# Hydrographic mesoscale structures and Poleward Current as a determinant of hake (*Merluccius merluccius*) recruitment in southern Bay of Biscay

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The relationship between the recruitment of European hake (*Merluccius merluccius*) and environmental conditions in southern Bay of Biscay is examined. The historical series of autumn bottom trawl surveys carried out in Galicia and Cantabrian Sea waters from 1983 show that the processes of hake recruitment lead to well-defined patches of juveniles, found in localized areas of the continental shelf. These concentrations vary in density according to the strength of the year-class, although they remain generally stable in size and spatial location. The size of the patches, estimated using basic geostatistical techniques, is found to be from 20 to 35 km in diameter. The existence of spatial correlation is assumed by computing variograms, and the year-on-year repetition of the spatial patterns is shown to be a way of linking them to environmental conditions.

In the eastern, progressively narrowing, shelf of the Cantabrian Sea, years of massive inflow of the eastward shelf-edge current produce low recruitment indices, due to larvae and pre-recruits being transported away from spawning areas to the open ocean. Under these conditions, high mortality is expected because of the difficulties juveniles have in finding the shelf grounds. On the other hand, the transport of larvae within anticyclonic mesoscale structures moving towards the recruitment areas will be an aid to recruitment. These eddies displace westward according to the condition of potential vorticity conservation. When orographic features, such as big capes, occur in their drift path their eastern edges are held back. This situation causes patches of recruits to be located east of the main capes of the western Cantabrian Sea.

The pattern of feeding of juvenile hake includes vertical migrations searching for small pelagic fish. Upward motions of nutrient-rich deeper water masses were found close to the recruitment areas, stemming from variations of the vorticity field by mesoscale eddies. The resulting enhanced primary production seems to affect the distribution and size of hake recruit concentrations.

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## Introduction

European hake (*Merluccius merluccius* L.) is both commercially and ecologically one of the most important species in the Bay of Biscay. The strength of annual recruitment has been monitored since 1983 in Galicia and the Cantabrian Sea waters off northern Spain by

means of a series of autumn bottom-trawl surveys. In recent years, the spawning biomass has been at a historical low level and outside safe biological limits (ICES, 1995), and there have been very important fluctuations in the inter-annual recruitment indices. This last observation led us to suspect that there is a degree of independence between the strength of recruitment and
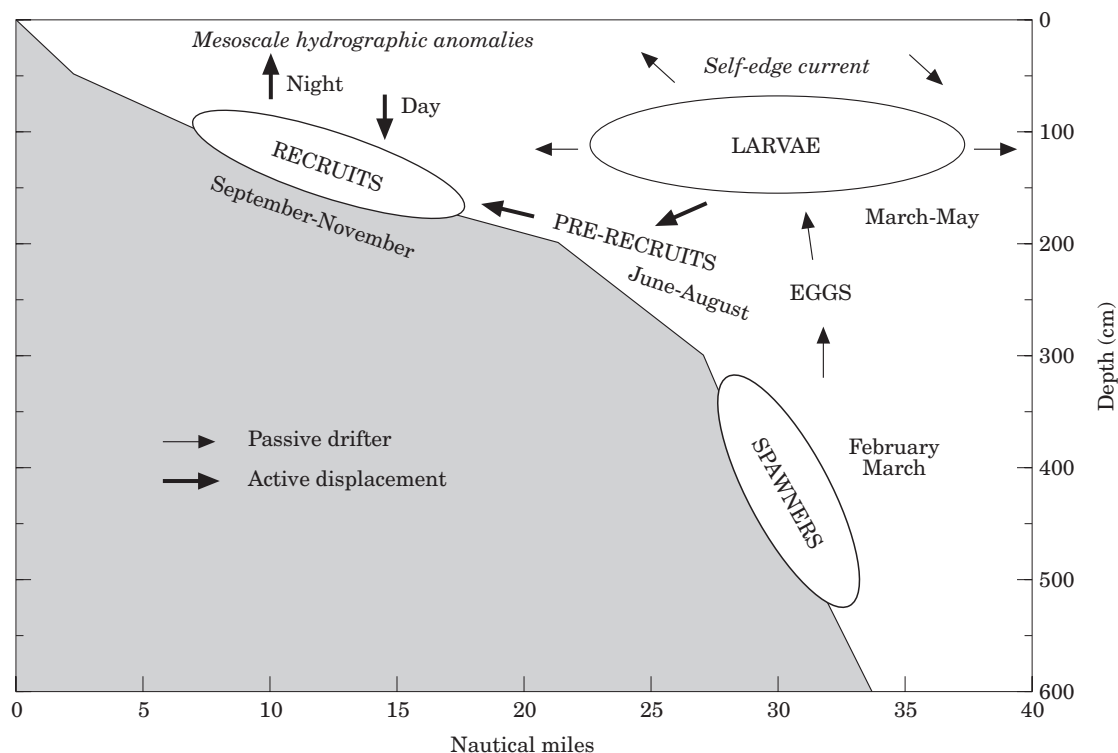
Figure 1. Recruitment processes of European hake in the Bay of Biscay.

spawning biomass, which implies the existence of significant environmental factors affecting the recruitment processes.

The biggest nurseries of European hake are located in the Bay of Biscay (Casey and Pereiro, 1995). Hake spawns in the study area from December to April, with a peak period in February and March, and the adults concentrate on certain sites, mainly canyons and rocky bottoms, of the shelf break area (Alcázar *et al.*, 1983; Pérez and Pereiro, 1985; Sánchez, 1993a, b). The maximum egg abundance occurs close to the 200 m isobath (Valdés *et al.*, 1996; Motos *et al.*, 1998). As embryonic development of eggs occurs over a period of a few days (Coombs and Mitchell, 1982) no significant displacement from the spawning sites can be observed during this developmental stage. Hake larvae remain resident in the plankton until they metamorphose to the juvenile stage, which takes about two months in depths of between 50 to 150 m (Motos *et al.*, 1998). Therefore, the drift of larvae from spawning sites to the nursery areas has been associated with the physical characteristics of the region, and particularly the current regime during the spring (Valdés *et al.*, 1996; Motos *et al.*, 1998). This mechanism can potentially act in favour or against the success of the recruitment by controlling the drift of larvae to either the nursery areas or the offshore oceanic waters. When the larval pelagic phase is concluded, hake

juveniles actively swim towards the bottom (prerecruits), starting the recruitment to the nursery area in early summer. Dense concentrations of juveniles have been found from September to November (Pereiro *et al.*, 1991; Sánchez, 1993a, 1994, 1995; Sánchez *et al.*, 1995). Once on the bottom, these juveniles, measuring between 8 and 14 cm in October, carry out vertical migrations at night to feed (Sánchez and Gil, 1995). In the spring of the following year they are dispersed on the shelf. Figure 1 summarizes the recruitment processes previously described for European hake in the Bay of Biscay.

In an extensive literature much has been discussed about hydrographic and dynamical features of the Bay of Biscay region. Vincent and Kurc (1969), Vincent (1973) and Le Cann (1982) described hydrographic structures off the French coasts, while Botas *et al.* (1989, 1990) performed hydrographic and biological studies on the Cantabrian shelf, and Koutsikopoulos and Le Cann (1996) compiled a recent review of papers about the Bay of Biscay. Oceanographic processes over the Cantabrian shelf area are highly influenced by seasonally-induced factors (Pingree and Le Cann, 1990; Pingree, 1993, 1994; Gil, 1995; Le Cann and Pingree, 1995; Koutsikopoulos and Le Cann, 1996). The annual cycle of currents along the study area is linked to the wind stress transferred from the atmosphere to the sea surface (Le Cann, 1982; Frouin *et al.*, 1990).

In the southern region of the Bay of Biscay, the most intense surface fluxes are experienced from October to February (Pingree and Le Cann, 1990), although an inversion of surface flow in deep layers points up important baroclinic effects (Huthnance, 1984). There is an eastward supply of warm water along the Cantabrian shelf and slope at 100–300 m (Frouin *et al.*, 1990; Bartsch *et al.*, 1996; Fiúza *et al.*, 1998). This current is a prolongation of the Poleward Current (PC), coming from the western edge of the Portuguese shelf. This phenomenon is also known as the *Corriente de Navidad*, or "Christmas Current", since it takes place during the last days of December; depending on its strength, it may last until February or March (Pingree, 1993, 1994; Le Cann and Pingree, 1995). The increased strength of the current is explained by a combination of: (i) the geostrophic adjustment of the large-scale oceanic zonal flow driven by the large-scale meridional baroclinic pressure gradient in the eastern North Atlantic as the flow reaches the upper continental slope of the western Iberian Peninsula; (ii) the onshore Ekman transport induced by southerly winds off Portugal (Frouin *et al.*, 1990). The latter provides about one fifth of the PC-induced geostrophic transports, although situations when more intense and sustained southerly winds off Portugal can contribute to the overall picture may occur (Frouin *et al.*, 1990). The onset of a southerly wind regime over the Portuguese coasts and onshore Ekman transport is triggered by a southward migration of the Icelandic Low at the beginning of November, implying the relaxation of the anticyclonic circulation associated with the Azores High, which prevails during the spring and early summer.

