Fish larvae distribution off Mejillones Peninsula (northern Chile) during a coastal upwelling event in Spring 1999: interactions with the cold upwelling plume

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ABSTRACT

We examined the interaction between vertical and horizontal distribution of fish larvae off Mejillones Peninsula (23°S), northern Chile, under conditions of active coastal upwelling. An oceanographic survey covered spatial variability in temperature, chlorophyll-*a* (chl *a*), dissolved oxygen, salinity and water density. Fish larvae were sampled during daytime and nighttime periods through two consecutive days in four stations: two inside and two outside of a well-developed upwelling plume, and at three depth strata: 0–20, 20–80 and 80–200 m. Eighteen taxa were analysed, of which the Myctophidae *Diogenychthys atlanticus*, *Diogenichthys laternatus*, and the anchovy *Engraulis ringens*, were most abundant. Our data showed little evidence for diel vertical migration and larvae were more abundant at depth (>80 m) under low temperature (~12°C) and low chl *a* (~2 mg m^{-3}), below the highly advective upper layer. The exploratory *K*-means analysis allowed the separation of data into two distinct habitats: upwelling and nonupwelling types. Most taxa were allocated in nonupwelling waters, i.e. outside the cold plume. However, short-term variations (<24 h) in the position of the upwelling plume influenced both horizontal and vertical occurrence as well as abundance of taxa, and caused variability in temperature, oxygen and chl *a*. These changes in oceanographic conditions, caused by upwelling circulation and the dynamics of the cold plume, may sharply modify the habitat of fish larvae and have an important role in survivorship and recruitment success.

Key words: advection, distribution, Humboldt current, ichthyoplankton, upwelling, vertical migration

INTRODUCTION

The Mejillones Peninsula is a well-recognized upwelling site in northern Chile (Rodriguez *et al.*, 1991; Marín *et al.*, 1993; Escribano, 1998). This area, like most upwelling systems, is dominated by small pelagic fishes, such as anchovy and sardine, which sustain their populations on high plankton productivity induced by nutrient-rich upwelled waters (Parrish *et al.*, 1983; Pauly and Tsukayama, 1987; Alheit and Bernal, 1993). However, fish populations in upwelling areas exhibit great variations in abundance, explained mostly by changes in recruitment strength (Hutching *et al.*, 1995). It has long been viewed that such fluctuations are substantially driven by environmental factors acting on early stages. Of these factors, advective losses of eggs and larvae have been considered as a key determinant of recruitment success in upwelling systems (Hutching, 1992; Bakun, 1996). Despite its importance for fish population dynamics, in the Humboldt-current system (HCS) the information on upwelling circulation and its effects on fish egg and larval survival is very scarce and limited to the anchovy, *Engraulis ringens* population of Central-South of Chile (Castro *et al.*, 2000).

During upwelling, eggs and fish larvae may be subjected to intense alongshore and cross-shelf flows, such that the ability to develop or adopt retention mechanisms near the upwelling centres may play a relevant role to maintain local populations (Sinclair, 1988) and hence successful recruitment. In northern Chile, fish larvae have been previously described as persistently appearing aggregated nearshore, associated with major concentrations of recently spawned eggs (Loeb and Rojas, 1988). Studies, however, do not provide clues on factors that may regulate nearshore retention of larvae. Among proposed retention

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mechanisms, diel vertical migration (DVM), allowing the use of reversing vertical flows (Peterson, 1998), has been hypothesized. In coastal waters off northern Chile, however, the rise of a shallow oxygen minimum (<0.5 mL O_2 L^{-1}) layer into the euphotic zone might impose a narrow limit for vertical movement (Morales *et al.*, 1996), forcing aggregation of planktonic organisms in the upper 50 m layer (Escribano and Hidalgo, 2000). An alternative retention factor may be a result of the spatial and temporal variability of the nearshore circulation. For example, flow structures termed 'upwelling shadows' have recently been proposed as an important flow-dependent retention mechanism (Graham and Largier, 1997; Wing *et al.*, 1998). Therefore, local upwelling circulation may play an important role in the distribution of fish larvae and eggs. The development of an upwelling plume also induces abrupt changes in 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. These changes, taking place mostly inside the upwelling plume, might influence larval distribution as well.

