Spawning of the chilean hake (*Merluccius gayi*) in the upwelling system off Talcahuano in relation to oceanographic features*

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SUMMARY: Previous studies have shown that the upwelling area off Talcahuano, in central-south Chile, is an important spawning zone for the hake *Merluccius gayi*. We document the results of a study designed to assess the importance of oceanographic features on the horizontal and vertical distribution of hake eggs and larvae. Ichthyoplankton samples and oceanographic data (CTDO casts, and wind speed and direction) were collected during a cruise carried out off Talcahuano (36º22'S-37º10'S) in early spring (October 1996), which included a grid of 61 stations up to 60 nm offshore. The oceanographic information obtained revealed the presence of an upwelling plume at Lavapie Point (southern zone) extending northward over the shelf, and the presence of a warmer water parcel close to shore in the northern area. Peak egg densities occurred in this northern area over the shelf, in a nucleus located at the shoreward moving deeper layer (40-100 m deep) and associated with the upwelling front about 20-30 nm from shore. The highest larval abundance also occurred in the northern area over the shelf and in the deeper layer but closer to shore than the egg nucleus. Because the timing (early spring) and location of spawning (at depth, over the shelf and in association with frontal structures) are also shared by other hake species in upwelling areas, we propose that they may be part of a more commonly developed strategy to enhance offspring survival in coastal upwelling areas of eastern boundary currents.

Key words: hake larvae, upwelling, spawning, ichthyoplankton.

INTRODUCTION

Coastal upwelling areas along the Eastern South Pacific have traditionally been recognised as some of the areas in which the highest landings of small pelagic and demersal fish are reached. Despite these tremendous fish productions, little information exists on the characteristics of the spawning areas and on the influence of oceanographic features on the distribution and survival of the early life stages of demersal fishes. In these coastal upwelling systems, hakes represent some of the economically most important demersal fisheries (Sandoval de Castillo, 1989; Espino and Wosnitza-Mendo, 1989; Ware, 1992). Along the Chile-Peru eastern boundary current, the hake *Merluccius gayi* is the most common demersal species occurring throughout a wide distribution range from 6°S through 47°S. Within this latitudinal range, two potential subspecies have been proposed: *Merluccius gayi peruvianus* from 6°S through 14°S (Espino *et al*., 1995) and *Merluccius gayi gayi* from 23°S through the 47°S (Aguayo, 1995).

The main hake spawning areas off the central-south Chilean coast that are traditionally observed extend from Papudo through Valparaiso (32°30'S-33°00'S) and from Constitucion to south of the Talc-

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ahuano area (35°30'S-37°30'S) (Aviles *et al.*, 1979, Rojas and Blanco 1981) (Fig. 1). More recently, however, the northern limit of the spawning area off Talcahuano has been confirmed but its southern limit has been extended to lat. 40°S (Bernal *et al.*, 1997). Like other coastal upwelling areas along the Chile-Peru Current, the spawning zones for hake are also utilized by a number of small pelagic species such as anchoveta (*Engraulis ringens*) and sardines (*Sardinops sagax* and *Strangomera bentincki*) (Castro *et al.*, 1997, 2000).

Throughout the southern hake spawning area, marked seasonal variations in wind patterns and oceanographic conditions occur yearly (Arcos and Navarro, 1986). From September to March south winds blow, inducing coastal upwelling of Subsurface Equatorial Waters of low temperature, low oxygen concentrations, high salinity and high nutrient concentrations at the coast and inside the bays. From April to August, alternatively, northern winds dominate inducing coastal downwelling and heavy rain, especially in the southern zone. Although hake eggs and larvae may occur most of the year, the main reproductive season goes from August to November, thus coinciding with the onset of the upwelling season (Balbontín and Fischer, 1981; Alarcon and Arancibia, 1993).

There are few studies that explore the relationship between the distribution of early life stages of *Merluccius gayi* and the oceanographic features in the spawning areas off central and southern Chile. In an extensive review of the egg and larval distribution information generated from multiple cruises from 1968 to 1991, Bernal *et al.* (1997) identified differences in the longitudinal distribution of egg and larvae (distance from shore) in the two main central-south spawning areas. In the central area (32°S-33°S), eggs and larvae occurred close to the coast, while in the southern area (35°S-37°S) they tended to occur further offshore (>15 mn offshore), probably as the result of their transport in the complex circulation of the area induced by the strong south wind regime. In this southern area, however, older larval hake have been collected over the continental shelf and inside the bays, suggesting that the subsurface shoreward flow below the Ekman layer may play an important role in larval transport toward the coast (Vargas *et al.*, 1997). Unfortunately, most studies on the distribution of hake egg and larvae in the southern spawning area have not benefited from stratified sampling of egg and larvae in the water column or assessed the effect of short term

