Small pelagic fish reproductive strategies in upwelling systems: A natal homing evolutionary model to study environmental constraints

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1. Introduction

Upwelling ecosystems support large populations of small pelagic fish, comprised mainly of anchovy and sardine species. These species exert a major control on the trophic dynamics of marine ecosystems (Cury et al., 2000), and are heavily exploited by industrial and artisanal fisheries. Recruitment of these small pelagic fish undergoes large interannual fluctuations, which may be related to environment instability, predator abundance and fishing pressure (Fréon et al., 2005). In particular, environmental conditions that prevail during spawning greatly influence the survival of eggs and larvae. Most of the pre-recruitment mortality occurs during the early life stages. Small pelagic fish populations in upwelling systems have a reproductive strategy resulting from past natural selection pressure which make them adapted to the constant structural instability of the upwelling area where they persist. Location and time of spawning, in particular, are crucial for successful recruitment (Bakun, 1996; Cury and Roy, 1989) and are important for the maintenance of marine fish population structure in general (Nielsen et al., 2005).

Natal homing is a reproductive strategy that relies on the mechanism of imprinting a record of the environmental condi-
tions, restricted to a brief period during the very first stage of life, which could account for successive generations reproducing at the same geographic location, even in open sea (Papi, 2006). Numerous studies have investigated natal homing in marine fish populations using individual tags (Svedang et al., 2007; Thorrold et al., 2001) or molecular genetic analysis (Chlaida et al., 2005). The observed spawning-site fidelity rates in these studies were often >50% (Bradbury and Laurel, 2007), and in some cases comparable to the scale of natal homing for birds and anadromous fishes (Thorrold et al., 2001). Herring also present high fidelity to their spawning site (Ruzzante et al., 2006) although the mechanism involved in this case seems to rely more on social transmission than imprinting (Corten, 2004; McQuinn, 1997). Indications of natal homing behaviour have been observed even in the very unstable upwelling areas of the ocean. In the northern Humboldt upwelling system off Peru, Mathisen (1989) suggested that the Peruvian anchovy (Engraulis ringens) stock “consists of a large number of local subpopulations of which each is genetically adapted to “home” to a different upwelling plume, and to spawn during a specific period of the year”. Hedgecock et al. (1994) observed genetic differences among the northern anchovy (Engraulis mordax) in the Californian current. More recently, in the central Canary upwelling system off Morocco, Chlaida et al. (2005) revealed genetic differences among sardine populations (Sardinia pilchardus) suggesting site fidelity. Lepage and Cury (1997) showed with a spatially explicit individual-based model (IBM) that only a population combining a low percentage of opportunists with a high proportion of “obstinate” (natal homing) individuals avoids extinction following drastic environmental events. Field observations (research surveys) show that anchovy and sardine spawning patterns off Peru, Chile and Morocco are very variable both temporally and spatially, suggesting a spawning strategy dominated by opportunists. A few frequently located “hot spots” and constantly occurring peak seasons do however, suggest some natal homing behaviour.

In this study we use an evolutionary individual-based model (IBM) which assumes a natal homing reproductive strategy to investigate the selective constraints which may be important during early life stages and may explain the observed spawning patterns. The IBM reproduced an evolutionary-based reproductive strategy for adult fish and passive transport of eggs and larvae based on environmental indices obtained from simulations of a realistic three-dimensional hydrodynamic model (ROMS) of the different areas. The IBM permits us to explore the effect of environmental selective constraints on the evolution of spatial (horizontal and vertical) and temporal spawning patterns. These patterns are compared to observed spawning patterns of sardine and anchovy following a Pattern-Oriented Modelling approach (Grimm et al., 2005). Mullon et al. (2002) used a similar model to investigate environmental constraints that select observed spawning patterns for anchovy (Engraulis encrasicolus) populations in the southern Benguela upwelling system off South Africa. They obtained a good match between simulated spawning patterns and observed ones by using simple environmental constraints. Here we apply a similar model in three different regions: the northern Humboldt (off Peru), southern Humboldt (off Chile) and central Canary (off Morocco) upwelling systems. The three upwelling systems have significantly different shelf extensions, widest off Morocco and narrowest off Chile. In each of these systems, sardine and anchovy larvae are distributed over areas where the continental shelf is the wider, apparently acting as an open nursery area. If the observed spawning patterns in these three systems can be reproduced, then it may be possible in the future to simulate the effect of climate changes on the distribution of pelagic fishes.