A spring–summer feature is the upwelling of deep cold water fringing the coast, as reported by Botas *et al.* (1989, 1990), Fernández and Bode (1991), Pingree (1994) and Koutsikopoulos and Le Cann (1996), because of the strengthening of the large-scale atmospheric Azores anticyclone (Frouin *et al.*, 1990). During the spring–summer seasons the eastern component of the wind stress parallel to the coast forces surface water offshore, causing a cross-shelf transport of light surface waters away from the coast. The upwelling of North Atlantic central water (NACW) tends to balance this transport, and breaks the thermocline. These displaced waters find their dynamic equilibrium as anticyclonic gyres which move westwards (Gil, 2000a).

Mesoscale dynamics are an important factor in the southern Bay of Biscay, and recent observations show that variations in mesoscale activity on shelf waters may have a significant impact both on the circulation and vertical motion (Gil, 1995). Topographic forcing and an unstable water column are known to be of importance in the formation and evolution of eddies. The circulation along the slope and shelf is known to be variable in this area, particularly in the neighbourhood of topographic or orographic unevenness. Gil (1995, 1998a, 1998b) reveals the presence of eddies and mesoscale structures as a result of the three-dimensional, quasi-geostrophic (QG) equilibrium balancing of a dynamic pattern closely adjusted to the coastal features. Likewise Pingree and Le Cann (1992) and Pingree (1993, 1994) describe, from drogued buoy deployments and satellite imagery, a conspicuous presence of SWODDIES (slope water oceanic eddies) shed from the slope poleward flow on orographic unevenness (Gil, 2000b).

Although the dynamics of the mesoscale eddies are still poorly understood because of the difficulty in dealing with the strong non-linear terms, a very close relationship between zones of great mesoscale activity and changes in relative geostrophic vorticity, with important areas of vertical motion, has been observed (Gil, 1995). This author found anticyclonic eddy structures, with a diameter of between 30 and 50 km, and values of normalized relative vorticity of approximately $-0.47$, to be highly correlated with areas of upwelling. A regime of such strong and conspicuous changes of vorticity is brought about by ageostrophic vertical motions. The superimposition of mesoscale anticyclone–cyclone pairs on the mean flow in the study area is a direct cause of vertical movements, which may contribute to the fertilization of the photic layer if they are in the form of upwelling.

The biological implications of mesoscale features in terms of the concentration and drift of eggs and larvae associated with SWODDY and eddy dynamics, and fertilization of upper layers of the water column, are of great importance (Pingree *et al.*, 1982; Robinson, 1984; Gil, 1995). Bartsch *et al.* (1996) found a mesoscale structure with some biological material being retained within it that overlapped with a hake larval patch. The possible advection of such a structure towards favourable nursery areas would enhance recruitment, whereas offshore transport would result the larvae having no chance of reaching the nursery areas on the shelf.

Environmental variables were studied during the bottom trawl surveys from 1993 under two main working hypotheses:

(1) The current pattern over the shelf-slope area determines the larval drift from the spawning grounds towards recruitment areas. Hence, an intense geostrophic flow towards the eastern part of the Bay of Biscay carries eggs and larvae away from the main nursery grounds, hampering the success of juvenile recruitment to the bottom.

(2) After the juveniles are recruited to the area and are mobile, their subsequent development is affected by the availability of food. Enriching processes of the surface layers which strengthen the food supply may, therefore, favour the presence of recruits on the bottom in such areas.

Here, the spatial distribution of hake recruits and the occurrence in space and time of their aggregations are described, together with some physical factors which may influence the recruitment process and food availability.

## Materials and methods

### Hake recruits' sampling and distribution analysis

The biological data used in this paper came from a series of bottom-trawl surveys carried out using standardized methodology in October in the northern continental shelf waters of the Iberian Peninsula. The survey area had been stratified according to depth and geographical criteria (Figure 2(a)) and a stratified random sampling scheme adopted (ICES, 1991, 1997; Sánchez and Pereiro, 1992; Sánchez 1993b, 1994). The number of hauls per stratum was proportional to the surface that could be trawled and, in accordance with the days available, the approximate coverage was one haul per 50 square nautical miles (Figure 2(b)). The sampling unit was made up of 30 minute hauls at 3.0 knots, using the baka 44/60 gear (Sánchez *et al.*, 1994; ICES, 1997). The length distributions of the hake population accessible to the gear has a well-defined mode of 10–11 cm in each year, which corresponds to the year-class recently moving to the bottom (Pereiro *et al.*, 1991; Sánchez *et al.*, 1995). The criterion used to dis-aggregate this year-class (recruits) has been to consider them all as specimens of less than 17 cm length, given the difficulty in reaching an agreement to determine correctly the age of this species (Pereiro *et al.*, 1991; Piñeiro and Pereiro, 1993). Figure 3 presents the catches of recruits from 1993 to 1995 surveys.

As a recruitment index, the stratified mean catch per trawl hour was used, following the methodology described by Cochran (1971) and Grosslein and Laurec (1982). The stratified mean and variance are, respectively:

$$\bar{Y}_{st} = \frac{1}{A} \Sigma A_h \bar{y}_h,$$

and

$$S^2_{\bar{Y}_{st}} = \frac{1}{A^2} \Sigma \frac{A_h^2 S_h^2}{n_h},$$

where A is the total surface area; $A_h$ is the surface of stratum h; $\bar{y}_h$ is the mean catch per haul in stratum h; $n_h$ is the number of hauls in stratum h and $S_h^2$ is the variance in stratum h.

The spatial distribution of hake recruits was analysed in each survey by means of geostatistical analysis techniques using the intrinsic method (Matheron, 1971; Petitgas, 1991). In order to determine the spatial

structure of the recruit aggregations, experimental variograms have been used in which the variance between pairs of values grouped into constant intervals of distance (5 km) is analysed. The spatial autocovariance estimator is:

$$\gamma(h) = \frac{1}{2n(h)} \sum_{i=1}^{N(h)} [Z(x_i + h) - Z(x_i)]^2,$$

where $\gamma(h)$ is the semi-variance between points located at a distance h apart; $n(h)$ is the number of pair of points $(x_i, x_i+h)$ separated by a distance h; $N(h)$ is the number of sampling points; $x_i$ is the location of the samples and $Z(x_i)$ is the density at point $x_i$ (number of recruits/hour trawl).

The lack of homogeneity in the distribution of hake recruits produces a high percentage of zero catches (close to 20%, Table 1). If the variogram is computed with all values, the consequence is a behaviour-type gaussian curve (very low values of semi-variance for short distances with horizontal tangent near h=0) that implies a high degree of spatial continuity. This is not observed in the data, where there are often high and low values close each other in the positive areas (Fig. 3). To correct this effect, hauls showing zero catches were excluded for the variogram parameters estimation.

Because of the absence of undetected spatial microstructures given the high density of hauls in the area, low values of semi-variance for short distances were obtained, and consequently the nugget effect (i.e. a jump at the origin when $\gamma(h)$ does not tend to $\gamma(0)=0$ as h tends to 0) was in general low. In fact it only occurred in the years 1990 and 1995, or was absent.

Spherical variograms were fitted, using EVA2 software (Petitgas and Lafont, 1997):

$$\gamma(h) = C_0 + C\left[\frac{3}{2}\frac{h}{a} - \frac{1}{2}\left(\frac{h^3}{a^3}\right)\right],$$

where $C_0$ is the nugget effect, C is the sill and represents the semi-variance value reached with a value of h=a and a is the distance (range) which represents the maximum distance where spatial covariance exists. The total variance given by the model over the area $\gamma_{vv}$ was employed to scale the variogram model to the data variance, as the two should be of the same order of magnitude. The anisotropy of spatial structure was not analysed because of the complexity of the continental shelf in the study area. The spherical model is used normally in spatial distributions of marine organisms, in general, and particularly for hake juveniles in other areas (Petitgas and Poulard, 1989).