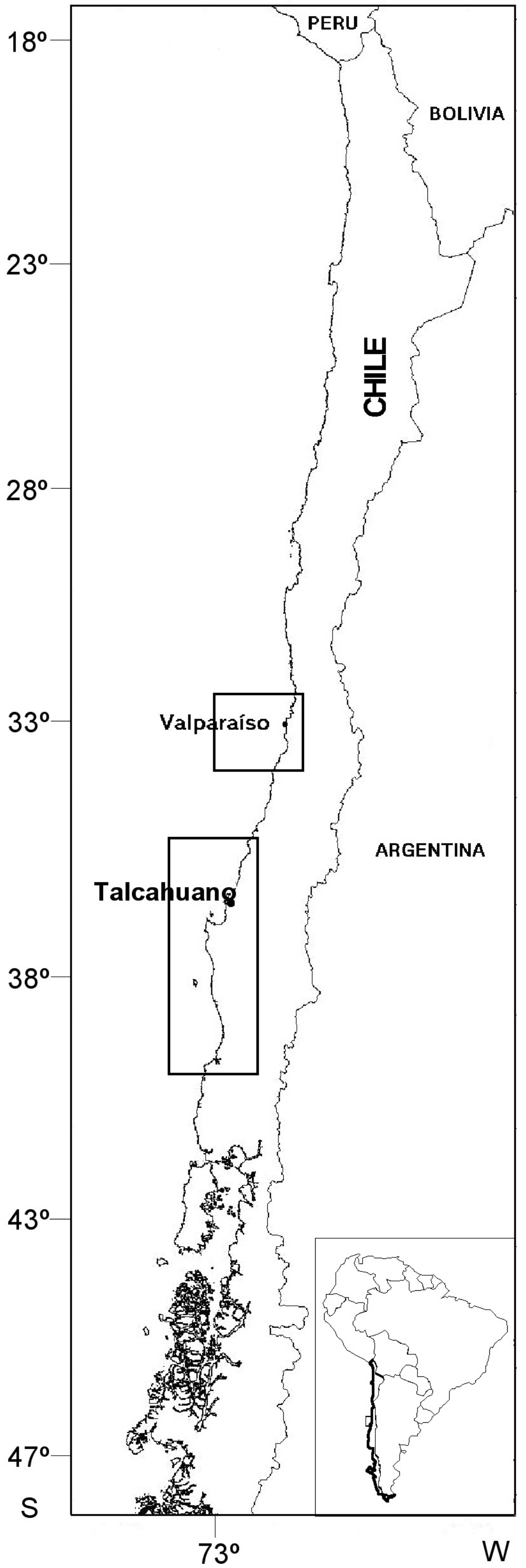

FIG. 1. – Spawning areas of *Merluccius gayi* along Chilean coast (according to Bernal *et al.* 1997).

variability in the oceanographic regime on the distribution of these early life stages. Consequently, the hypotheses on the role of oceanographic processes in the transport and distribution of hake egg and larvae remain to be tested until basic information on these variables can be obtained.

In the present study: i) we document the horizontal and vertical distribution (0-40 m and 40-100 m) of egg and larval hake *Merluccius gayi* in its southernmost spawning area (36°S-37°S) during the main reproductive season; ii) we identify some oceanographic features associated to the zones of peak egg and larval abundance; and iii) we assess the potential role of short term variability in the wind and some oceanographic processes in transporting young stages or modifying their distribution across the continental shelf.

MATERIAL AND METHODS

The oceanographic cruise was carried out along the coastal zone off Central Chile (October 15-28, 1996) aboard the research vessel Kay-Kay (Universidad de Concepcion). The cruise plan included a grid of 60 stations off Talcahuano (36°22´S-37°10´S), where the widest continental shelf occurs in central Chile. The grid included stations distributed in 6 transects perpendicular to the coast (Transects 11 to 16) with 4 to 8 stations each (2, 5, 10, 15, 20, 30, 40 and 60 nm from shore), and also stations located within the larger bays (Coliumo Bay, Concepcion Bay and Arauco Gulf) (Fig. 2).

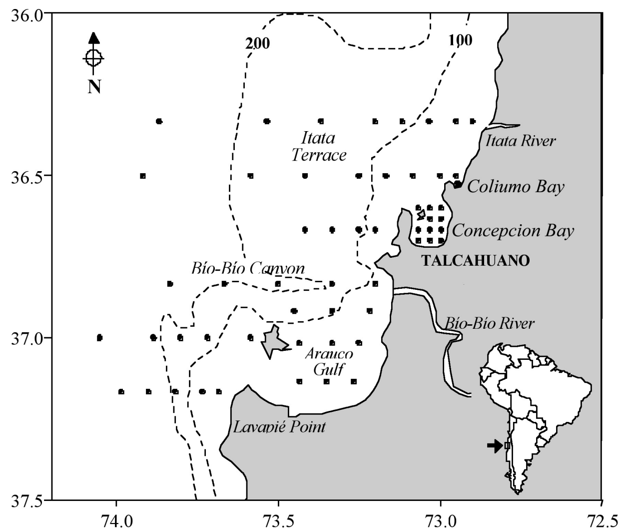

FIG. 2. – Area of study off Talcahuano, central-southern Chile, showing the location of oceanographic stations. The 100 and 200 m bathymetric contours are shown.

Ichtyoplankton samples were obtained using a 1 m^2 Tucker trawl net equipped with a 250 µm mesh nitex and a calibrated flowmeter. At each station, a single oblique tow was made to obtain samples at two-depths (from 100 to 40m and from 40 to the surface). Plankton samples from each station were split on board and one fraction was preserved in 5% formaline and the other in 96% ethanol. In the laboratory, all fish eggs and larvae from each subsample were separated and counted. Hake *M. gayi* eggs and larvae were identified and the eggs were staged in three classes according to Fischer (1959): Stages I-III (undeveloped embryo), Stage IV (early embryo), and Stage V (pre-hatching). Ichtyoplankton abundance was standardized to 1000 m^3 of seawater sampled. Standard length (SL) was measured for all *M. gayi* larvae using a Zeiss stereomicroscope with a calibrated ocular micrometer (50x).