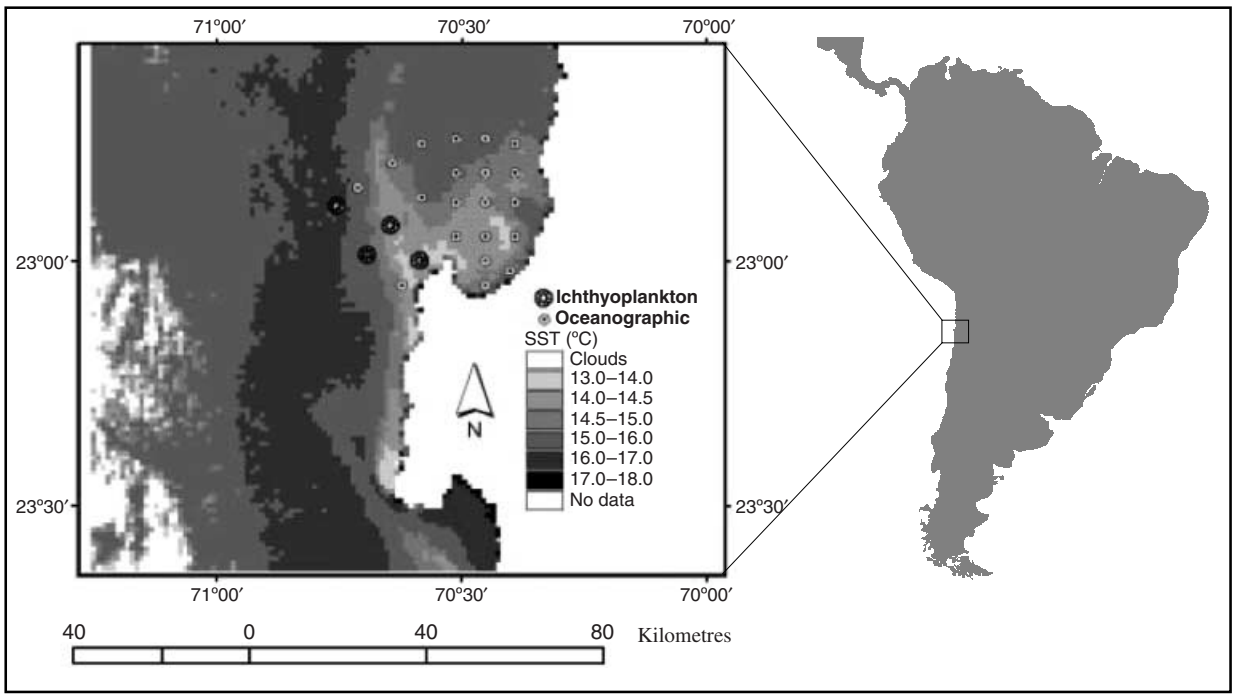
As part of an ongoing oceanographic research programme of zooplankton populations in coastal upwelling areas at the northern area of the HCS, we studied the oceanographic conditions during coastal upwelling. In this work, we report the response of the fish larval assemblage to the oceanographic features associated with upwelling. We examined the role of physical structures that arise after development of the upwelling plume have on vertical and horizontal distribution of fish larvae.

MATERIALS AND METHODS

Sampling design and procedures

During November 1999, we established a sampling grid of 24 stations at the northern end of Mejillones Peninsula (23°S) (Fig. 1). This grid was sampled for 26 h on board the L/C *Purihaalar* from the University of Antofagasta. At each station, vertical profiles of temperature, salinity and dissolved oxygen (DO) were made from surface to 200 m depth with a SeaBird SBE-19 conductivity temperature depth (CTD), 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. Fluorescence units were converted to chl *a* concentration through a linear algorithm derived from an *in situ* calibration (Escribano and McLaren, 1999). For fish larvae sampling, we used four fixed stations (Fig. 1): two inside and two outside the upwelling plume, in accordance with a

Figure 1. Satellite NOAA image of SST of Mejillones Peninsula at northern Chile illustrating the cold upwelling plume on 6 November 1999 and location of the stations for the oceanographic survey and ichtyoplankton sampling.



satellite NOAA image of sea surface temperature (SST) obtained on November 6, a day before the start of our sampling. Detailed information on satellite-derived SST is described in Marín *et al.* (2001). The next 2 days after the oceanographic grid was finished, fish larvae were sampled at four stations during two daytime and two nighttime periods. This design considered upwelling/nonupwelling conditions as the main treatment, i.e. inside/outside the cold plume, and variability introduced by daytime/nighttime effect, as well as temporal changes after 24 h. Diel changes in vertical distribution of larvae were evaluated by sampling three depth strata each time: 200–80, 80–20 and 20–0 m. According to a previous study in this zone (Escribano *et al.* 2001), during upwelling the upper 20 m was found to represent the Ekman layer, the 80–20 m stratum having a reversal flow, and the 200–80 m stratum as a deep and more stable layer.

Ichtyoplankton sampling and analysis

Ichtyoplankton 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 2 days. In the laboratory, fish eggs and larvae were removed for counting and identification. Abundance per each depth stratum was expressed as number per 10 m^{-2}.

Data analysis

The effects of upwelling vs. nonupwelling locations (inside and outside the upwelling plume), day/night, and depth strata on total abundance of larvae were examined by ANOVA on log-transformed data, excluding counts with zero larvae. Because of low occurrence for many species, we did not use ANOVA on each species separately. To assess short-term variability, we analysed changes in oceanographic conditions and total larval abundance at stations separated by 12 h intervals. In order to study the influence of upwelling on the larval assemblage as a whole, we distinguished upwelling and nonupwelling waters using the exploratory *K*-means analysis (Wilkinson, 1990). This method allows partitioning of the data set as a function of their oceanographic attributes by maximizing variance between groups and minimizing variance within groups for selected variables (Hartigan and Wong, 1979). The selected variables were temperature, salinity, DO and chl *a*. *K*-means method uses the Euclidean distance and calculates the *F*-ratios between and within groups, partitioning the locations into clusters according to the highest between-variance and the smallest within-variance. The first-order partitioning would be between surface and deep waters, given the sharp vertical gradient for most variables. Thus, we decided to use *K*-means analysis separately for each depth layer for grouping two types of data, either representing upwelling or nonupwelling habitats. The partitioning of data as a function of oceanographic variables may help to distinguish upwelled and nonupwelled waters. However, we did not know which taxa were associated with those water masses. As larval counts from samples were usually small (<5), we examined relative occurrence and abundance of taxa within each sorted group of data by *K*-means, such that presence of taxa rather than absolute abundance might be more relevant to evaluate the influence of the cold upwelling plume.