2. Methods

2.1. The model

The evolutionary individual-based model (IBM) used here comprised two main parts: (1) the transport of eggs and larvae, based on the ichthyoplankton dynamics IBM Ichthyop (Lett et al., 2008) with specific selective environmental constraints (see below), and (2) an evolutionary-based reproductive strategy, based on the method developed by Mullon et al. (2002), in which all adults spawned in the vicinity of their natal place and date. Recruited individuals were spawners of the next simulated generation, which were confronted by different environmental conditions (see below), but had the same goal of spawning at their location of birth (Fig. 1). Using this approach, spatial and seasonal spawning patterns progressively emerged at the population level from the selective constraints imposed at the individual level (Mullon et al., 2002).

2.1.1. Environmental conditions

Environmental conditions were obtained from archived simulations of a three-dimensional hydrodynamic model (ROMS) (Shchepetkin and McWilliams, 2005) of the different regions, using climatological and/or interannual forcing.

For the northern Humboldt (Peru) region the domain extends from 5°N to 22°S and from 70°W to 92°W with a horizontal resolution of 1/9° and includes 32 vertical levels (terrain-following curvilinear coordinates) (Penven et al., 2005). Since the mesoscale activity could be variable between the different simulation years due to intrinsic model variability (Marchesiello et al., 2003), a set of four years was chosen randomly from those used by Penven et al. (2005). This climatological configuration, previously used in other (non-evolutionary) IBM experiments (Brochier et al., 2008a; Lett et al., 2007), was complemented with a nine-year (1992–2000) interannual simulation, which includes the 97-98 ENSO event (Colas et al., 2008; Echevin pers.com.). This produced a pool of 13 different hydrodynamic years.

For the southern Humboldt (Chile) region, model outputs were extracted from a large grid which includes the South-Eastern Pacific and the equatorial Eastern Pacific. The extracted sub-domain extends from 18°S to 40°S and from 80°W to 69.5°W with an horizontal resolution of ~7.5 km and contains 30 vertical levels. The pool of hydrodynamic years used for the simulations comprised 7 years of a climatologic simulation and 6 years of an interannual simulation (1994–1999) developed and validated by Colas et al. (2008) and Capet et al. (2008).

For the central Canary (Morocco) region, the model domain extends from 21°N to 32°N and from 9°W to 20°W with a horizontal resolution of 1/12° (~8 km) and includes 32 vertical layers (Machu et al., 2009; Marchesiello and Estrade, 2007). We used a 7-year

Fig. 1. Diagram representing the algorithm used in the evolutionary individual-based model.
(1996–2002) interannual simulation, which has been used previously to study the main ichthyoplankton transport patterns along the African shelf and from this shelf to the Canary archipelago (Brochier et al., 2008b).

2.1.2. Selective constraints

Three selective constraints were considered in the model for individuals to recruit and contribute to the next generation of spawners, together and in isolation.

First of all, the temperature experienced by eggs and larvae during the transport phase determines their survival. Individuals recruited when they did not encounter temperatures below a given lethal limit. The actual effect of cold is to slow swimming and growth and directly or indirectly to increase mortality rates. Temperature can also be considered as a proxy for oxygen, with cold waters associated to the oxygen minimum zone, especially in the Humboldt Current system (Morales, 2000). The lethal temperature was set in the model to 10 °C to cover the range of minimal temperatures allowing sardine and anchovy egg and larval survival reported in the literature (Hernandez and Castro, 2000; King et al., 1978; Tarifeño et al., 2008).