Beginning with this model, and using the ordinary punctual kriging technique (Isaaks and Srivastava,
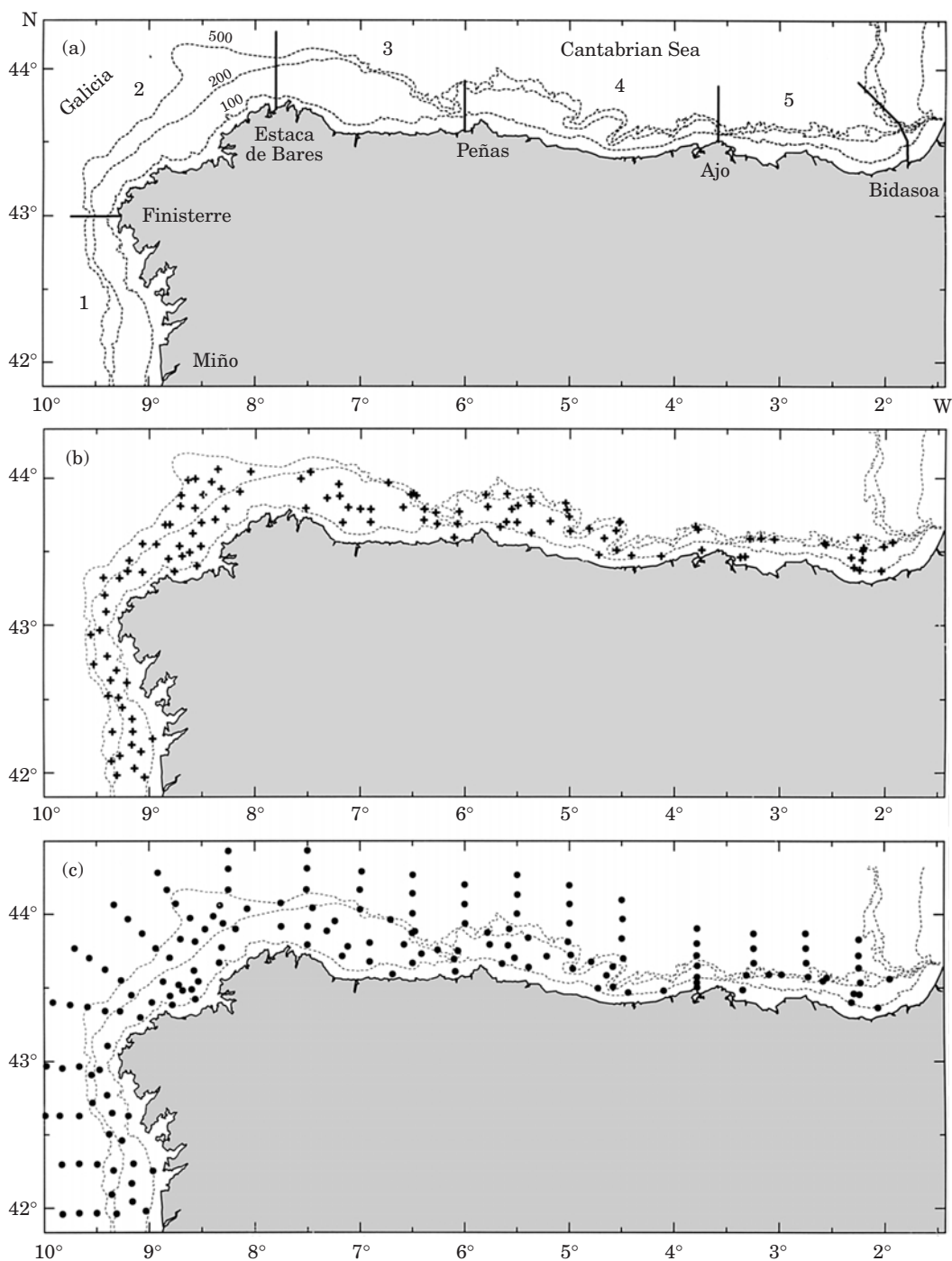
Figure 2. Survey stratification (a), hauls in 1995 (b) and hydrographic stations in 1995 (c).

1989), estimates of the abundance of recruits and their distribution in the bottom layers have been obtained. Density was estimated on the nodes of a 5 × 5 nautical miles grid (original random sampling survey protocol grid), covering the area between isobaths of 30 and 1000 m. The isolines of abundance provided by this methodology have allowed us to estimate the size and location of patches.
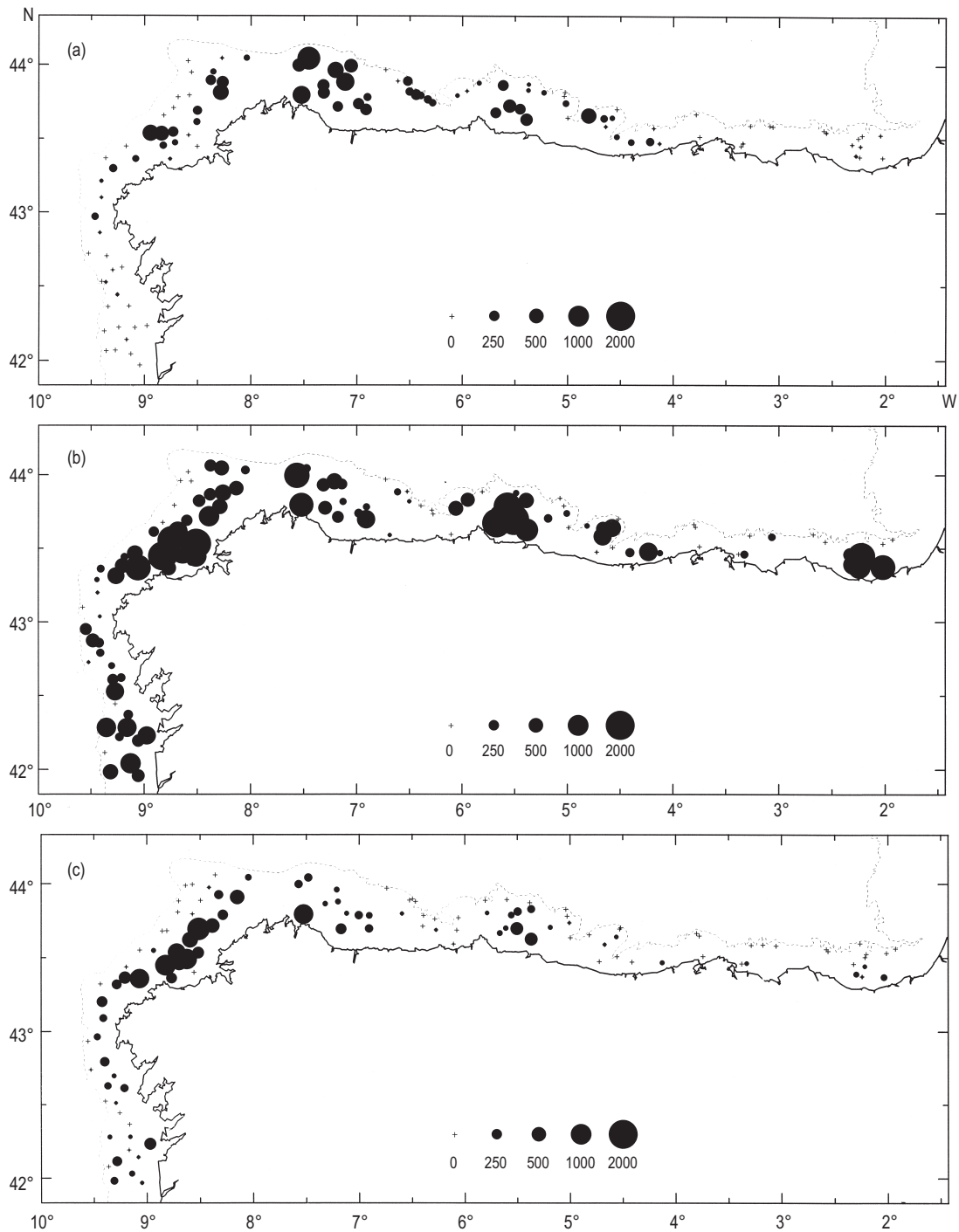
Figure 3. Number of hake recruits per hour trawl during the surveys of 1993 (a), 1994 (b) and 1995 (c).

## Hydrography

The hydrographic characteristics were determined by conductivity–temperature–depth (CTD) systems (SBE 19 and SBE 25). Sampling stations were distributed throughout the area of study covering the continental shelf, slope, and adjacent oceanic area, according to mesoscale structure resolution criteria, and were occupied during the trawl survey (Fig. 2(c)). For this region (taking an upper water layer between 40 and 100 m

Table 1. Hake recruitment indices and parameters of the variogram spherical models fitted for each survey.

| Year | Data statistics (recruits/h) | | | | Stratified mean | | Variogram parameters | | | | |
| | Hauls | 0 catch | Average | Variance | No./hour | SE | Nugget | Sill | Range (km) | Est. Var. | $\gamma_{vv}$ |
|------|-------|---------|---------|----------|----------|------|--------|---------|------------|-----------|---------------|
| 1990 | 108 | 33 | 143.1 | 50 531 | 146.3 | 16.5 | 10 000 | 59 000 | 30 | 1124.2 | 58 638 |
| 1991 | 118 | 24 | 336.3 | 167 571 | 315.3 | 29.6 | 0 | 125 000 | 20 | 2262.3 | 124 575 |
| 1992 | 110 | 28 | 100.0 | 18 109 | 99.0 | 9.9 | 0 | 19 680 | 20 | 294.3 | 19 613 |
| 1993 | 120 | 24 | 132.0 | 42 799 | 134.5 | 15.5 | 0 | 45 000 | 35 | 912.5 | 44 555 |
| 1994 | 122 | 16 | 453.7 | 321 140 | 468.3 | 49.0 | 0 | 334 000 | 25 | 4706.9 | 332 259 |
| 1995 | 122 | 39 | 127.1 | 52 712 | 130.8 | 14.8 | 15 000 | 66 500 | 30 | 1322.5 | 71 084 |

SE, standard error; Est. Var., estimation variance; $\gamma_{vv}$, total variance given by the model over the area.

thick, with a density of between 1025 and 1027; lower water layer 500 m thick, and a density of 1029) values for the internal Rossby radius of deformation were obtained $(Rd = (g'H)^{1/2}/f)$, where $g'$ is the reduced gravity, H the layer thickness and f the Coriolis parameter, between 10 and 17 km. This indicates that mesoscale structures can be found between 30 and 70 km. Since the CTD sampling consisted of radial lines of stations perpendicular to the coast, with a mean separation between stations of 12 km and a separation between radials of 35 km (Fig. 2(c)), it can be deduced that over the continental shelf and in a direction perpendicular to the coastline, mesoscale structures should be adequately resolved. In the outer oceanic area, the smaller structures have not been resolved.