Oceanographic data (temperature, conductivity and dissolved oxygen) were obtained using a CTD Sensordata SD2003 equipped with a oxygen sensor and also from water samples collected with 5 l Niskin bottles at six depths (surface, 10, 20, 30, 40, 60 and 80 m). From these samples, salinity was determined in the laboratory with an induction salinometer (Beckman III) and dissolved oxygen concentrations were determined through the Winkler method (Carpenter, 1965; Knapp *et al.*, 1993). Throughout the entire cruise, hourly wind data were obtained on board with a Delta-T automatic meteorological station.

RESULTS

Egg and larval distribution

M. gayi eggs were more abundant in the northern zone of the area surveyed and in the deeper layer (i.e. below 40 m; Wilcoxon paired-sample test, $p < 0.05$) (Fig. 3; Table 1). Spawning, as evidenced by the presence of eggs, was not observed inside the bays. The spatial distribution in the bottom layer showed a high concentration of eggs recently spawned (Stage I-III) in a nucleus located in the northern zone over the continental shelf, about 30-40 nm from shore (Fig. 3b). However, they were not restricted to this stratum because eggs at a more advanced stage (Stage V) were also present in the surface layer at most stations in the northeast area, but in very low density (Fig. 3e). In this area, eggs were also present up to 60 nm offshore, the furthest offshore stations sampled at both strata.

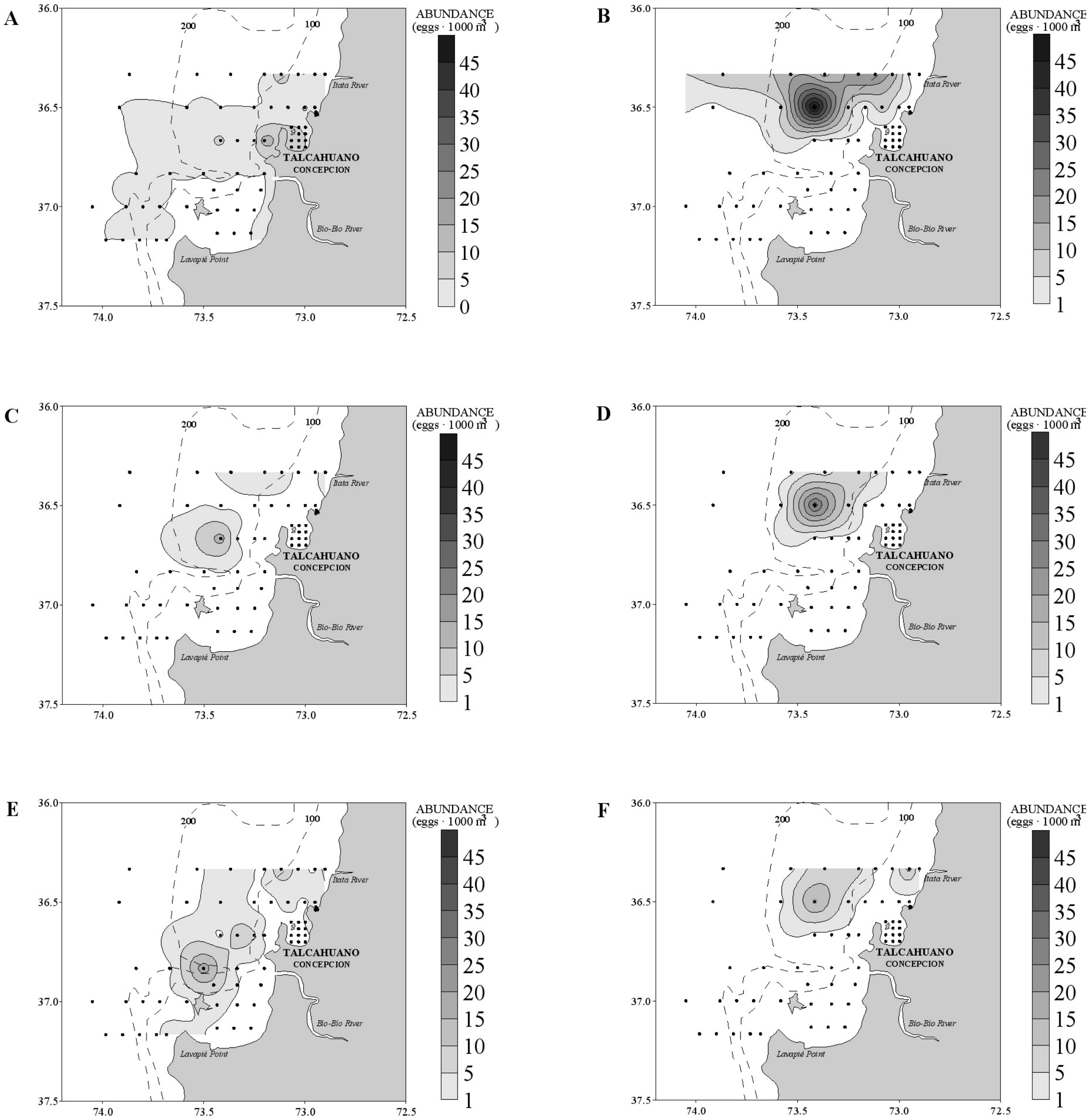

FIG. 3. – Horizontal distribution of hake, *Merluccius gayi* eggs: Stage I-III at the (a) shallow and (b) deep layer; Stage IV at the (c) shallow and (d) deep layer, and Stage V at the (e) shallow and (f) deep layer, off Talcahuano (15-28 October).