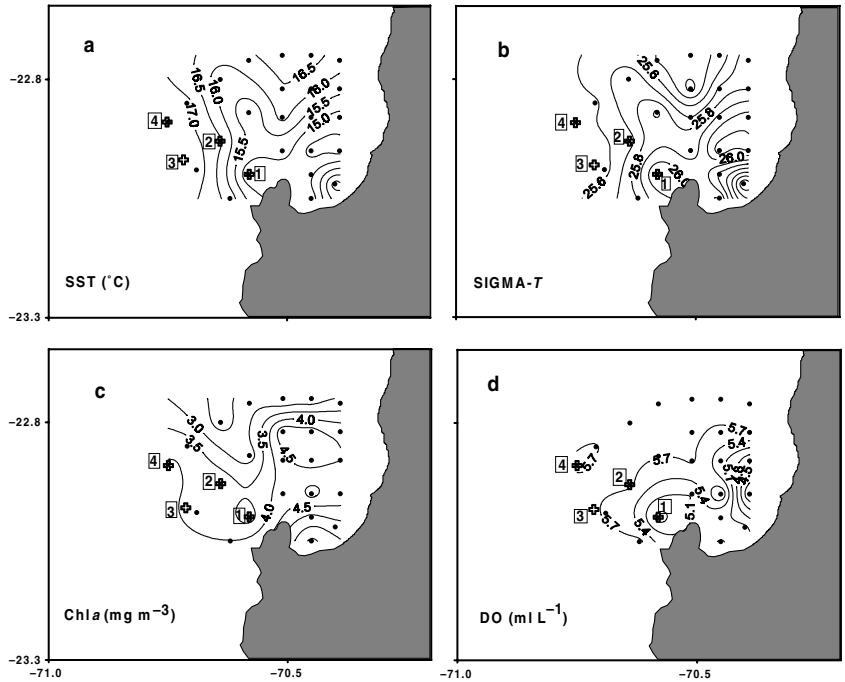
RESULTS

Oceanographic conditions

As shown by the satellite image of SST on the previous day before sampling (Fig. 1), the upwelling plume was orientated northward about 15 km, having its origin located at the northern point of the Peninsula. As ichthyoplankton stations were fixed according to a satellite image of SST on the previous day, we did not know how conditions could have changed during the sampling (~40 h). In fact, after examining the *in situ* SST (Fig. 2a), we noted that one of the stations (station 2) was indeed in a frontal area of the plume rather than inside. SIGMA-*T* distribution illustrates the density-gradient across the plume (Fig. 2b). Surface chl *a* levels were nearly 4 mg m^{-3} and seem rather uniformly distributed, without a clear pattern (Fig. 2c), whereas DO appeared slightly lower inside the cold plume (Fig. 2d). These *in situ* measurements of SST revealed a difference of about 2.5°C between the sites inside and outside the upwelling filament.

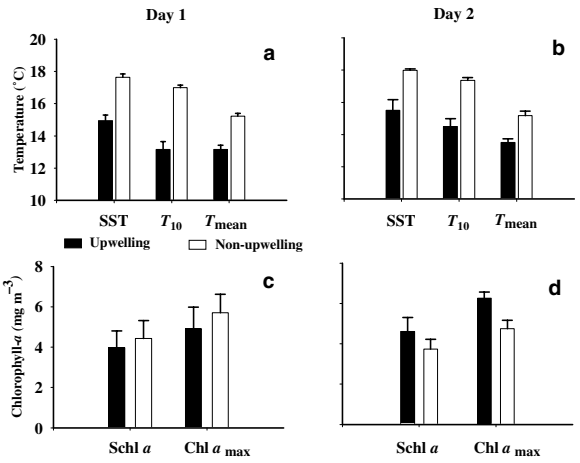
Mean values of SST differed significantly ($F_{1,14} = 41.5$, $P < 0.01$) between upwelling and nonupwellling locations (inside and outside the plume), whereas mean surface chl *a* was not significantly different ($F_{1,14} = 0.06$, $P > 0.05$). Inside the cold-filament and associated with cold SST, the surface DO was slightly lower (<5 m L^{-1}) as compared to areas outside the plume (>5 m L^{-1}), but the differences were not significant. Significant ($P < 0.05$) differences in the temperature between locations affected the whole water column on both days of the sampling

Figure 2. Distribution of *in situ* measured SST, surface density (SIGMA-*T*), surface chlorophyll *a* (chl *a*) and surface dissolved oxygen (DO) after the oceanographyc survey in November 1999, and location of the ichthyoplankton stations.



(Fig. 3a,b). Figure 3c,d also illustrates the lack of differences in chl *a* between sites, on both sampling days. Profiles of DO at stations 1 and 4, inside and outside the plume, respectively, revealed the ascent of the oxygen minimum layer at the upwelling location and the much more oxygenated layer in the nonupwelling area (Fig. 4).

Figure 3. Temperature and chl *a* inside (upwelling) and outside (nonupwelling) of the cold upwelling plume on 7 November 1999. Values are means from two stations in both sites. SST = sea surface temperature, $T10$ = temperature at 10 m, T_{mean} = mean temperature of the water column (0–200 m), Schl *a* = surface chl *a* and chl *a* max = maximum peak of chl *a* in the water column.



As vertical profiles of temperature and fluorescence were made every 12 h, at each ichthyoplankton sampling, we examined variability of oceanographic conditions while sampling. Station 1, located in the upwelling focus, appeared well-stratified with a very shallow thermocline, within 20 m depth (Fig. 5a). Station 2, located inside the temperature gradients, within the plume, was also stratified, although the thermocline was deeper (Fig. 5b). Stations 3 and 4, although showing stratification, were much warmer and with a deeper mixed layer (Fig. 5c,d). Changing conditions in the water column temperature at 12 h intervals, affected the mixed layer of all stations. This caused warming and cooling of the upper layer in about 1–2°C at stations inside the plume, whereas temperature variation outside the plume was mostly observed within the thermocline Fig. 5c,d. Short-term variability while sampling was also observed when looking at chl *a* profiles (Fig. 6). These changes were consistently associated with changes in temperature and caused large variations in chl *a* concentration at all stations (Fig. 6), in particular at station 2 (Fig. 6b).