A water column stabilization programme was applied to the data with the aim of smoothing anomalous density distributions due to analytical errors. After that, the Barnes Objective Data Analysis (Barnes, 1964) was applied to build the total field of concerned variables at several depths. Subsequently, the dynamic topography field was calculated on the 200 m reference level: this level being the optimum for station coverage.

We estimated the vertical motion by the omega (ω) equation. The ω-equation results by combining the QG vorticity and thermodynamic equations. Using the classical notation (Pedloski, 1987):

$$\left(\frac{\partial}{\partial t} + v_g \cdot \nabla_h\right)\zeta_g - \frac{f_0}{\rho_0}\frac{\partial}{\partial z}(\rho_0 w) = 0 \quad (1)$$

$$\left(\frac{\partial}{\partial t} + v_g \cdot \nabla_h\right)\frac{g}{\rho_0}\rho' - N^2 w = 0, \quad (2)$$

the QG vorticity equation (1) tells us that ageostrophic vertical motions (w), i.e. stretching or shrinking of the vortex lines, are a consequence of the geostrophic advection of potential vorticity ($\zeta_g$) and of changes in vorticity associated with the geostrophic motion. The thermodynamic equation (2) relates density variations and horizontal density advection with vertical velocity.

Thus, the ω-equation combines both concepts (Holton, 1979):

$$N^2\nabla^2 w + f_0^2\frac{\partial^2 w}{\partial z^2} = f_0\frac{\partial}{\partial z}(v_g\nabla_h\zeta_g) + \frac{g}{\rho_0}\nabla^2(v_g \cdot \nabla_h\rho'). \quad (3)$$

In a regime of strong meanders as with our study area, and since geostrophic velocity $V_g$ decreases with depth, it implies that if:

$-v_g \times \nabla_h \zeta_g < 0$, it means negative vorticity advection, then w is negative (or bottomward motion)
$-v_g \times \nabla_h \zeta_g > 0$, it means positive vorticity advection, then w is positive (or upward motion).

We used the form of the omega equation introduced by Hoskins et al. (1978), where terms on the right side of the equation appear as $2\nabla Q$, being:

$$Q = g/\rho_0[(\partial u_g/\partial x)(\partial \rho'/\partial x) + (\partial v_g/\partial x)(\partial \rho'/\partial y), (\partial u_g/\partial y)(\partial \rho'/\partial x) + (\partial v_g/\partial y)(\partial \rho'/\partial y)$$

Thus, the diagnostic equation yields than if:

$2\nabla Q > 0$, then w is negative (or downward motion)
$2\nabla Q < 0$, then w is positive (or upward motion),

i.e. the convergence of this vector indicates regions where upward motion exists (Hoskins and Pedder, 1980).

## Results and discussion

### Recruits abundance and distribution

Hake recruitment indices were characterized by sharp variations during the period studied, with four years of poor recruitment (1990, 1992, 1993, and 1995) and two years (1991 and 1994) of good recruitment (Table 1). The process of the recruitment of the hake year class to the bottom leads to concentrations of individuals with a high level of spatial correlation. The extent of the spatial effects in the variograms varied between 20 and 35 km (Table 1 and Fig. 4) and implies a relatively stable
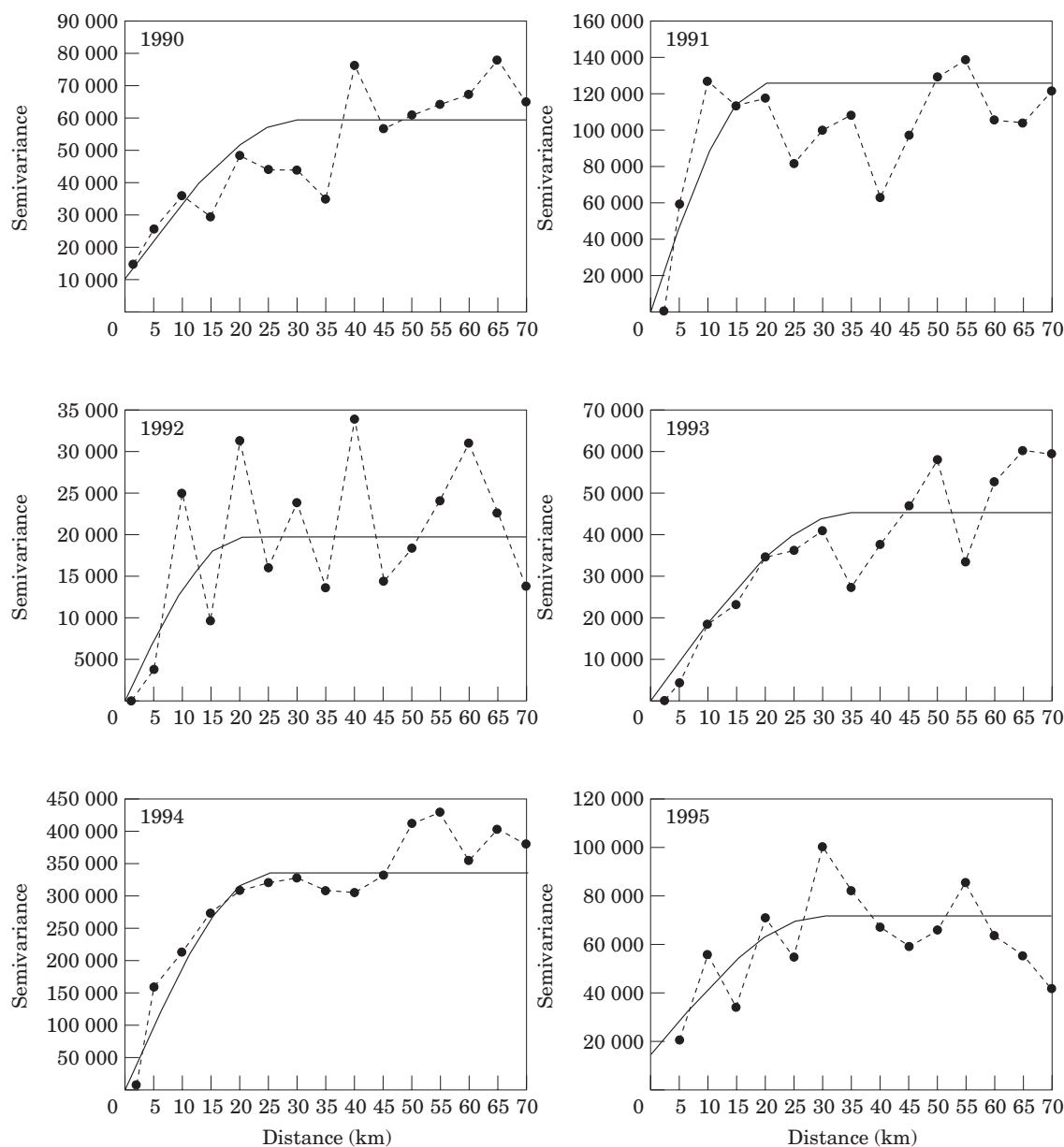
Figure 4. Experimental variograms and fitted spherical model corresponding to the hake recruits of surveys from 1990 to 1995.

spatial structure in different years, which is, in some way, independent of the abundance of recruits (Table 1). This could indicate that hake recruits tend to aggregate in mesoscale patches of this diameter. In the three last years they formed several patches of similar dimensions but of different density (e.g. high recruitment index in 1994 and low in 1993 and 1995).

The distributions of juveniles in the area investigated over the last decade (Sánchez, 1993a, 1995) and here show the highest concentrations in three defined areas, repeated every year, called La Coruña, Ribadeo and

Peñas, shown in Figure 5. In some years, two smaller concentrations, Rías Bajas and Guetaria also appear (Sánchez, 1995). These areas of high concentration, more than 200 individuals $h^{-1}$, are found between 90 and 180 m depth and predominantly have muddy bottoms. The persistence of these nurseries in the historical series of surveys since 1983 may be caused by their special environmental characteristics compared with the rest of the continental shelf.