The second selective constraint was the retention of larvae over the continental shelf at the end of the transport phase. In the three regions under study, the continental shelf is an area with high chlorophyll a concentrations (Carr and Kearns, 2003), high food availability for larvae, and therefore constitutes a potentially suitable nursery area. It is generally accepted that advective loss of larvae away from nursery areas has a negative effect on recruitment, especially in upwelling areas where offshore larval loss might be considerable (Bakun, 1996; Bakun and Parrish, 1982; Cury and Roy, 1989).

The last selective constraint considered was the non-dispersion of individuals, which was used as a proxy for whether food and larval distribution remain patchy: a factor which enhances larval feeding efficiency (Bakun, 1996; Lasker, 1975; Lasker and Smith, 1976), and the onset of schooling (Hunter and Coyne, 1982). In that case, individuals were considered as recruited if the distance to their nearest neighbour at the end of the transport phase was less than or equal to that at the beginning of the transport phase (when eggs were just spawned).

2.2. Simulations

The temperature constraint was always present with either the retention constraint alone, the non-dispersal constraint alone or both constraints combined. This leads to nine sets of simulations in each system. Simulations were run for 100 generations, a value that was empirically chosen as being adequate for spawning patterns to emerge under the various selective constraints scenarios considered. The transport phase lasted for 30 days, a duration covering the planktonic stage of sardine and anchovy larvae (Santos et al., 2007). Individuals initially spawned randomly over the whole domain and the entire year, at depths ranging from 0 to 100 m in the southern Humboldt and central Canary and from 0 to 50 m in the northern Humboldt, based on available data of egg vertical distribution patterns and oxygen limitations (Ayón, 2004; Rodríguez et al., 2006).

To allow robust spatio-temporal spawning patterns to emerge, recruited individuals did not spawn at their exact natal location and time of birth, but within a margin: ±50 km (horizontal) and ±3 m (vertical) for location, ±3 days for time. The continental shelves were defined according to the specific characteristics of each region to ensure that they covered the chl-a rich area, as visible by satellite measurements. Offshore extensions of the retention zone were set to isobaths 200 m, 500 m and 1500 m in the central Canary, northern Humboldt and southern Humboldt areas, respectively.

Fig. 2. Emerging spawning patterns in the central Canary Current system (off Morocco) with a lethal temperature of 10 °C and different selective constraints: (a) shelf retention, (b) non-dispersion, and (c) shelf retention and non-dispersion.
3. Results

3.1. Central Canary Current system

The larval lethal temperature had no effect on the selected spawning patterns in the central Canary Current system within the range of values tested. Results obtained with a 10 °C lethal temperature (Fig. 2) were similar to those obtained with 12 °C and 14 °C lethal temperatures (not shown).

When using the selective constraint based on shelf retention, the selected spawning area was between 22°N and 26°N extending relatively far offshore (~100 km), corresponding to the large extension of the shelf in that region. There was a secondary spawning area of much lower intensity between 28°N and 29°N. The selected seasonal pattern was maximum spawning in November–January (winter) and minimum in May–July (summer). The selected vertical spawning pattern was maximum around 15 m (Fig. 2a).

Using the non-dispersion criterion a weaker spatial spawning pattern was obtained, concentrated in the surface layers, with slightly more spawning along the coast from 24°N to 26°N, 28°N to 31°N and 22°N to 23°N. The selected maximum spawning season was May–July (Fig. 2b).

Finally, combining the selective constraints of shelf retention and non-dispersion, a horizontal spatial pattern similar to the one obtained with the shelf retention constraint alone was obtained, except that there was very little spawning south of 24°N. There was also, like for the shelf retention constraint alone, a second spawning area of much lower intensity between 28°N and 29°N. The seasonal pattern was similar to the one obtained with the non-dispersion criterion alone. The selected vertical distribution was maximum near the surface and almost constant from 10 m to 30 m after which a rapid decrease was observed until 60 m, i.e., a combination of the patterns obtained using each constraint alone (Fig. 2c).