Taxonomic composition and larval distribution

A total number of 48 samples were analysed, of which 40 contained fish larvae. Total larvae had a mean

Figure 4. Vertical profiles of DO at station 1 (upwelling) and station 4 (nonupwelling), showing the rise of the oxygen minimum layer inside the upwelling plume (continuous line), and the more oxygenated upper layer (broken line) outside the plume in November 1999, off Mejillones Peninsula.

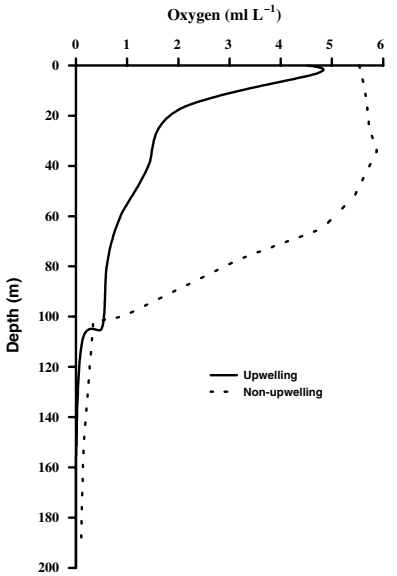
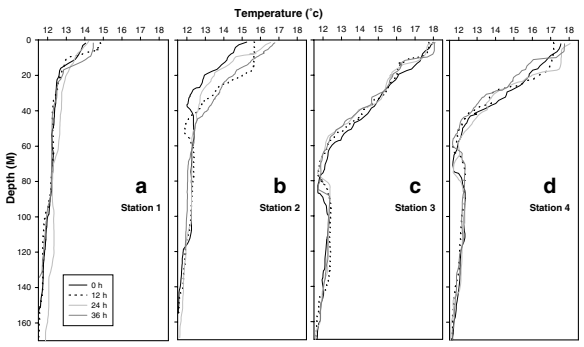
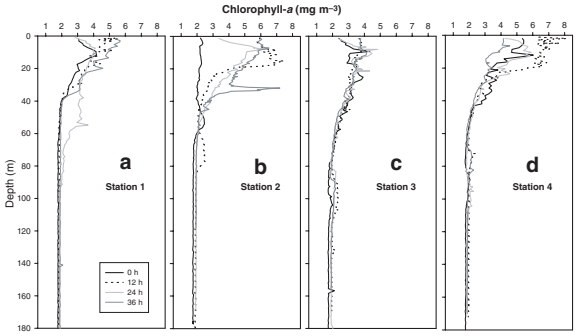


Figure 5. Short-term (12 h) variability in temperature at each ichthyoplankton station sampled on two subsequent days inside (stations 1 and 2) and outside (stations 3 and 4) of the upwelling plume in November 1999, off Mejillones Peninsula.



abundance of 36 larvae per 10 m^{-2} (SD = 34). Fifteen taxa were identified, which represented 63.4% of the total larvae (Table 1). These species had been previously described for the area (Loeb and Rojas, 1988). In their study, the three most abundant species were *Diogenychthys atlanticus*, *Diogenychthys laternatus*, and *E. ringens*, and these were present in many of our samples. We did not identified fish eggs, except for

Figure 6. Short-term (12 h intervals) variability in chl *a* at each ichthyoplankton station sampled in two subsequent days inside (stations 1 and 2) and outside (stations 3 and 4) of the upwelling plume in November 1999, off Mejillones Peninsula.



E. ringens. Eggs of *E. ringens* were mostly concentrated in the upper 80 m and their vertical distribution did not show diel differences ($F_{1,9} = 0.04$, $P > 0.05$). Pooled data of total larvae, from both the sampling days and stations inside and outside the cold plume, showed that larvae were not restricted to one or two strata, but were usually found in each one of them, although with a trend to increase in abundance with depth (Fig. 7). ANOVA revealed no significant diel or upwelling vs. nonupwelling effects on total abundance ($F_{1,108} < 1$, $P > 0.05$), but significant differences in larval abundance among depth strata ($F_{2,108} = 12.64$, $P < 0.001$).

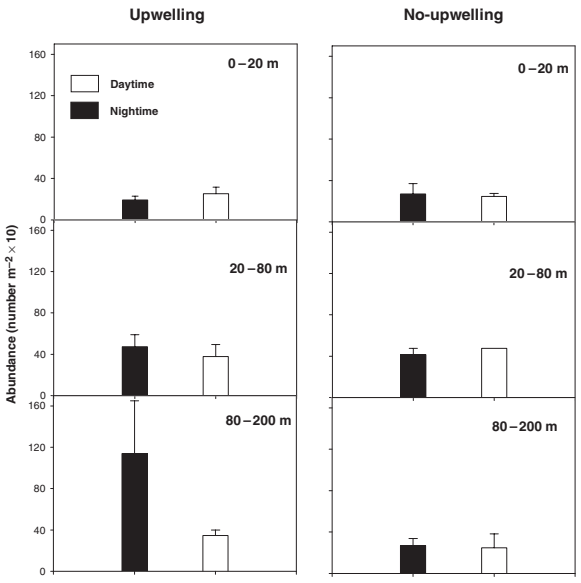
Even though ANOVA did not reveal significant effects of spatial location, i.e. either inside or outside the upwelling plume, on total abundance of larvae, we thought that any possible influence could have been obscured by vertical layering and diel effects, as well as eventual mixing and changes in position of the upwelling plume while sampling, as shown above (Figs 5 and 6). All these sources of variance may also be taxon-dependent. Therefore, vertical distribution of the taxa may still depend on the spatial location of our sampling stations, but observed distributions do not consider changes in abundance and composition over the 40 h period. In this regard, *K*-means analysis allowed us to allocate data on larval abundance according to their associated oceanographic conditions, independently from the location of stations and at the time of sampling. Table 2 shows ANOVA from *K*-means for each of the two water types, upwelling vs. nonupwelling, separated by depth strata. According to the *F*-ratios in the upper layer (0–20 m), as expected, SST explained most variance between upwelling vs. nonupwelling waters. We then assumed that one group corresponded to oceanographic data from the sample