Density isolines of hake concentrations obtained via kriging are not only defined by the narrowness of the
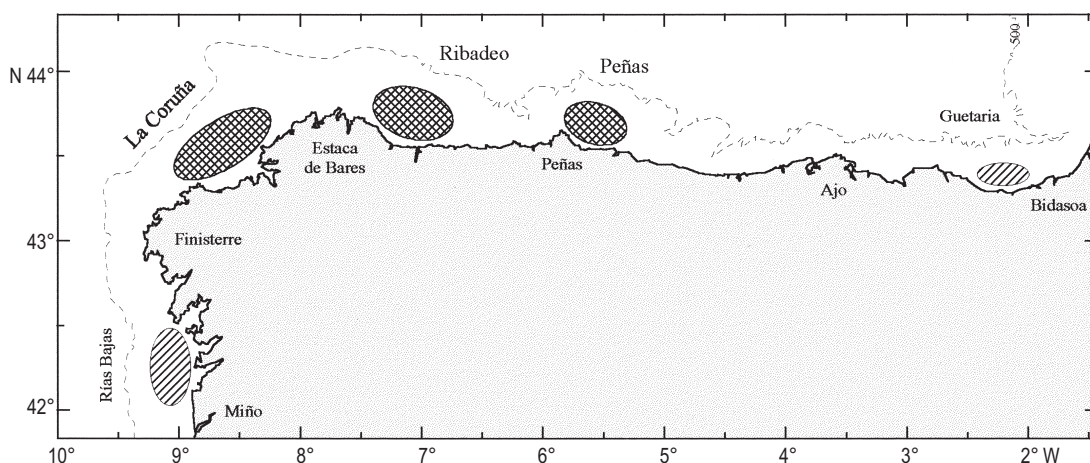
Figure 5. Main nursery areas of hake in the last decade (based in Sánchez, 1995). Shaded in a diagonal cross for the main areas appearing all years and shaded in a forward slash for the concentrations which only appear in some years.

continental shelf but also are concentrated in areas 20 to 35 km of diameter (Figs 8(c), 9(c) and 10(c)). This nesting structure is also present in years of high recruitment, since juveniles are not spread throughout the continental shelf, but increase in density in the nursery areas, with a maximum of 2400 recruits $h^{-1}$ in 1994. By combining the sweep area and kriging methods, it is estimated that 90% of the recruits are in areas with more than 200 recruits $h^{-1}$ that the remaining areas are irrelevant as far as total recruitment is concerned. The years of good recruitment (1991 and 1994) are manifested mainly by a considerable increase of the density in the patches of the western Cantabrian Sea and Galicia (La Coruña, Ribadeo and Peñas) and secondly by the contribution of the other two smaller aggregations (Guetaria and Rias Bajas). These results contradict the views of Casey and Pereiro (1995) who suggest that the distribution area of hake recruits seems to vary with year-class strength, contracting for poorer year classes and expanding for good year classes. Bearing in mind our analyses, the spatial distribution of recruits can be said to follow, in general terms, the criteria of fixed geometry and variable density.

Besides the concentrations of recruits previously described, another important nursery of European hake is located on that part of the shelf of the Bay of Biscay in the French Coastal Zone. However, the aggregation patterns are different in that the Spanish patches are smaller and denser. Those in the French zone reaching a size of 300 km in diameter (Grande Vasière area) and maximum densities of only 600–800 recruits $h^{-1}$ (Petitgas and Poulard, 1989).

## Environmental scenarios

Hydrographic conditions at the time of hake recruitment vary greatly from year to year. One scenario is that of the existence of an intense and persistent PC in the previous winter months (Pingree, 1994). This would bring warm, saline waters with a high degree of mixing on to the Cantabrian shelf and slope and leave colder water off the shelf with a weak easterly wind regime along the coast. This combination would undoubtedly lead to a weak summer upwelling, warm water over the shelf and cold water off-shelf. Since the Rossby number is very small for the study area (Gil, 1995) the flow is strongly influenced by the Earth's rotation and may be calculated via the QG theory. A weak and uncertain eastward current broken up by a number of instabilities would result. On the other hand, if either the supply of warm and saline water from the PC is not very intense, or the spring–summer appearance of the (easterly) longshore component of the wind stress is strong and persistent, or both effects occur together, two consequences result. First of all, the subsequent Ekman transport of coastal waters off the shelf produces spring–summer upwelling. The intrusion of deep cold water over the shelf area forms vertical temperature profiles characterized by a thin surface layer with a prominent thermocline from summer warming. A horizontal density front with upwelling at the coast forms. Secondly, the dynamics of surface waters dragged off the shelf by the wind stress are initially inertial, although forced by friction and pressure gradient damping. Because of shallow water processes and coastal influence, the inertial motion degenerates in a QG adjustment as linearized westward flow alongside the slope with orographic features causing intensification of the current, as proposed by Bartsch et al. (1996). The central Cantabrian Sea is characterized by this upwelling process, present throughout the period of thermal stratification, i.e. late spring and summer. It is considered to be an important mechanism of fertilization of the photic layer (Fernández and Bode, 1991). This seems to have been
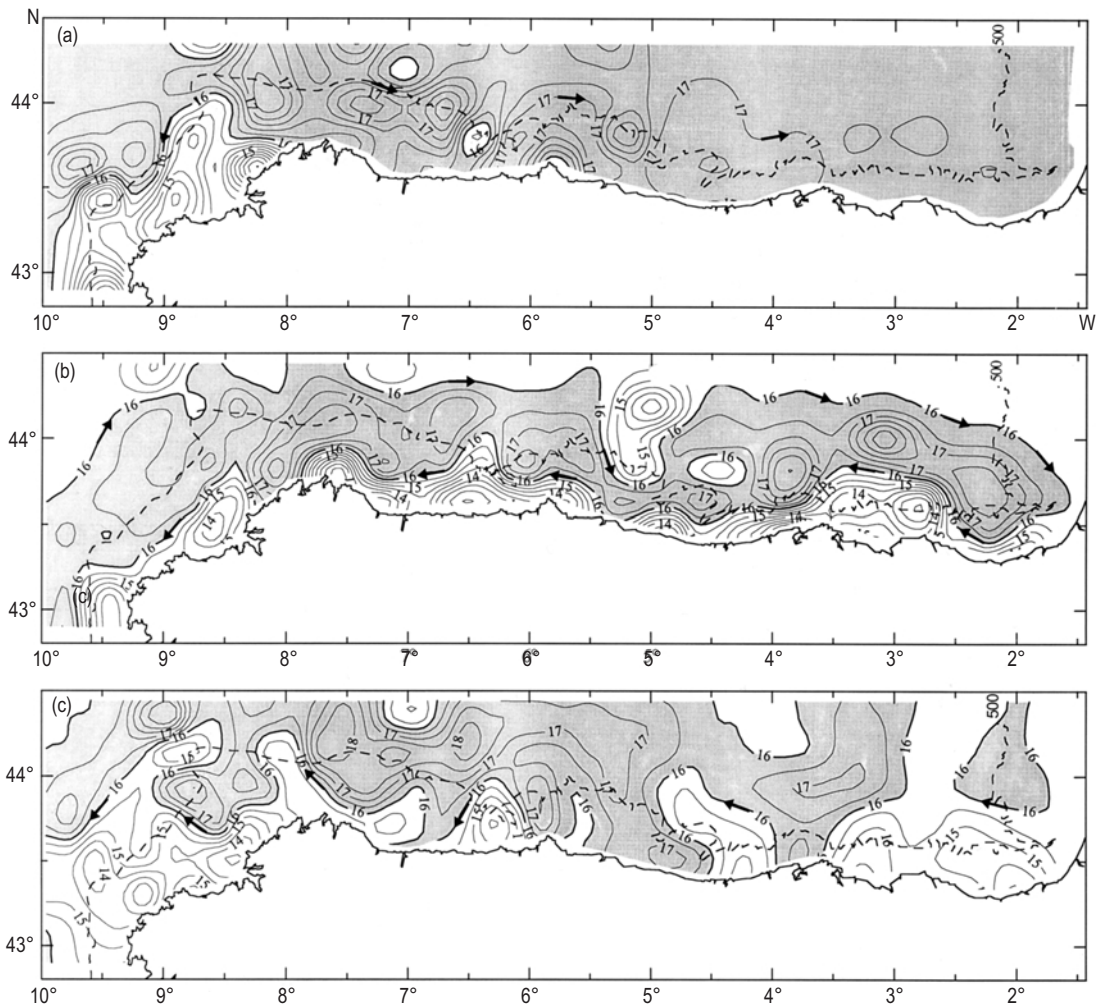
Figure 6. Temperature (°C) at 40 m in October during the years 1993 (a), 1994 (b) and 1995 (c).

the situation in 1994 and 1995, and it is noticeably different from that of 1993. In 1993, a thin, warm surface layer and lower temperatures in the sub-surface layers of the continental shelf characterized the summer upwelling.

Three features characterize the picture:
- a coastal fringe of cold, upwelled water over the shelf area;
- an intermediate anticyclonic zone of warm-core mesoscale eddies;
- the exterior region with the Bay of Biscay oceanic waters.

Between the first two zones, a density front is set up along which a QG flow circulates westwards, whereas between the last two, a secondary front causes a QG adjustment towards the east, closing the anticyclonic loop over the shelf-break area. The anticyclonic mesoscale structures displace westward according to the

condition of conservation of potential vorticity due to the variation of the Coriolis parameter, f, with latitude (β-effect).

Year-to-year variations in the location and strength of the density fronts vary according to the resulting states of equilibrium between the stratification conditions at the end of the winter and the atmospheric forcing. Therefore, in autumn the slope current may be directed either towards the west or the east, depending on the processes that occurred during the previous summer; this gives the QG adjustment among the water masses over the shelf, shelf break and oceanic area.

Three different situations occured in the years 1993 to 1995. The temperature at 40 m in 1994 (Fig. 6(b)) shows a well-defined example of the situation outlined above. A strip of warm water (over 16°C) separates the coastal fringe of upwelled water (below 16°C) from the oceanic background water (below 16°C). Between

the anticyclonic zone and the coastal upwelling, a westward flow occurs linked to the shelf break orography. Off the shelf, an eastward counter-current closes the anticyclonic loop. The narrowness of the coastal upwelling permits a succession of anticyclonic cores to be placed over areas relatively close to the shelf, although it is possible to observe disruptions of the coastal upwelling by invasions of warm waters over the shelf area. These cores are found in the La Coruña zone (8°W), in the vicinity of Cape Peñas (5–6°W) and around the Guetaria zone (2–2.5°W).