TABLE 1. – Frequency of stations at which egg and larval hake stages were collected off Talcahuano (15-28 October 1996), indicating their mean density (± std. Dev.), peak density at each layer (shallow layer: 0-40 m; deep layer: 40-100 m) and percentage of each stage in relation to the total number of eggs and larvae in each layer. Densities are ind./1000 m^3 (Total number of sampled stations: shallow = 60 and deeper = 32).

	EGGS			LARVAE	
	Stage I-III	Stage IV	Stage V	Small (<4 mm SL)	Large(<4 mm SL)
Number of positive stations					
Shallow	7	5	11	13	5
Deep	5	5	5	12	12
Mean density at positive stations					
Shallow	1.2 ± 2.9	0.7 ± 2.3	1.9 ± 3.8	11.5 ± 8.6	5.8 ± 4.3
Deep	4.2 ± 9.4	1.5 ± 5.6	1.3 ± 4.0	38.2 ± 64.4	4.7 ± 1.8
Max density at any station					
Shallow	12.9	12.5	18.1	29.0	12.1
Deep	48.1	32.1	18.7	216.8	7.8
Percentage (%) by depth interval					
Shallow	31.0	19.1	49.9	83.6	16.4
Deep	59.3	21.7	19.0	89.0	11.0

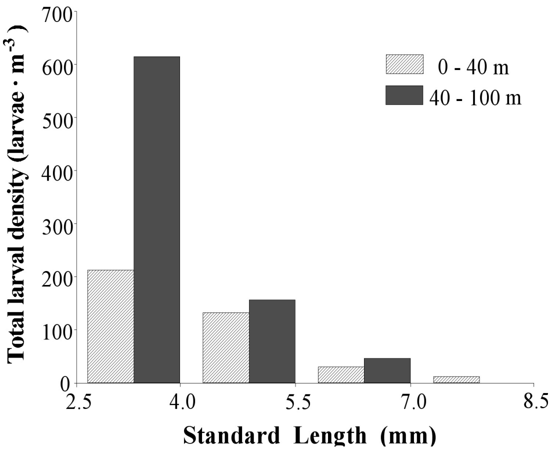

FIG. 4. – Length frequency (SL) distribution of larval hake, *Merluccius gayi*, off Talcahuano, 15-28 October 1996

The larval hake size distributions ranged from 2.5 to 7.5 mm SL. At both strata the highest larval densities were of smaller size larvae (yolk sac to 4.0 mm larvae), and the densities decreased monotonically in both layers as the larval sizes increased (Fig. 4). The total number of small larvae at the deepest strata was higher than the total number of small larvae in the surface layer.

The horizontal distribution of small size (<4.0 mm SL) *M gayi* larvae at the surface layer (Figure 5a) resembled the egg distribution, almost entirely covering the northern area over the continental shelf. In the bottom layer, a nucleus of small size larval hake occurred closer to the coast than the egg nucleus. Some small larval hake occurred in several offshore stations located in the southwestern zone (Figure 5a-b). The larger size hake larvae (>4.0 mm SL) showed a different distribution than the eggs and small size larvae: while in the shallow layer larger larvae occurred close to shore in the central part of the area, in the deeper layer they were patchily distributed over the entire area surveyed (Fig. 5c-d). No evidence of any strong nucleus of larger larvae was detected over the entire area in either stratum.

Egg and larval distributions in relation to environmental variables

The horizontal distribution of sea temperature, salinity and density revealed a clear upwelling plume extending south to north with a cold nucleus at Lavapie Point, the south western tip of the Arauco Gulf

