

Escribano, R. & I.A. McLaren. 1999. Production of *Calanus chilensis* from 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. U.K., 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. Hidrobiologia, 453/454: 143-151.

Fahay, M.P. 1983. Guide to the early stages of marine fishes occurring in the western North Atlantic Ocean, Cape Hatteras to the southern Scotian Shelf. J. NW. Atl. Fish. Sci., 4: 1-432.

Fiksen, Ø & J. Giske. 1995. Vertical distribution and population dynamics of copepods by dynamic optimization. ICES J. Mar. Sci. J. Cons., 52: 483-503.

Fortier, L. & W.C. Leggett. 1983. Vertical migrations and transport of larval fish in a partially mixed estuary. Can. J. Fish. Aquat. Sci., 40: 1543-1555.

Fortier, L. & R.P. Harris. 1989. Optimal foraging and density-dependent competition in marine fish larvae. Mar. Ecol. Prog. Ser., 51: 19-33.

Gjösaeter, J. & K. Kawaguchi. 1980. A review of the world resources of mesopelagic fish. FAO Fish. Tech. Rep., 193: 151 pp.

Giesecke, R. & H.E. González. 2004. Feeding of *Sagitta enflata* and vertical distribution of chaetognaths in relation to low oxygen concentrations. J. Plankton Res., 26(4): 475-486.

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.

Guizien, K., T. Brochier, J.-C. Duchéne, B.-S. Koh & P. Marsaleix. 2006. Dispersal of *Owenia fusiformis* larvae by wind-driven currents: turbulence, swimming behaviour and mortality in a three-dimensional stochastic model. Mar. Ecol. Prog. Ser., 311: 47-66.

Hare, J.A & J.J. Govoni. 2005. Comparison of average larval fish vertical distributions among species exhibiting different transport pathways on the southeast United States continental shelf. Fish. Bull., 103: 728-736.

Heath, M.R., K. Brander, P. Munk & P. Rankine. 1991. Vertical distributions of autumn spawned larval herring (*Clupea harengus* L.) in the North Sea. Cont. Shelf Res., 11: 1425-1452.

Hernández-León, S., M. Gómez & J. Arístegui. 2007. Mesozooplankton in the Canary Current System: the coastal-ocean transition zone. Prog. Oceanogr., 74(2-3): 397-421.

Hunter, J.R. 1984. Feeding ecology and predation of marine fish larvae. In: R. Lasker (ed.). Marine fish larvae: morphology, ecology and relation to fisheries. pp. 90-131.

Hurst, T.P., D.W. Cooper, J.S. Scheingross, E.M. Seale, B.J. Laurel & M.L. Spencer. 2009. Effects of ontogeny, temperature, and light on vertical movements of larval Pacific cod (*Gadus macrocephalus*). Fish. Oceanogr., 18(5): 301-311.

Inda-Díaz, E.A., L. Sánchez-Velasco & M.F. Lavín. 2010. Three-dimensional distribution of small pelagic fish larvae (*Sardinops sagax* and *Engraulis mordax*) in a tidal-mixing front and surrounding waters (Gulf of California). J. Plankton Res., 32: 1241-1254.

Job, S.D. & D.R. Bellwood. 2000. Light sensitivity in larval fishes: Implications for vertical zonation in the pelagic zone. Limnol. Oceanogr., 45: 362-371.

John, H.-C. & P. Re. 1995. Cross-shelf zonation, vertical distribution and drift of fish larvae off northern Portugal during weak upwelling. Arquivos do Museu Bocage. Nova serie, Lisbon, 2: 607-632.

Lampert, W., E. McCauley & B. Manly. 2003. Trade-offs in the vertical distribution of zooplankton: ideal free distribution with costs? Proc. R. Soc. London, B-270: 765-773.

Landaeta, M., R. Veas, J. Letelier & L. Castro. 2008. Larval fish assemblages off central Chile upwelling ecosistema. Rev. Biol. Mar. Oceanogr., 43(3): 569-584.

Leis, J.M., A.C. Hay & T. Trnski. 2005. *In situ* ontogeny of behaviour in pelagic larvae of three temperate, marine, demersal fishes. Mar. Biol., 148: 655-669.

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

Marín, V., L. 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. 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.

Moku, M., A. Tuda & K. Kawaguchi. 2003. Spawning season and migration of the myctophid fish *Diaphus theta* in the western North Pacific. Ichthyol. Res., 50(1): 52-58.

Morales, C.E., M. Braun, H. Reyes, J.L. Blanco & A.G. Davies. 1996. Anchovy larval distribution in the coastal zone off northern Chile: the effect of low dissolved oxygen concentrations and a cold-warm sequence (1990-1995). Invest. Mar., Valparaíso, 24: 77-96.

Morgan, S.G. & J.L. Fisher. 2010. Larval behavior regulates nearshore retention and offshore migration in an upwelling shadow and along the open coast. Mar. Ecol. Prog. Ser., 404: 109-126.

Morgan, S.G., J.L. Fisher & A.J. Mace. 2009. Larval recruitment in a region of strong, persistent upwelling and recruitment limitation. Mar. Ecol. Prog. Ser., 394: 79-99.

Moser, H.G. 1996. The early stages of fishes in the California Current region. Calcofi, Atlas, 33: 1-1505.

Munk, P., T. Kiørboe & V. Christensen. 1989. Vertical migrations of herring, *Clupea harengus*, larvae in relation to light and prey distribution. Environ. Biol. Fish., 26: 87-96.

Neilson, J.D. & R.I. Perry. 1990. Diel vertical migrations of marine fishes: an obligate or facultative process? Adv. Mar. Biol., 26: 115-168.