A radically different situation occurred in 1993 (Fig. 6(a)). In this year the generalized intrusion of warm water over most of the Cantabrian Sea shelf area produced minor upwelling events at the beginning of autumn, except for the La Coruña zone. Elsewhere, in contrast to the situation in 1994, slightly warmer waters occur inshore rather than offshore and result in an inverted density front that causes eastward flows over the slope area.

In 1995 (Fig. 6(c)) the considerable width of the cold coastal fringe that defines the summer upwelling suggests the strongest and most intense episode of the 1993–1995 period occurred, although it does not appear as a continuous feature along the shelf area. As a consequence of the broad extension of the coastal upwelling, the succession of anticyclonic eddies is placed further away from the shelf-break than in other years for all areas except the vicinity of Cape Peñas (6°W) and west of Cape Ortegal (8.5°W). Other intrusions of warm water over the shelf region are not associated with eddy features (5°W). The anticyclonic loop has not been closed in this case because the missing segment probably lies outside the sampling area.

Below the 90 m level the seasonal atmospheric influence is weak. Therefore, the thermal pattern at 90 m is formed by the addition of a macroscale ambient distribution and thermal anomalies caused by the mesoscale eddies. In the Galicia-Cantabrian Sea at 90 m depth, the most frequent temperature values (from an historical dataset not presented here) range from 12–13°C. Mesoscale structures with temperatures above 14–15°C will be anticyclonic eddies superimposed on the macroscale pattern. A warmer macroscale thermal pattern will also be anomalous and as a consequence of a large-scale phenomenon such as the PC. This situation appears to have occurred during autumn 1993 when a general warming of the sub-surface layers was observed compared with 1994 and 1995 (Fig. 7). This warming was a consequence of the increase in the thickness of the water layer above the thermocline, stemming from an influx of relatively low-density water in winter months (PC).

The different combinations of all inputs appears to be the driving mechanism for the year-to-year variation of the circulation pattern (Gil, 1998a). The fluxes of the different mass and energy inputs form the distribution of water masses set up the initial field conditions for hake recruitment, namely stratification in the vertical and the formation of fronts in the horizontal. The absence of a permanent circulation pattern over the shelf and slope during this period and the seasonal nature of most of the hydrographic phenomena are the reasons why the mesoscale field is more important than the macroscale field (Gil, 1998a). QG adjustment of the mass field formed after the spring–summer season involves detachment and geostrophic isolation of warm mesoscale eddies over the mid-oceanic area (Gil, 1995).

## Links

Over the three years studied, mesoscale activity evidenced by anticyclonic eddies is clear, with an easily identifiable repetition of gyres, La Coruña, Ribadeo and Peñas, with negative vorticity over the shelf break (Figs 8(a), 9(a) and 10(a)). The repeated presence of these eddies in the same areas in the three years studied may be due to topographic factors that induce negative vorticity. These locations in which to various degrees the main concentrations of hake recruits are found, are repeated every year (Figs 8(c), 9(c) and 10(c)). This may be consequence of larval aggregation within isolated mesoscale structures and subsequent transport towards the main nursery areas.

On the other hand, it seems logical that if, during the winter and at the beginning of spring, a flow of surface water sweeps the whole continental shelf-slope area (PC), an eastward displacement of eggs and larvae would bring about an increase in mortality and result in low recruitment over the western nursery areas. Transport is particularly important for recruitment where nurseries are in localized areas or where the continental shelf is narrow and juveniles are associated with the bottom (Wooster and Bailey, 1989). The poor recruitment of 1993, one of the lowest of the last ten years, (Table 1 and Fig. 8(c)) corresponds to this situation. It could be that because of the massive intrusion of warm water (PC) in winter and the progressive narrowness of the Cantabrian Sea shelf, eggs and larvae were advected from the spawning areas to the open ocean. As a result, high mortality would be expected. Hollowed and Bayley (1989) have demonstrated for the Pacific hake (*Merluccius productus*) that the relative year-class strength is determined at the larval and early juvenile stages and is associated with the degree of offshore advection. Survival may be inhibited in the open ocean environment due to growth decrease resulting from lower prey abundance. This unfavourable situation in 1993 for recruiting hake larvae was made worse by the low level of upwelling intensity, which diminished the food availability for larvae and juvenile survivors due to a reduction in nutrients.
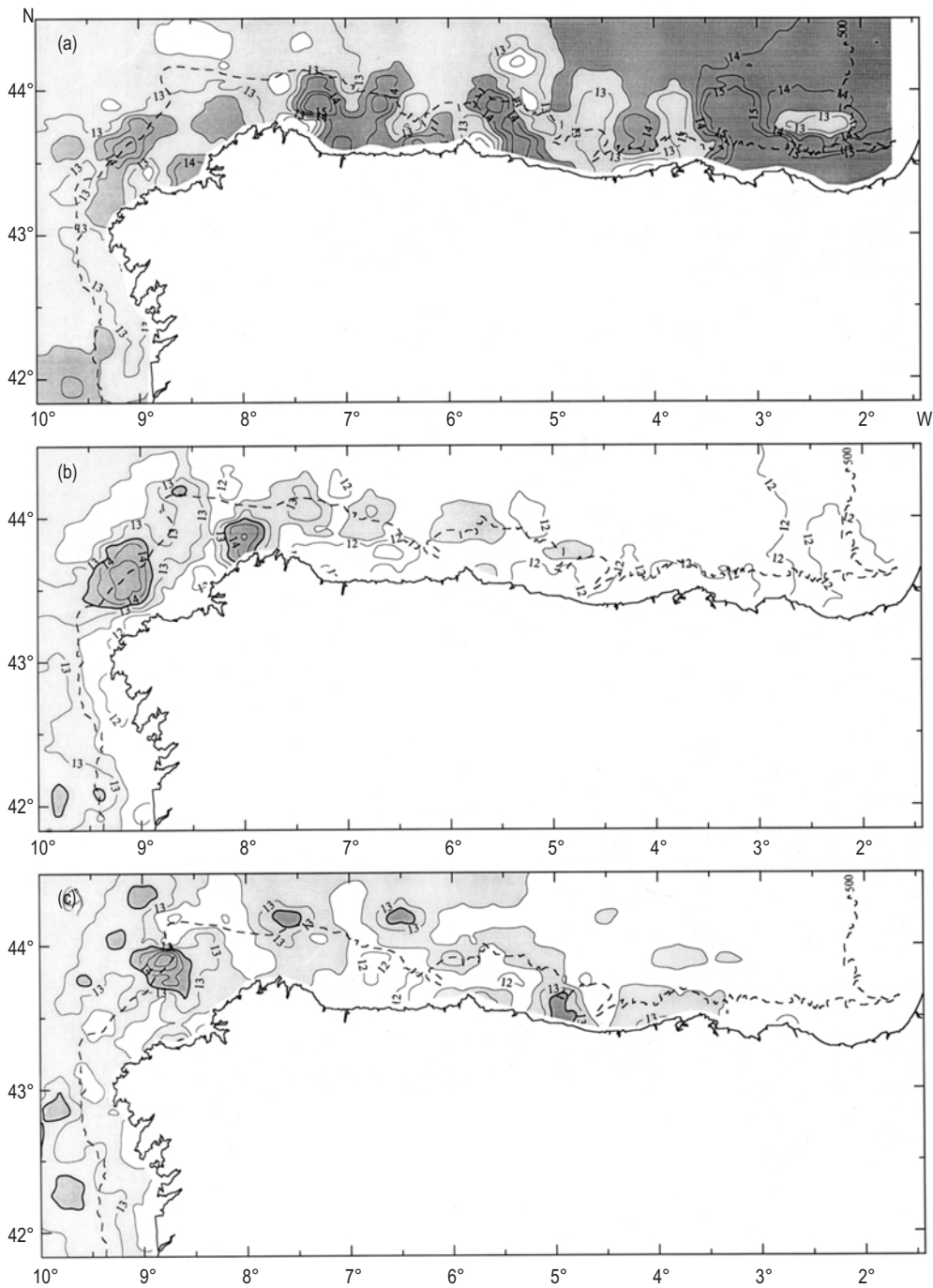
Figure 7. Temperature (°C) at 90 m in October during the years 1993 (a), 1994 (b) and 1995 (c).