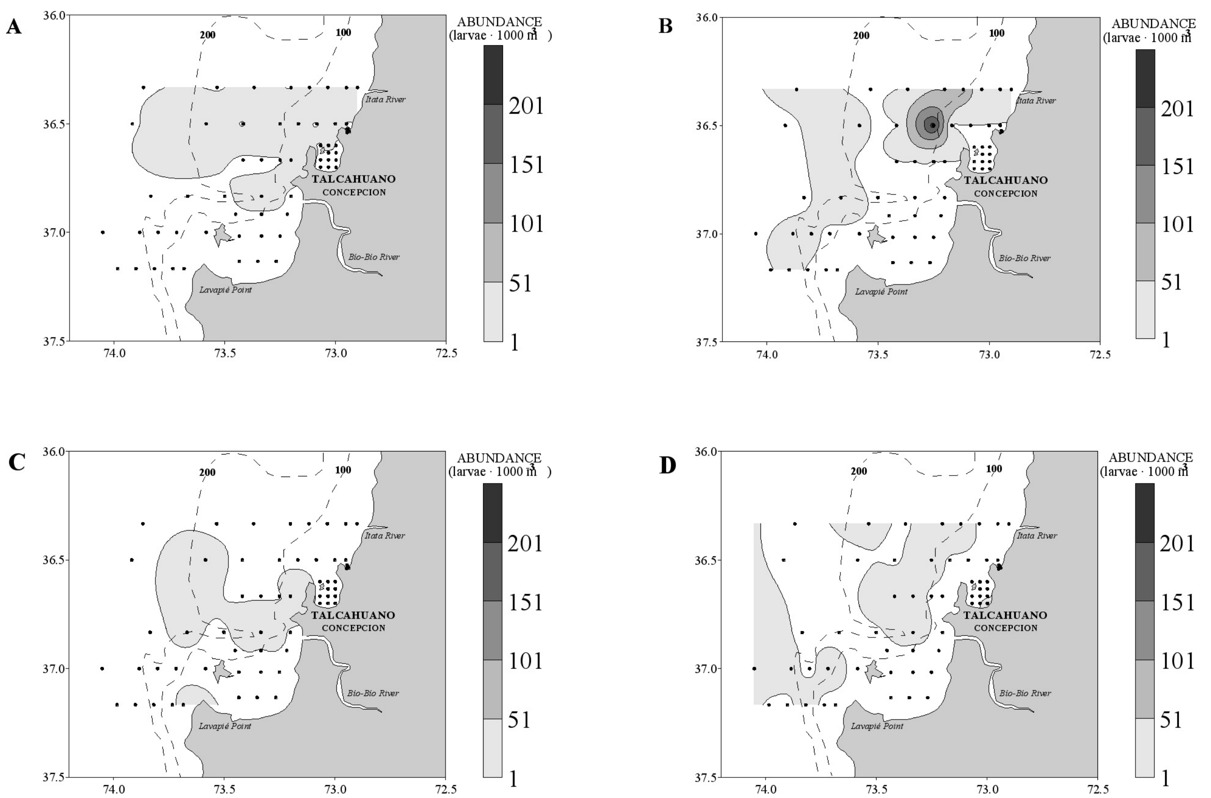

FIG. 5. – Horizontal distribution of hake, *Merluccius gayi,* larvae: small larvae (<4 mm SL) at the (a) shallow and (b) deep layer, and larger larvae (> 4mm SL) at the (c) shallow and (d) deep layer, off Talcahuano (15-28 October).

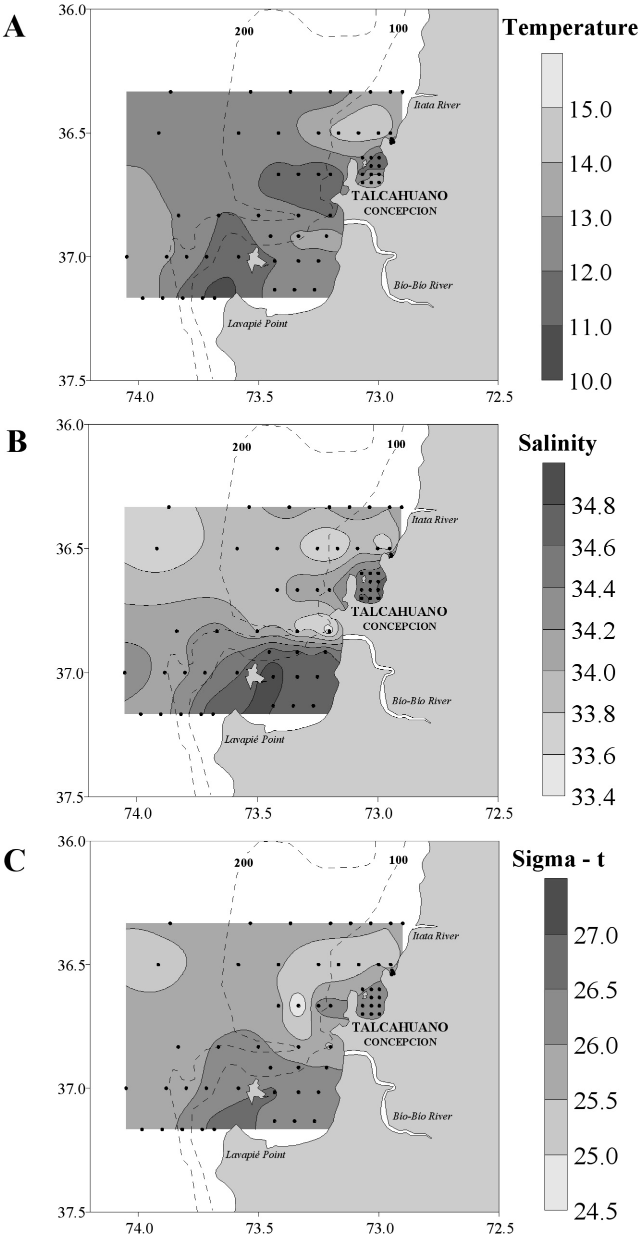

FIG. 6. – Horizontal sections of sea surface a) temperature, b) salinity, and c) density (Sigma-t), off Talcahuano, 15-28 October 1996.