Neira, F.J., A.G. Miskiewicz & T. Trnski. 1998. Larvae of temperate Australian fishes. Laboratory guide for larval fish identification, University of Western Australia Press, Nedlands, 474 pp.

Norcross, B.L. & R.F. Shaw. 1984. Oceanic and estuarine transport of fish eggs and larvae: a review. T. Am. Fish. Soc., 113: 153-165.

Olivares, G. 2001. Mecanismos de interacción físico-biológicas en una zona de surgencia costera: retención de larvas y cierre del ciclo de vida de *Euphausia mucronata*. M.Sc. Ciencias Biológicas, Universidad de Chile, Santiago, 80 pp.

Olivar, M.P. 1990. Spatial patterns of ichthyoplankton distribution in relation to hydrographic features in the Northern Benguela region. Mar. Biol., 106: 39-48.

Olivar, M.P. & L.E. Beckley. 1994. Influence of the Agulhas current on the distribution of lanternfish larvae off the southeast coast of Africa. J. Plankton Res., 16: 1759-1780.

Paris, C.B. & R.K. Cowen. 2004. Direct evidence of a biophysical retention mechanism for coral reef fish larvae. Limnol. Oceanogr., 49: 1964-1979.

Parrish, R.H., C.R. Nelson & A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr., 1: 175-203.

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

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., Valparaiso, 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(5): 670-675.

Rodriguez, J.M. 1990. Contribución al conocimiento del ictioplancton del Mar de Alborán. Bol. Inst. Esp. Oceanogr., 6: 1-20.

Rodríguez, J.M., S. Hernandez-Leon & E.D. Barton. 1999. Mesoscale distribution of fish larvae in relation to an upwelling filament off Northwest Africa. Deep-Sea Res., Part I, 46(11): 1969-1984.

Rodriguez, J.M., S. Hernández-Leon & E.D. Barton. 2006. Vertical distribution of fish larvae in the Canaries-African coastal transition zone in summer. Mar. Biol., 149: 885-897.

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.

Rodríguez-Graña, L., L. Castro, M. Loureiro, H.E. González & D. Calliari. 2005. Feeding ecology of dominant larval myctophids in an upwelling area of the Humboldt Current. Mar. Ecol. Prog. Ser., 290: 119-134.

Rojas, P.M., R. Escribano & V. Marín. 2002. The influence of coastal upwelling on fish larvae distribution off Mejillones Peninsula, northern Chile. Fish. Oceanogr., 11(4): 233-244.

Roughan, M., A.J. Mace, J.L. Largier, S.G. Morgan, J.L. Fisher & M.L. Carter. 2005. Subsurface recirculation and larval retention in the lee of a small headland: a variation on the upwelling shadow theme. J. Geophys. Res., 110: C10.

Sakuma, K.M. & R.J. Larson. 1995. Distribution of pelagic metamorphic-stage sanddabs *Citharichthys sordidus* and *C. stigmaeus* within areas of upwelling off central California. Fish. Bull., 93: 516-529.

Sassa, C. 2001. Ecological study of myctophid fish larvae and juveniles in the western North Pacific. Ph.D. Thesis, University of Tokyo, Tokyo, 274 pp.

Sassa, C. & K. Kawaguchi. 2005. Larval feeding habits of *Diaphus theta*, *Protomyctophum thompsoni*, and *Tarletonbeania taylori* (Pisces: Myctophidae) in the transition region of the western North Pacific. Mar. Ecol. Prog. Ser., 298: 261-276.

Sassa, C., K. Kawaguchi, T. Kinoshita & C. Watanabe. 2002a. Assemblages of vertical migratory mesopelagic fish in the transitional region of the western North Pacific. Fish. Oceanogr., 11(4): 193-204.

Sassa, C., K. Kawaguchi, Y. Oozeki, H. Kubota & H. Sugisaki. 2004b. Distribution patterns of larval myctophid fishes in the transition region of the western North Pacific. Mar. Biol., 144: 417-428.

Send, U., R.C. Beardsley & C.D. Winant. 1987. Relaxation from upwelling in the coastal ocean dynamics experiment. J. Geophys. Res., 92(C): 1683-1698.

Siegel, S. & N.J. Castellón. 1988. Non-parametric statistics for the behavioral sciences. McGraw-Hill International Editions, Statistics Series, 399 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.

Received: 17 August 2012; Accepted: 12 April 2014

Sokal, R.R. & F.J. Rohlf. 1985. Biometry. Blume, Barcelona, 587 pp.

Stenevik, E.K., S. Sundby & R. Cloete. 2007. Diel vertical migration of anchovy *Engraulis encrasicolus* larvae in the northern Benguela. Afr. J. Mar. Sci., 29(1): 127-136.

Tsukamoto, Y., H. Zenitani, R. Kimura, Y. Watanabe & Y. Oozeki. 2001. Vertical distribution of fish larvae in the Kuroshio and Kuroshio-Oyashio transition region in early summer. Bull. Nat. Res. Inst. Fish. Sci., 16: 39-56.

Watanabe, H., M. Masatoshi, K. Kawaguchi, K. Ishimaru & A. Ohno. 1999. Diel vertical migration of myctophid fishes (family Myctophidae) in the transitional waters of the western North Pacific. Fish. Oceanogr., 8(2): 115-127.

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.

Yamashita, Y., D. Kitagawa & T. Aoyama. 1985. Diel vertical migration and feeding rhythm of the larvae of the Japanese sandeel *Ammodytes personatus*. Bull. Jpn. Soc. Sci. Fish., 51: 1-5.