Taxa	Total larvae	Relative abundance (%)	Frequency of occurrence ($n = 48$)	Mean abundance (number, 10 m^{-2})
Diogenichthys atlanticus	914.0	18.5	17	37
Diogenicthys laternatus	847.0	17.2	21	36
Engraulis ringens	831.0	16.9	14	37
Unidentified Myctophidae	547.0	11.1	14	35
Strangomera bentincki	534.0	10.8	7	37
Vinciguerria lucetia	416.0	8.4	9	37
Triphoturus mexicanus	218.0	4.4	5	37
Diaphus theta	154.0	3.1	4	34
Normanichthys crockeri	118.0	2.4	3	34
Lampanyctus sp.	72.0	1.5	2	38
Diogenichthys sp.	57.0	1.2	2	35
Undetermined spp.	53.0	1.1	2	26
Unidentified Macrouridae	47.0	1.0	2	23
Unidentified Genipteridae	34.0	0.7	2	17
Unidentified Blennidae	29.0	0.6	1	29
Protomyctophum crockeri	23.0	0.5	1	23
Hygophum brunni	20.0	0.4	1	20
Myctophum nitidulum	18.0	0.4	1	18

Table 1. Abundance, relative abundance and frequency of occurrence of fish larvae species found off Mejillones Peninsula in November 1999. Total larvae represents all larvae captured during the sampling.

of cold upwelled waters, and the other data are from the sample of warmer nonupwelling waters. Again, this analysis does not depend on sampling location, but on oceanographic conditions. For example, some samples that clustered into the nonupwelling waters, had indeed originated from stations 1 and 2 (Fig. 2), which were initially upwelling stations (inside the plume). We thus estimated the number and percentage of cases that were allocated into the 'wrong' water type and considered it as a result of the short-term variability as shown above, possibly associated with changes in the position of the upwelling plume. In the upper layer, about 38% of the cases were allocated into a 'wrong' water type. *K*-means yielded a more effective separation for the mid-layer (20–80 m), with only 9% mixed cases. In this layer, however, oxygen concentration explained most variance (Table 2). Thus, upwelling waters are less oxygenated in this layer, as shown in Fig. 4. Finally, the deep layer (80–200 m) is also well described by temperature, with 9% mixed cases, such that colder waters corresponded to upwelling waters (Table 2). In the three layers, all the cases allocated into the 'wrong' water type were upwelling and classified as nonupwelling waters.

Figure 7. Total abundance of fish larvae in three depth strata sampled at nighttime and daytime in stations located inside (upwelling) and outside (nonupwelling) of the cold upwelling plume off Mejillones Peninsula, in November 1999.



The corresponding taxa allocated within each water type, when examined in terms of occurrence and larval density, should give us insight into which species represented either upwelling or nonupwelling waters. The abundances and occurrences of the three most abundant species, *D. atlanticus*, *D. laternatus* and *E. ringens*, were different, according to water type into which data were allocated (upwelling/nonupwelling). *D. atlanticus* was distributed in all the layers inside the upwelling waters and more abundant in the mid-layer, whereas in the nonupwelling waters it was not found

Table 2. Oceanographic conditions allocated into upwelling and nonupwelling water types, according to the exploratory analysis *K*-means. Temp. = temperature, chl *a* = chlorophyll a, SAL = salinity and DO = dissolved oxygen represent mean values of each corresponding stratum. *F*-ratios and *P*-values are for comparison of variances between both groups.

		Upwelling				Nonupwelling					
Strata	Variable	Min	Max	Mean	*n*	Min	Max	Mean	*n*	*F*-ratio	*P*-value
0–20 m	Temp. (°C)	13.06	14.57	13.85	10	15.63	17.66	16.96	16	1641.53	< 0.01
	chl *a* (mg m^{-3})	2.19	5.09	4.08	10	3.10	6.42	4.97	16	45.02	< 0.01
	SAL (psu)	34.74	35.02	34.91	10	34.74	35.02	34.95	16	7.99	< 0.01
	DO (mL L^{-1})	4.56	5.81	5.25	10	4.56	5.81	5.49	16	15.18	< 0.01
20–80 m	Temp. (°C)	11.68	12.59	12.26	30	11.68	12.59	12.17	33	10.34	< 0.01
	chl *a* (mg m^{-3})	1.81	2.84	2.14	30	1.81	2.84	2.04	33	10.03	< 0.01
	SAL (psu)	34.99	35.11	35.04	30	34.19	34.67	34.43	33	863.48	< 0.01
	DO (mL L^{-1})	0.70	1.34	1.02	30	4.04	4.80	4.42	33	6641.50	< 0.01
80–200 m	Temp. (°C)	11.36	11.81	11.65	7	11.81	12.15	11.97	21	502.14	< 0.01
	chl *a* (mg m^{-3})	1.75	1.94	1.82	7	1.71	1.97	1.88	21	37.53	< 0.01
	SAL (psu)	35.14	35.42	35.31	7	35.14	35.42	35.24	21	29.98	< 0.01
	DO (mL L^{-1})	0.00	0.16	0.07	7	0.00	0.16	0.09	21	3.65	0.06

in the upper 20 m layer. *D. laternatus* showed an inverse distribution compared with *D. atlanticus*. It was observed in all the layers in the nonupwelling waters, but absent in the upper stratum inside the upwelling water (Table 3). The abundant *E. ringens* was aggregated in the upper layer although present in all layers in the nonupwelling waters. Other species, although less abundant, were allocated to either the upwelling or the nonupwelling waters, but there seems to be a decrease in the number of species (occurrence) and in abundances within the upwelling waters (Table 3). For other species, we noted that some of them were only present in nonupwelling waters. Only two much less abundant groups unidentified, Macrouridae and *Lampanyctus* sp., were allocated in upwelled waters.