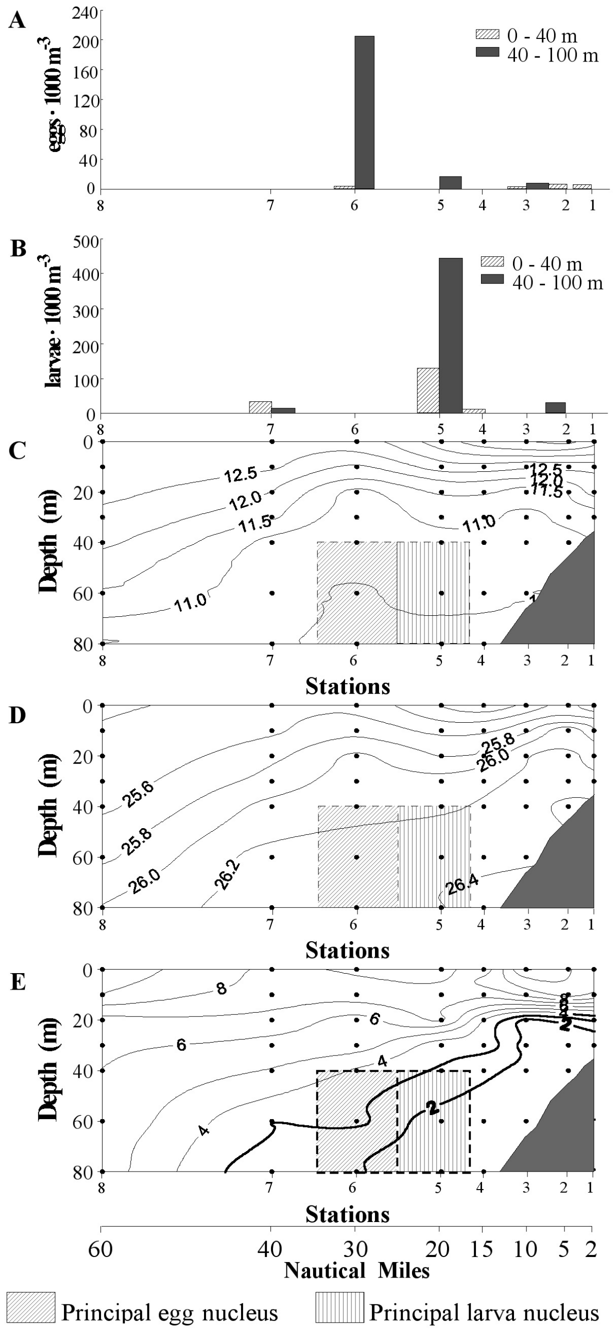

FIG. 7. – Distance from shore of a) egg and b) larval hake, and the vertical section of c) temperature, d) density (Sigma-t) and e) dissolved oxygen (ml O_2 l^{-1}), along a normal to the coast transect off Talcahuano (36.5°), 15-28 October 1996.

(Fig. 6a-c). In the gulf itself and also in Concepcion Bay, some evidence of upwelling also existed at the surface. In the northeast zone of the area surveyed, some parcels of warmer and less saline water, surrounded by the recently upwelled water over the rest of the shelf, were still present at the surface.

A vertical section of temperature and density along the transect where the peak egg and larval hake densities were collected, revealed that upwelling occurred between 20 and 40 miles from shore (Fig. 7). Closer to the coast, warmer and less dense water occurs at the surface and a strong thermocline between the surface and 30 m could be identified. Peak egg and larval hake densities occurred in the deeper layer at temperatures around or below 11.5°C and was also coincident (but at depth) with the area where cold water was reaching the surface.

Spatially, however, the peak egg and larval densities did not co-occur in the area where maximum