3.2. Northern Humboldt Current system

Similarly to that found for the Canary Current system, changing the larval lethal temperature had no effect on the emerging spawning patterns in the northern Humboldt Current simulations. Results obtained with a 10 °C lethal temperature (Fig. 3) were similar to those obtained with 12 °C and 14 °C lethal temperatures (not shown). The selected pattern obtained with the shelf retention constraint was concentration of spawning over the shelf from 6°S to 12°S, maximum from December to March (austral summer) and minimum from June to October (extended austral winter). The selected vertical spawning pattern was essentially sub-surface depths (from 20 m to 50 m, Fig. 3a). With the non-dispersion selective constraint, four distinct spawning areas emerged along the coast: around the northwest corner of the domain, 8°S, 11°S and 14°S. Spawning was concentrated near the surface (up to a depth of 20 m), and the seasonal pattern was weak (Fig. 3b). Finally, the combination of the shelf retention and the non-dispersion selective constraints lead to two distinct spawning areas and seasons, August spawning from 6°S to 12°S mainly in deeper waters and March–April spawning from 2°S to 4°S close to the surface (Fig. 3c).

3.3. Southern Humboldt Current system

In the southern Humboldt Current system larval lethal temperature had a major impact on the selected spawning patterns. When we used the shelf retention constraint with a 10 °C lethal temperature, the main spawning area was essentially from 33°S to 38°S (Fig. 4a). 38°S was the southern limit of the physical simulation, which explains why the spawning area is cut at this latitude, but some complementary experiments with the same set of constraints and a domain limit extended to 40°S (not shown) showed that it may extend further south at least until 40°S. The seasonal pattern for this spawning area showed a peak in July (austral win-
When the larval lethal temperature was increased to 12 °C, the southern limit of the spawning shifted north to 37°S and the spawning season slightly shifted to a peak in August. For both 10 °C and 12 °C lethal temperature, there was a secondary spawning area in the north of the domain, from 18°S to 21°S, with a very little number of individuals compared to the main area and an extremely weak seasonality. On the other hand, with a 14 °C larval lethal temperature this area became the main one, with a seasonal maximum in November–December (austral spring) while the southern area shrank (Fig. 4a). The vertical distribution of spawning was maximum around 50 m for both areas, and was not sensitive to changes in lethal temperature (Fig. 4a).

With the non-dispersion selective constraint the selected horizontal spawning pattern was very weak, with some coastal maximum from 18°S to 21°S and from 30°S to 38°S when simulating a 10 °C lethal temperature. The southern area was reduced to 30–36°S when using a 12 °C threshold and to 30–34°S with 14 °C. Spawning peaked from November to January and was concentrated near the surface, independently of the lethal temperature applied (Fig. 4b).

Finally, when we combined the non-dispersion and shelf retention constraints we obtained a single clear spawning peak in February for a 10 °C lethal temperature and in March–April at 12 °C and 14 °C, concentrated off the northernmost part of the domain, from 18°S to 21°S, with a vertical bimodal distribution peaking primarily near the surface and secondarily between 80 m and 120 m (Fig. 4c), i.e., a combination of the distributions obtained when each selective constraint was used in isolation. The vertical pattern was not sensitive to the lethal temperature changes. There were very few individuals spawning in the south of the domain with 10 °C and 12 °C lethal temperatures, and none for 14 °C.

### 4. Discussion

Horizontal, vertical and seasonal spawning patterns for sardine and anchovy observed in the different systems are summarized in Table 1. We now compare model results and observed patterns for each region. A synthesis of this comparison is reported in Table 2.