Finally, based on mean abundances and percentages of occurrence of species within each group of data that resulted from *K*-mean analysis (Table 3), the dominant habitat of each species was inferred (Table 4). Most species predominate in nonupwelling waters, although the abundant *D. atlanticus* and *D. laternatus* were equally present in both the water types. The dominant habitats, according to depth stratum, suggest some vertical partitioning (Table 4).

When looking at the role that temperature and chl *a* could have had on observed larval density, we found that the greatest abundances were associated with low temperature (~12°C) (Fig. 8a) and low chl *a* (~2 mg m^{-3}) (Fig. 8b). This was because at 'upwelling stations' larvae were mostly concentrated in the cold and low chl *a* in the middle and deep layers (>20 m), as shown in Fig. 7.

Changes in oceanographic conditions while sampling and exchanges of species between upwelling and nonupwelling waters, as shown by *K*-mean analysis, suggested that observed abundance of larvae and their vertical distribution also resulted from these short-term variations. In the upwelling stations, the proportion of larvae relative to the water column showed that any DVM pattern may be obscured by this temporal variability. In fact, the relative abundance of larvae seems to vary most consistently with the mean temperature, at least in the upper 20 m (Fig. 9). At the nonupwelling locations, which did not exhibit much variation in the upper layer, larval depth was also more uniform through time, but changes still appeared associated with variations in temperature in the upper 80 m (Fig. 10).

DISCUSSION AND CONCLUSIONS

Presence of recently spawned eggs and larvae of *E. ringens* in nearshore-upwelling areas of the HCS has

Table 3. Taxa of fish larvae allocated into upwelling/nonupwelling waters from *K*-means analysis, and their corresponding mean abundance (n = number 10 m^{-2}) within each group of data. Ocurrence (%) represents the number of cases (samples) the taxon was present relative to total number of cases allocated to a group of data by *K*-means. The analysis was performed separated for each depth stratum.

		Upwelling		Nonupwelling	
Strata	Taxa	*n*	%	*n*	%
0–20 m	*D. atlanticus*	39.5	4.2	–	
	D. laternatus	–		68.3	6.3
	E. ringens	32.5	4.2	77.7	8.3
	Unidentified Myctophidae	31.0	4.2	32.5	4.2
	D. theta	–		33.0	4.2
	T. mexicanus	39.0	2.1	32.0	2.1
	S. bentincki	–		136.0	6.3
	V. lucetia	–		72.5	4.2
	N. crockeri	–		49.5	4.2
	Diogenichthys sp.	–		33.0	2.1
20–80 m	*D. atlanticus*	70.3	6.3	65.4	14.6
	D. laternatus	67.6	14.6	29.0	8.3
	E. ringens	46.5	4.2	37.7	6.3
	Unidentified Myctophidae	41.7	6.3	45.2	12.5
	D. theta	26.0	2.1	23.5	4.2
	Unidentified Genipteridae	–		22.0	2.1
	T. mexicanus	21.0	4.2	52.0	2.1
	S. bentincki	38.0	4.2	25.0	4.2
	V. lucetia	19.0	4.2	35.7	10.4
	N. crockeri	20.0	2.1	–	
	Lampanyctus sp.	36.0	4.2	–	
	Macrouridae	23.5	4.2	–	
	H. brunni	–		20.0	2.1
	M. nitidulum	–		18.0	2.1
80–200 m	*D. atlanticus*	15.7	6.3	40.0	4.2
	D. laternatus	23.0	6.3	25.3	8.3
	E. ringens	23.0	2.1	25.5	4.2
	Unidentified Myctophidae	–		24.0	2.1
	T. mexicanus	–		15.5	4.2
	D. theta	–		15.0	2.1
	Diogenichthys sp.	–		24.0	2.1
	Unidentified Genipteridae	11.0	2.1	11.0	2.1
	Unidentified Blennidae	29.0	2.1	29.0	2.1
	P. crockeri	23.0	2.1	23.0	2.1

been recently viewed as part of a large reproductive strategy, in which maximal peaks of abundance appear coupled with favourable oceanographic conditions (Castro *et al.*, 2000). Off Mejillones Peninsula, dense aggregations of phytoplankton and zooplankton are usually associated with upwelling plumes, or their surrounding areas (Escribano, 1998; Escribano and Hidalgo, 2000). Thus, retention nearby the upwelling plume will provide a favourable habitat for larval survival and hence successful recruitment. The presence of frontal zones surrounding the upwelling plume will further aid in retaining larvae and eggs (Hutchings *et al.*, 1995; Roy, 1998). In fact, we noted the opposite pattern: larvae predominantly occupied the nonupwelling habitat (Table 4), i.e. surrounding the upwelling plume rather than inside of it. Only two appeared associated with the upwelling plume, Macrouridae and *Lampanyctus*, albeit with rather low occurrences. The two most abundant species, *D. atlanticus* and *D. laternatus*, occurred similarly in both habitats, although they were concentrated in the middle and deep layers, respectively. This could help prevent offshore advection, as the highly advective Ekman layer in this zone was estimated as comprising the upper 20 m (Marín *et al.* 2001) and below that current shear may help retention (Peterson *et al.*, 1979; Wroblewski, 1982).