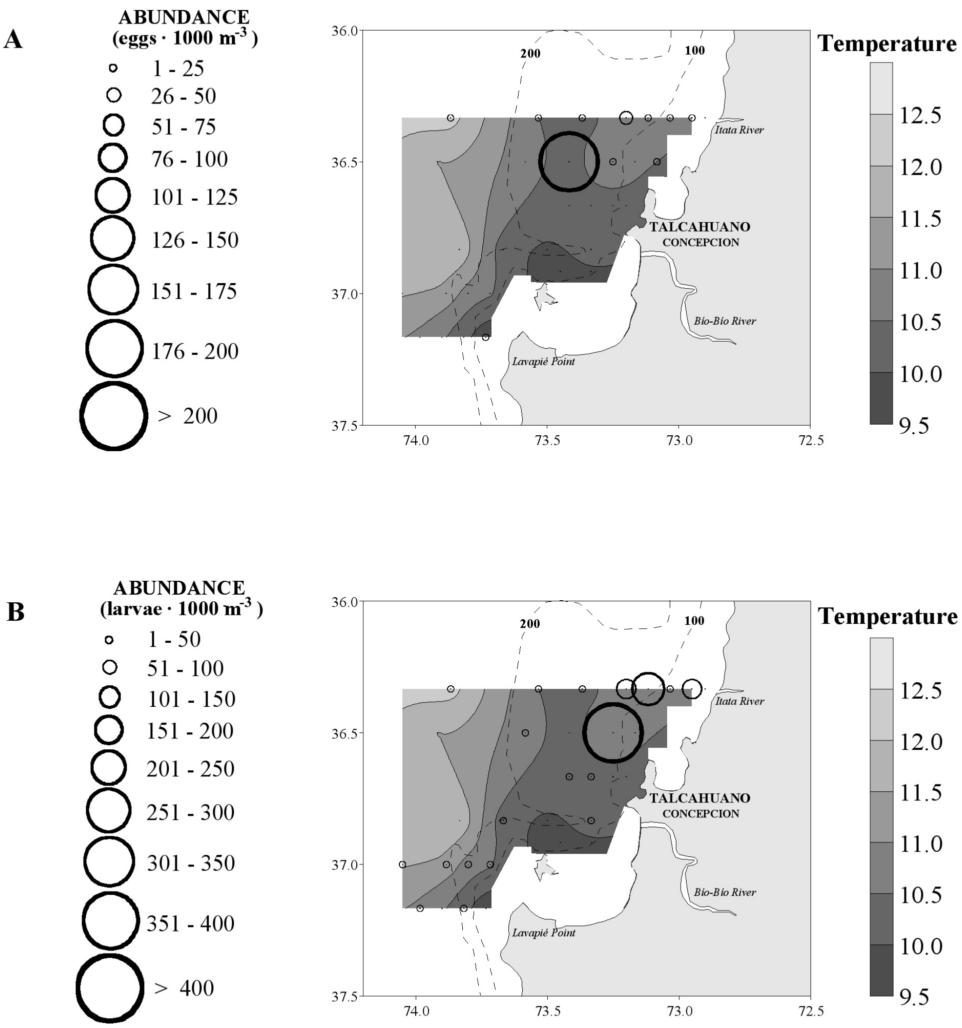

FIG. 8. – Horizontal sections of temperature at 60 m showing the areas where peak densities of hake, *Merluccius gayi,* a) eggs and, b) larvae, occurred off Talcahuano, October 1996. Dimensions of the circles are proportional to egg and larval densities.

upwelling took place over the entire region, as evidenced by the absence of eggs and larvae in the origin of the upwelling plume and inside the Arauco Gulf (Fig. 8). Instead, peak egg and larval densities occurred at the upwelling front but at depth (below 40 m), in waters that show the influence of Equatorial Subsurface Water (ESSW) (temperature: 10-12°C and density: 26.2-26.4) which do not correspond to the coldest (<8-9°C), more saline or oxygen minimum layers (<1.0 ml l^{-1} O_2) that typically approach the coast and upwell at Lavapie Point during spring and summer at this latitude (Bernal *et al.*, 1983).

DISCUSSION

The hake *Merluccius gayi* spawns in two main areas along the central-south Chilean coast (32°30'S-33°00'S and 35°30'S-40°S; Fig. 1). Although in both areas eggs and larvae occur close to shore, in the southern area eggs tend to occur further offshore (>15 nm offshore) than in the northern area (<15 nm offshore; Bernal *et al.*, 1997). In the present study, peak hake egg densities occurred offshore (30-40 nm offshore), as previously reported in cruises from 1961 through 1991 (Bernal *et al.*, 1997) with peak density restricted mostly to the northern zone of the wide continental shelf and the deepest stratum (40-100 m deep). Recent studies in the same area, but covering only the 25 nm close to shore (Vargas *et al.*, 1996, 1997) also reported maximum egg densities in the northern area, but have not reported on the vertical distribution of eggs. The first result of this study, therefore, was to determine that spawning of the hake *M. gayi* in this spawning area occurs over the continental shelf in a stratum deeper than 40 m.

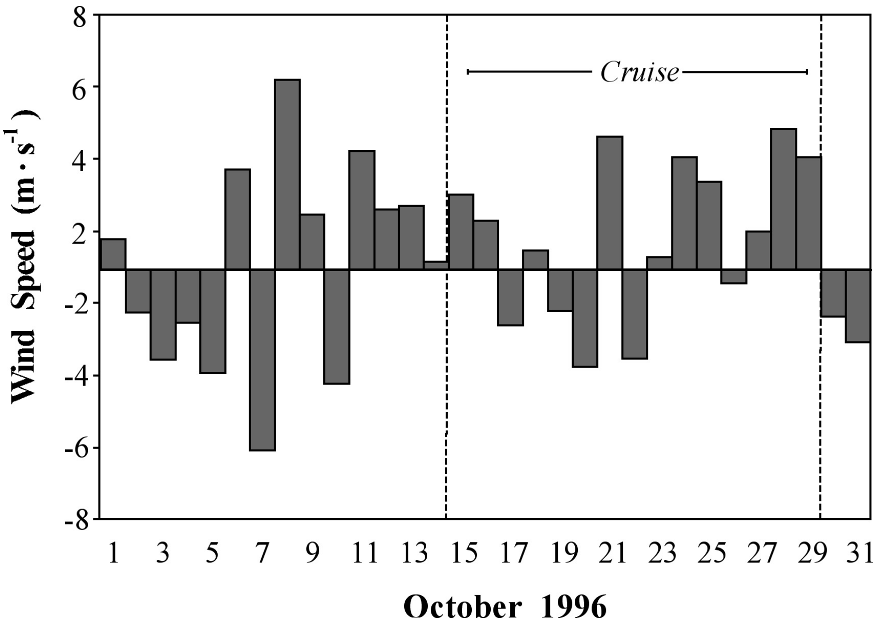

FIG. 9. – Mean daily north-south component of wind intensity during October 1996 at the Talcahuano area calculated from hourly wind data recorded on board. Upwelling favorable winds blow from south to north (positive values).