Conversely, the excellent recruitment of 1994 (Table 1 and Fig. 9(c)), which surpassed the expectations derived from a spawning stock at a historical low point (ICES, 1995), may have been favoured by the lower influx of water of the PC allowing eggs and larvae to remain close to nursery grounds. Afterwards, the anticyclonic eddies, each with its entrained eggs and larvae, remained close to the break shelf in their slow westward displacement inside the inter-mediate fringe of warm-core mesoscale eddies (Fig. 6(b)). In the Gulf of Alaska the eddies entrapping individuals are capable of both enhancing and
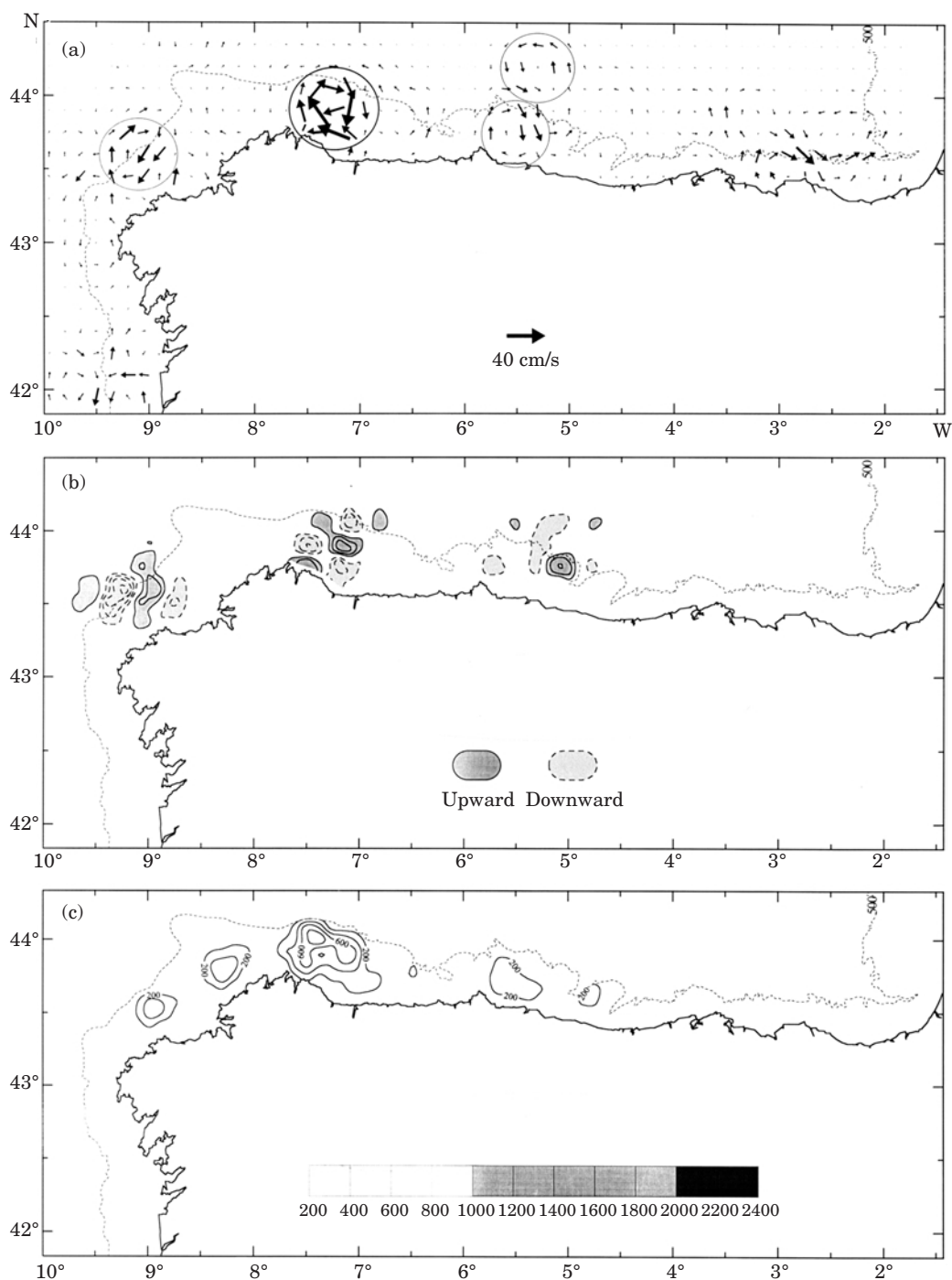
Figure 8. Geostrophic current (a), water vertical motion ($\Delta = 10^{-17}$ s$^{-3}$ m$^{-1}$) (b) and hake recruitment (number/h) estimated by kriging (c) in October of 1993.

destroying the patchiness of young walleye pollock (*Theragra chalcogramma*) depending on the time of year (Hermann *et al.*, 1995). Larvae outside the eddies will be subjected to greater degree of horizontal mixing when such mesoscale features are abundant. On the other hand, the important level of upwelling close to the nurseries areas in 1994 (Fig. 6(b)) undoubtedly enhanced food availability.
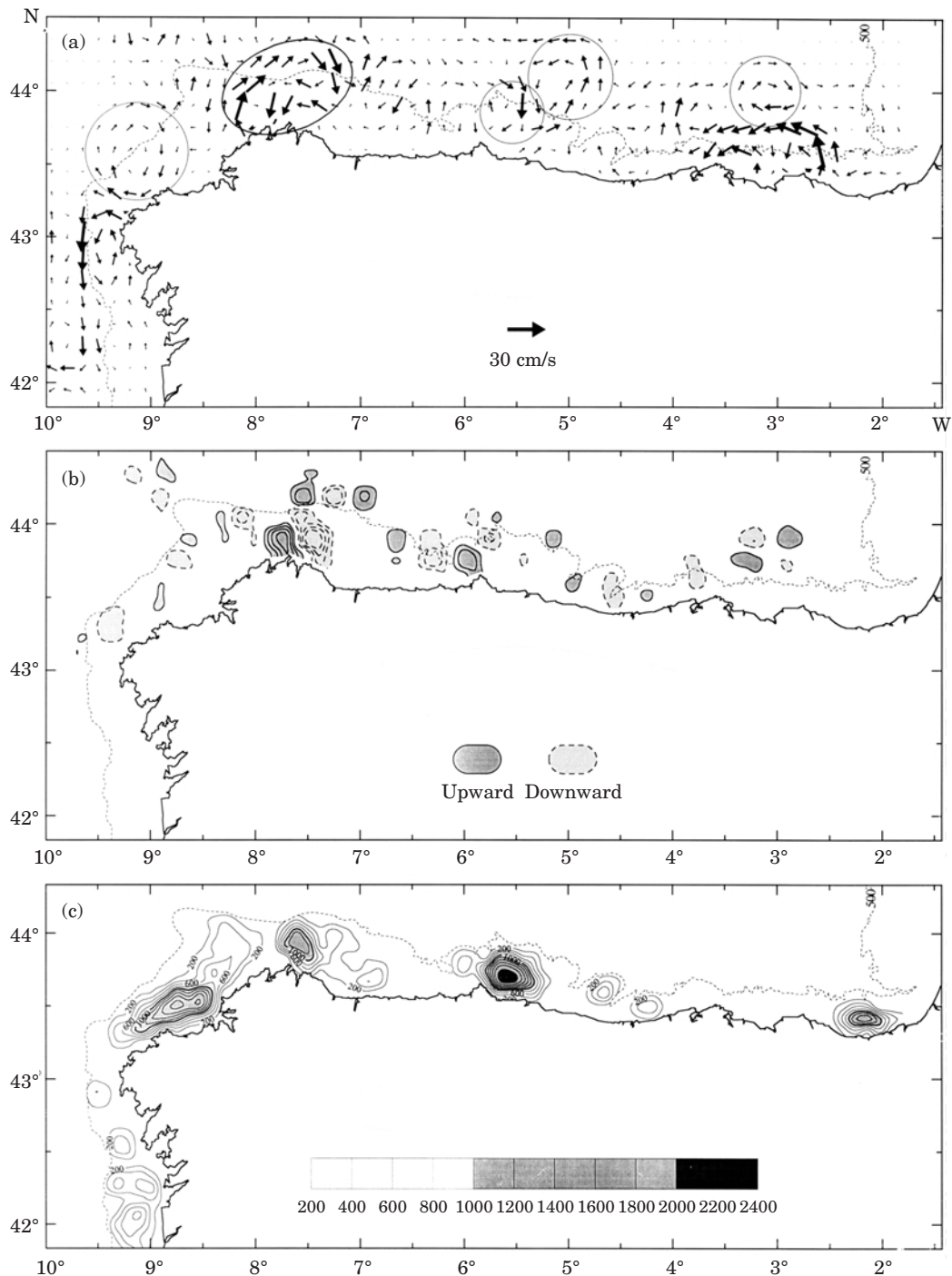
Figure 9. Geostrophic current (a), water vertical motion ($\Delta = 10^{-17}$ s$^{-3}$ m$^{-1}$) (b) and hake recruitment (number/h) estimated by kriging (c) in October of 1994.