Another well-documented mechanism that may prevent offshore transport of fish larvae is DVM. There are a large number of examples that show the importance of DVM for fish larvae (Ahlstrom, 1959; Bailey, 1981; Bakun and Parrish, 1982; Neilson and

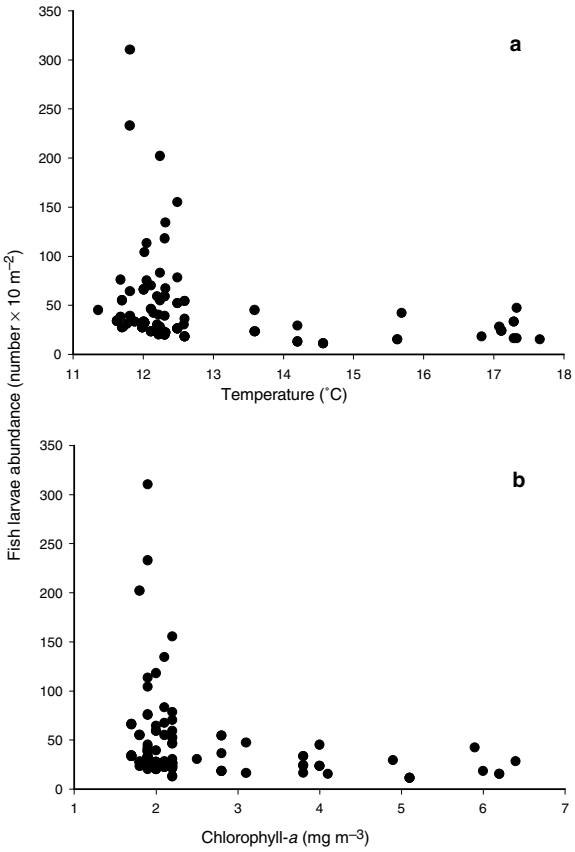
Table 4. Dominant habitat of fish larvae during coastal upwelling off Mejillones Peninsula. Allocation was based on abundance and occurrence (%) after *K*-means analysis. Waters type represents either upwelling or nonupwelling habitat. Strata are: upper = 0–20 m, mid = 20–80 m and deep = 80–200 m.

Species	Waters type	Strata
D. atlanticus	Both	Mid
D. laternatus	Both	Deep
E. ringens	Nonupwelling	All three
Unidentified Myctophidae	Nonupwelling	Mid
S. bentincki	Nonupwelling	Upper/mid
V. lucetia	Nonupwelling	Upper/mid
T. mexicanus	Nonupwelling	Mid
D. theta	Nonupwelling	Upper
Lampanyctus sp.	Upwelling	Mid
Unidentified Macrouridae	Upwelling	Mid
N. crockeri	Nonupwelling	Upper/mid
Unidentified Genipteridae	Both	Deep
P. crockeri	Both	Upper
H. brunni	Nonupwelling	Mid
M. nitidulum	Nonupwelling	Mid

Perry, 1990; Hutchings *et al.*, 1995). Maintaining position, optimization of energy usage, and avoiding predation are among the suggested advantages of DVM (Brewer and Keppel, 1986; de Lafontaine and Gascon, 1989). Our data, however, manifest as in comparisons of daytime and nighttime samples, showed little evidence for DVM. In Mejillones Peninsula, presence of a very shallow oxygen minimum layer nearshore (Morales *et al.*, 1996) may be the major constraint for the extension of DVM. The oxygen minimum layer, bringing low oxygen (<1 mL L^{-1}), shoals within the photic zone in coastal waters to 40–50 m depth (Escribano and Hidalgo, 2000), limiting the extension of DVM of actively migrating euphausiids (Escribano *et al.*, 2000). However, fish larvae in our study were more abundant below the thermocline (Fig. 7). Their restricted nighttime ascent to the upper chl *a*-rich layer might be a mechanism developed not only to avoid the highly advective and variable mixed layer but also to cope with potentially increased predation in the upper layer.

Although the position of our ichthyoplankton stations (Fig. 1) was supposed to equally sample upwelling/nonupwelling habitats, i.e. inside/outside the plume, changed conditions through time indicated that station 2 was indeed located in a temperature gradient, therefore representing a transition zone between upwelling and nonupwelling waters. This may have affected observed distributions of larvae. However, larvae exchanges between the upwelling plume and surrounding zones occurred mostly in the upper layer, where many taxa were not found (Table 4). Nevertheless, this short-term variability, in a time scale of hours and days, may considerably alter both spatial and vertical distributions of fish larvae during upwelling. For instance, major inconsistences between observed distributions based on geographical location and actual habitat, as derived from the *K*-means analysis, indicate that larvae may undergo drastic changes in oceanographic conditions on a day-to-day basis during active upwelling. This is especially true for larvae occupying the upper, advective layer. The observed oscillations in water temperature and chl *a* concentration, at about 12 h intervals, may be driven by short-term changes in position and extension of the upwelling plume upon varying upwelling intensities, because of current reversals associated with changes in

Figure 8. The relationship between *in situ* measured temperature (a) and chl *a* (b) and fish larvae abundance (all species) sampled from three depth strata, at four stations, in two subsequent days, off Mejillones Peninsula, in November 1999. Mean values of temperature and chl *a* for each stratum from which larvae were sampled were used.



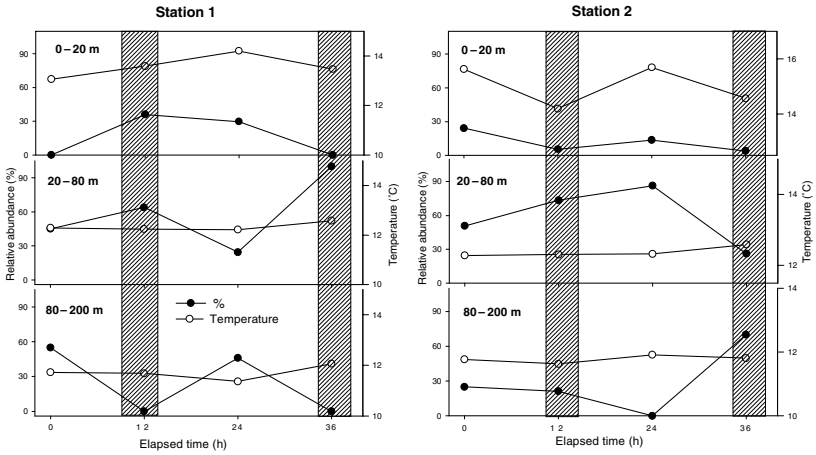


Figure 9. Short-term (12 h) variation in temperature (open circles) and fish larvae proportion (filled circles) sampled from two stations located inside the upwelling plume in three depth strata. The relative abundance (%) for each stratum was estimated with respect to abundance of the whole water column (0–200 m). Mean temperature is used for each stratum. Shaded areas indicate nighttime samplings.