While recently spawned eggs (Stage I-III) occurred in the deepest layer, a significant (Table 1) fraction of more developed eggs and larvae also occurred in the shallow layer (Figs. 3, 4), showing upward movement as the individuals develop. The mechanisms by which these stages reached the surface layer are not yet known. However, changes in egg density during ontogeny have been proposed as an important mechanism affecting the vertical egg distribution (e.g. Coombs *et al.* 1985; John and Kloppmann 1993). Changes in vertical distribution at the larval stage may also occur as changes in depth residence layer as it have been observed for other gadiforms (Lough, 1984; Page *et al.*, 1989; Grønkjaer and Wieland, 1997). In our study, however, some evidences of ontogenetic changes in vertical distribution were detected, despite the coarse sampling depth range utilized. A finer stratified sampling will be necessary to determine whether these types of changes in vertical positioning occur as egg and larval *M. gayi* develop.

The horizontal distribution of egg, small size and larger size hake larvae were not uniform and were affected by mesoscale oceanographic features over the shelf. Peak egg and larval densities occurred at the upwelling front (about 40 nm offshore), but at depths below 40 m, in water of intermediate temperature (10-12°C) and oxygen concentrations above 2 ml O_2 l^{-1}. As our sampling covered only up to 100 m deep, some eggs could have been deeper and exposed to a lower oxygen concentration that usually occurs over the shelf in spring and summer. Off Peru, *M. gayi* eggs have also been reported associated with frontal areas and primarily at a depth between 25 and 75 m (Gorbunova *et al.*, 1986). Since eggs of other hake species (e.g. *Merluccius capensis*) have also been reported at mid-depth offshore over the continental shelf in the Benguella System (Olivar *et al.*, 1988, 1992), this shared pattern of egg distribution seems to be the result of a more generalized spawning behaviour of *Merluccius* species in upwelling areas.

The potential advantages of spawning associated with mesoscale oceanographic features in upwelling areas may result from several sources:

i) Spawning in association with frontal areas may be advantageous because fronts tend to concentrate larval food such as phytoplankton, microzooplankton, copepod stages, etc. (Kiørboe *et al.*, 1988, Muck *et al.*, 1995). However, peak egg and larval densities in this study occurred in a layer below the frontal zone. Unless some of the increased food concentrations sink or get vertically mixed into the deeper layer, spawning associated with fronts to enhance subsequent larval feeding may not be so advantageous. During this study, however, strong switches in wind direction and intensity occurred periodically (Fig. 9), which may have induced vertical mixing of the potential food particles concentrated in the frontal zone. Alternatively, larvae may also feed on the organisms located at the bottom of the thermocline, especially in the inshore area (Fig 7).

ii) Spawning at mid-depth may also be advantageous because egg and larvae may be transported onshore (Vargas *et al*., 1997), where benign feeding, higher temperature and higher water column stability occur. Spawning in this layer, however, may only be advantageous in an upwelling system if the oxygen concentrations in the deeper layer are sufficient to allow egg and larval survival and development. During this study, dissolved oxygen concentrations at the layer of peak hake egg and larval densities were above 2 ml O_2 l^{-1}, which are substantially higher concentrations than those occurring in the area under more intense upwelling conditions in late spring and summer (< 1.0 ml O_2 l^{-1}; Bernal *et al*., 1983). For adult *M. gayi*, the low oxygen concentration in the upwelling waters is seemingly not a limiting factor, as the largest biomasses of *M. gayi peruanus* have been observed at depths where the oxygen values ranged from 0.25 to 1.5 ml/l (Samame *et al*. 1983; Espino *et al*. 1995). A similar pattern has been determined for *M. gayi* at the Chilean coast, where Avilés *et al*. (1979) and Arancibia (1992) propose a strong relationship between the low oxygen water masses (i.e. ESSW) and the presence of *M. gayi* off central-southern Chile. In the California Upwelling System, Ermakov (1974) reported that in spring and early summer schools of *Merluccius productus* begin to migrate over the continental shelf for spawning, suggesting that these movements are similar to the dynamics of the California Undercurrent.

iii) Finally, spawning at the deeper layer may also be advantageous for avoiding egg and larval predation by the extremely abundant clupeiform populations typical of coastal upwelling areas (Espino and Wosnitza-Mendo, 1988; Sandoval de Castillo *et al*., 1989; Castro *et al*. 2000). In the Talcahuano area, the most common and important clupeiforms are the anchovy *Engraulis ringens* and sardine *Strangomera bentincki*, which usually occur in the shallowest strata and represent together the second largest pelagic fisheries of the area (205732 and 421054 tons respectively, SERNAP, 1998). Spawning below the usual anchovy and sardine residence layer, therefore, may confer a surplus advantage to enhance survival of early hake life stages.

Mesoscale oceanographic features such as fronts, subsurface shoreward flow and nearshore larval-food rich zones are common in most upwelling systems. Since most hake species in upwelling areas or other zones share some of the spawning behaviours in terms of timing and location (Bailey, 1981; Gorbunva *et al*., 1986; Olivar *et al*., 1988, 1990; Podestá, 1989, Vargas *et al*., 1996, 1997; Bernal *et al*., 1997), our results suggest that spawning in association with these mesoscale features may be advantageous to enhance egg and larval survival, and may therefore be part of common reproductive strategy of hake species of coastal upwelling areas. Future studies might try to determine whether the observed spatial and temporal patterns of spawning are also shared by other demersal fish species in coastal upwelling systems.

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