The situation during 1995 was different from that in 1993 and 1994 with adverse consequences for hake recruitment. The flow of the PC was small, therefore it is unlikely that the eggs and larvae were displaced outside of the continental shelf by this water mass. However in spring–summer, strong upwelling took place that transported the mesozooplankton toward the oceanic area (Fig. 6(c)). Parrish *et al.* (1981) hypothesized that the
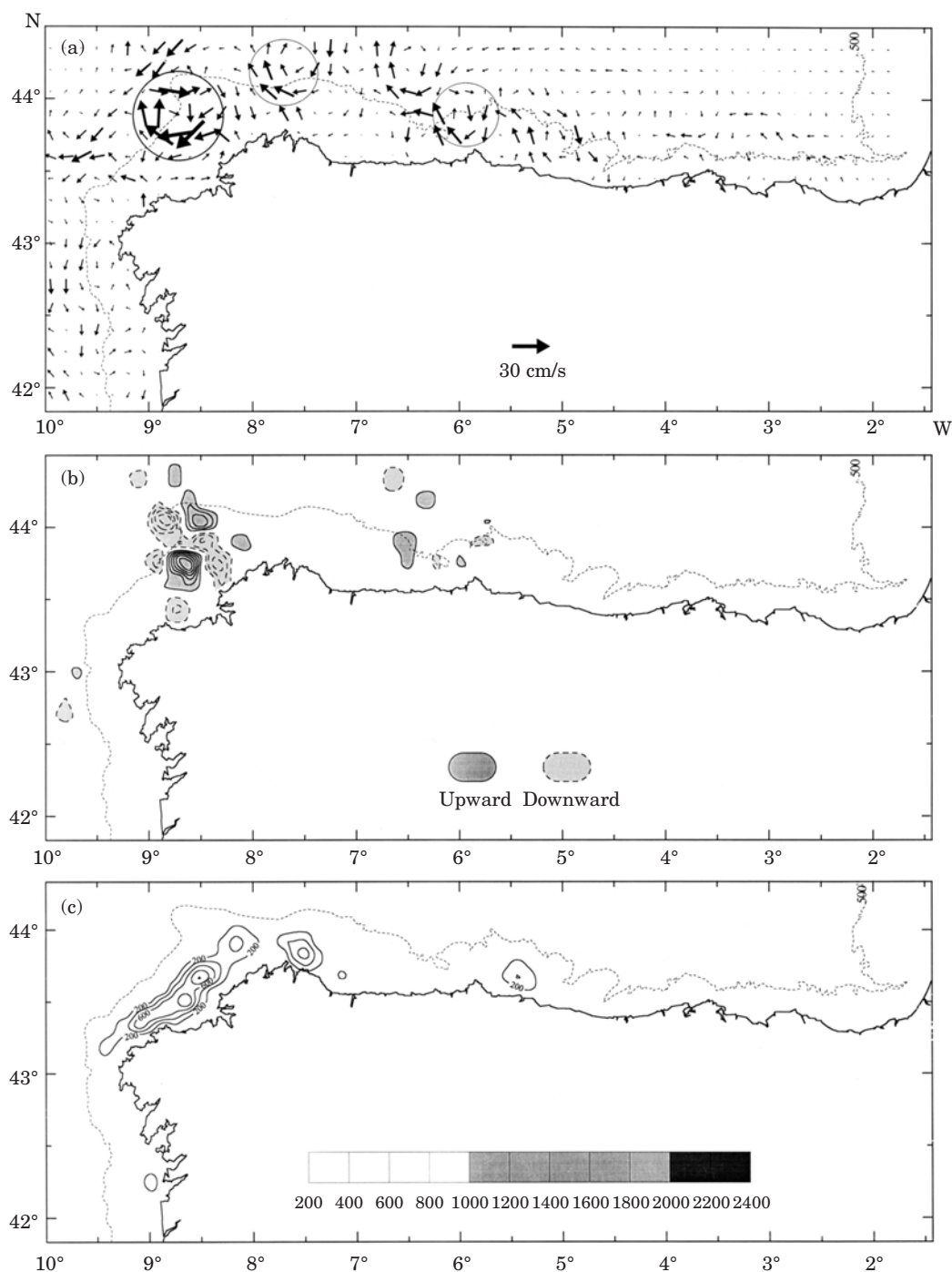
Figure 10. Geostrophic current (a), water vertical motion ($\Delta = 10^{-17}\,\mathrm{s}^{-3}\,\mathrm{m}^{-1}$) (b) and hake recruitment (number/h) estimated by kriging (c) in October of 1995.

spawning of fishes in the upwelling zone of the Californian Current is adapted to the adverse effects of offshore transport of eggs and larvae. The late-larval or juvenile (pre-recruits) mortality may be critical in determining the relative size of year class in this scenario and Sissenwine (1984) suggests the importance of this critical period for fish recruitment. For the Pacific hake, years of cold water temperatures on the spawning ground are

assumed to be years of high offshore transport and low larval survival (Francis *et al.*, 1989).

Vertical motion, the mechanism by which nutrients are brought into the photic layer, is related to variations in the geostrophic relative vorticity (Tintoré *et al.*, 1991; Gil, 1995). Vertical forcing is more intense in areas where mesoscale anomalies and instabilities are present and, therefore the advection of vorticity is higher. In 1993 the highest forcing appeared to be restricted to the areas of La Coruña, Ribadeo and Peñas (Fig. 8(b)). It was in these areas, where the thermocline was disrupted by the upwelling of cold water containing nutrients associated with intrusions of warm surface water, that the main aggregations of recruits were found. In 1994 there was a more significant and generalized vertical motion along the Cantabrian Sea continental shelf, with a maximum at Ribadeo and Peñas (Fig. 9(b)). This year saw the highest recruitment in the Cantabrian Sea in the whole historical series, with the appearance of additional smaller patches of juveniles, particularly the aggregations of Peñas and Guetaria. In 1995 the vertical motion was concentrated mainly off La Coruña (Fig. 10(b)) where the largest concentration of recruits was found (Fig. 10(c)). In the Cantabrian Sea there was very little vertical circulation. The aggregations of Ribadeo and Peñas were not very dense, and no concentrations of hake juveniles were found in Guetaria.

The spatial distributions of marine fish are significantly influenced by the vertical migration of each individual according to its life stage and size (Hermann *et al.* 1995). The possible explanation of the dependence of hake juvenile density on vertical forcing may be in their feeding behaviour as we have suggested earlier (Gil and Sánchez, 1996). Hake is considered to be a top carnivore and feeds on a variety of organisms mainly at night (Casey and Pereiro, 1995). Hake recruits make nocturnal vertical migrations in search of food in the upper layers. During the 1994 survey, some experiments were carried out to look into this behaviour in the area of La Coruña, and the following abundance indices over the bottom were obtained: day 251($\pm$ 52) individuals/haul; night 5($\pm$ 2.1) individuals/haul. Hickling (1927) described vertical migrations of hake from fishery observations and reported that this species is entirely independent of the sea bottom for its food supply. Hake juveniles feed on small fish, mainly anchovy and silvery pout, and pelagic crustaceans in autumn in the study area (Olaso, 1990; Olaso *et al.*, 1994). These prey species are found in upper layers and directly depend on planktonic organisms that exist in high primary production areas and are linked to vertical motion of nutrients to the photic layer. There is evidence that diel vertical migrations enable other gadoids, cod, haddock, whiting, etc., to maximize their feeding rate and maintain station in a food-rich environment in the North Sea (Bromley and Kell, 1995). Like hake, these species are demersal by

day and pelagic at night and there was evidence that these migrations were also food-related.

The differences between the aggregation patterns of recruits described by us and those found in the French area of the Bay of Biscay (Petitgas and Poulard, 1989; Petitgas, 1991) are not only a consequence of the different widths of the continental shelves. The production mechanisms found in Spanish waters are stronger, so that they support a higher density of recruits, and smaller in size (mesoscale) that those found on the French shelf. In the latter case the physical factors at work are based mainly on the effect of tidal dynamics caused by a bigger continental shelf (Le Cann, 1990) and on the fronts that occur in big estuaries such as the Gironde (Jegou and Lazure, 1995).

## Conclusion

Hake recruits were found aggregated in patches of 20–35 km along the Galician and Cantabrian Sea continental shelf in the same areas throughout the six years of the surveys reviewed here.

The spatial distribution of the hake recruits seems to obey the criteria of fixed geometry and variable density. The concentrations of recruits maintain their size within the mesoscale range and the strength of recruitment mainly depends on the density of these aggregations and on the number of patches that develop.

The size of patches and their location over the continental shelf seems to be influenced by mesoscale anomalies, "eddies", which appear to retain the larvae and juveniles and favour the feeding behaviour of recruits. Consequently these aggregations are located in areas of the continental shelf where the anomalies are repeated to a greater or lesser extent every year.

The PC may increase the mortality of the larval and pre-recruit phases of hake by increasing the displacement of water over the continental shelf towards the oceanic area and so reducing recruitment on the bottom. On the other hand this current generates eddies over the continental shelf and, as a consequence, ageostrophic vertical forcing, which provides nutrients to the upper layers and seems to have a positive effect on the abundance and distribution of recruits.

The transport of larvae inside the nuclei of the anticyclonic eddies toward the recruitment areas will be favourable when they move toward the west, close to or over the continental shelf. When they are far from the shelf, however, the numbers of larvae reaching the nurseries will be very low, and the strength of recruitment will be reduced.

Table 2 is a summary of the main environmental conditions that conditioned the hake recruitment in the last three years studied. The three factors considered were unfavourable to recruitment in 1993 and beneficial

Table 2. Interannual variability in Poleward Current, upwelling, mesoscale activity close to shelf and hake recruitment.

| Year | Poleward Current | Upwelling | Mesoscale activity close the shelf | Hake recruitment |
|------|------------------|-----------|------------------------------------|------------------|
| 1993 | Strong | Weak | Weak | Weak |
| 1994 | Weak | Moderate | Good | Strong |
| 1995 | Weak | Strong | Weak | Weak |

in 1994. The 1995 recruitment figures show that the negative influence of only one factor harms recruitment, irrespective of the other factors being favourable.

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