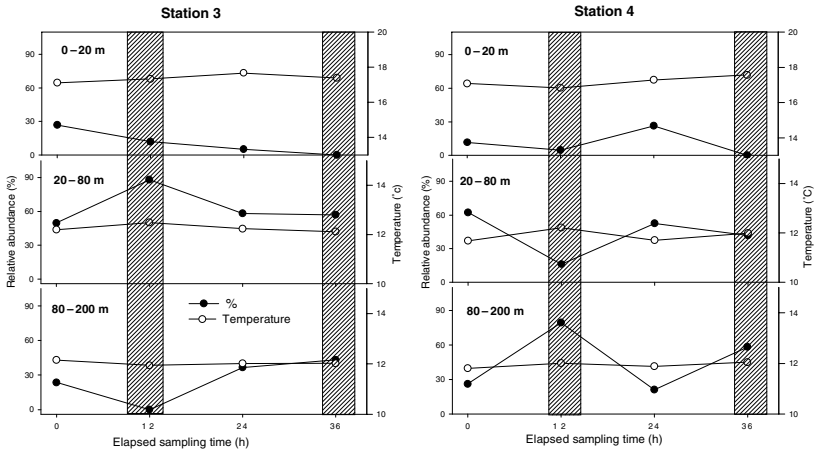


Figure 10. Short-term (12 h) variation in temperature (open circles) and fish larvae proportion (filled circles) sampled from two stations located outside the upwelling plume in three depth strata. The relative abundance (%) for each stratum was estimated with respect to abundance of the whole water column (0–200 m). Mean temperature is used for each stratum. Shaded areas indicate nighttime samplings.

the wind field in this zone (Marín *et al.*, 2001). This type of variability might be an important factor determining not only actual conditions of temperature, which may affect physiological responses of larvae, but also may modulate encounter rates with highly patchy food. Off Mejillones Peninsula, food does not seem to be a limiting factor for zooplankton growth (Escribano and McLaren, 1999), and this might also be true for fish larvae. Our data showed that, either inside or outside of the upwelling plume, the phytoplankton biomass appeared as high as 7 mg chl *a* m^{-3} within the upper 20 m, suggesting that larval starvation is unlikely. Even those larvae aggregated below the thermocline at low chl *a* may be subject to rapid changes in oceanographic conditions, precluding long-term exposure to low food. These changes indicate highly heterogeneous habitats in terms of temperature, oxygen levels and advective forces, which may in turn be important for larval survival, as suggested for *E. ringens* larvae in a southern area of the HCS (Castro and Hernandez, 2000). The interaction between vertical and horizontal distribution and the dynamics of cold upwelling plumes may thus strongly influence fish larvae survival and recruitment in coastal waters off Mejillones Peninsula, and this might be a more general feature of fast growing and short-living small pelagics from upwelling ecosystems.

Larvae of mesopelagic species were more abundant in our study, mostly represented by the myctophids *D. atlanticus* and *D. laternatus*. Mesopelagic species are important components of upwelling systems (Hulley and Prosch, 1987; Moser, 1996) although, in other upwelling regions, they seem to be more independent of upwelling plumes. For example, in the Benguela Current, *Lampanyctodes hectoris* tended to occur below the Ekman layer, avoiding the more advective upper layer (Olivar and Shelton, 1993), whereas the abundant *Protomyctophum chilensis* and *Symbolophorus boops* remained offshore (Olivar *et al.*, 1992; Olivar and Shelton, 1993). In the California system, the

Protomyctophum crockeri remains near the coastal front, also avoiding the upwelling plume (Moser and Smith, 1993). In our study, mesopelagic larvae were associated with the upwelling plume and hence they were subject to short-term variability. However, they appeared to occur below the Ekman layer (>20 m), which was more affected by changing oceanographic conditions. In a previous study in the North Pacific gyre, larvae of the same species had been described as remaining at depth (Loeb, 1980). In northern Chile, the continental shelf is very narrow (<20 km) and the cold upwelling plume develops near the shore, but at depths >1000 m off Mejillones Peninsula. Thus, the upwelling plume may interact with both oceanic and coastal waters, consequently affecting mesopelagic species as well as small pelagics, such as anchovy and sardine, whose eggs and larvae are expected to be more abundant nearshore (Castro and Hernandez, 2000). Mesopelagic species are known to feed on copepods and euphausiids (Hopkin *et al.*, 1992; Pakhomov *et al.*, 1996), whereas anchovy and sardine larvae may alternate a diet on diatoms and copepod eggs, and nauplii and copepodites (Hunter, 1984; Hutchings *et al.*, 1995; Castro *et al.*, 2000). Therefore, high-frequency variability in oceanographic conditions, driven by upwelling intensity, and timing and position of the cold plume, may not only influence the success of a highly diverse larval assemblage, comprised of taxa with very different life strategies, but also give rise to interactions of species using the same habitat and similar food resources. Ecological consequences of such interactions deserve further considerations in the Mejillones Peninsula upwelling system and elsewhere.

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