#### 4.1. Central Canary Current system

The main feature of the Central Canary system is the presence of the Canary Islands situated at a distance ranging between 100 km to 450 km from the coast. The southward flowing Canary Current is disrupted by the presence of the islands, which creates a large eddy field downstream of the archipelago (Barton et al., 2004). These eddies interact with enriched upwelling filaments which extend out from the continental shelf resulting in an eddy-filament system which constitutes a suitable environment for larval development and transport towards the Canary Islands (Brochier et al., 2008b; Rodriguez et al., 1999). This eddy-filament system may explain the emerging spawning peak that we found off Cape Boujador (~26°12′N) during summer (Fig. 2b) with the non-dispersion selective constraint. Applying this constraint led to the emergence of an area south of Dakhla (~24°N) where no spawning occurred (Fig. 2b and c). This corresponds to an area with enhanced dispersion that matches the permanent upwelling core (Wooster et al., 1975). This area is situated too far from the eddy field generated by the Canary archipelago to interact with it, so that ichthyoplankton spawned there would gain no benefit from it (Brochier et al., 2008b). However, with the shelf retention selective constraint this area was selected for winter spawning (Fig. 2a), which suggests that even if dispersion is high, individuals spawned there mostly remained...
over the continental shelf, either retained there or advected northwards by the sub-surface poleward current, or southwards by the main surface flow (Brochier et al., 2008b; Pelegri et al., 2005). The two main small pelagic species present in the central Canary Current system are sardine (S. pilchardus) and anchovy (E. encrasicholus). They are known to have opposite seasonal spawning patterns (Table 1): sardine spawn mainly in winter while anchovy spawning is elevated in summer, during the period of maximum upwelling (Aristegui et al., 2006; Berraho, 2007). These observations are in line with observations in the California Current system which show that anchovy prefer to spawn during periods of strong upwelling while sardine prefer to spawn during periods of moderate upwelling (Lluch-Belda et al., 1991). Opposite seasonal patterns also appeared in our model results. The shelf retention constraint resulted in maximum spawning in winter (Fig. 2a), i.e. during the sardine spawning season, while the non-dispersion constraint resulted in maximum spawning in summer (Fig. 2b), during the main anchovy spawning season (Table 2).

There are two genetically distinct sardine populations off Morocco (Chlaida et al., 2005). The southern population has a natal home area located from Tarfaya to Dakhla (24°–28°N), which matches the northern part of the main spawning area selected with the shelf retention selective constraint in our model (22°–26°N, Fig. 2a). The northern population of sardine which has a natal home area located north of Cape Ghir (~30°38’N) migrates southwards during the feeding season (summer) to an area between 28°N and 31°N, known as a “transition zone” (Chlaida et al., 2008), which is also the main distributional area of anchovy (Table 1). This area coincides with the secondary spawning area obtained in the model between Cape Juby and Cape Draa (28°–29°N, Fig. 2a and c). The model selected a maximum spawning depth around 17 m (retention constraint, Fig. 2a) or close to the surface (non-dispersion constraint, Fig. 2b, retention and non-dispersion, Fig. 2c), which compares well to information available for anchovy in the Canary and sardine in the nearby Bay of Biscay (Tables 1 and 2).

### Table 1

<table>
<thead>
<tr>
<th>Region species</th>
<th>Horizontal distribution</th>
<th>Vertical distribution</th>
<th>Seasonality</th>
</tr>
</thead>
<tbody>
<tr>
<td>Central Canary</td>
<td>Ankovy: 28°–31°N</td>
<td>Sardine: no data</td>
<td>Winter</td>
</tr>
<tr>
<td>(Anchovy</td>
<td>(C. Juby – C. Ghir)</td>
<td>in Canary, but</td>
<td></td>
</tr>
<tr>
<td>Engraulis</td>
<td></td>
<td>0–50 m for same</td>
<td></td>
</tr>
<tr>
<td>encrasicolus</td>
<td></td>
<td>species in Bay of</td>
<td></td>
</tr>
<tr>
<td>Sardina</td>
<td></td>
<td>Biscay (Coimbs</td>
<td></td>
</tr>
<tr>
<td>pilchardus</td>
<td></td>
<td>et al., 2004)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sardine: 24–26°N</td>
<td>Ankovy: 0–100 m,</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(Dakhla – C. Boujdur)</td>
<td>but mostly (80%)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>and 28–31°N (C. Juby</td>
<td>concentrated in</td>
<td></td>
</tr>
<tr>
<td></td>
<td>– C. Ghir)</td>
<td>the surface layer</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0–35 m) (Rodríguez</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>et al., 2006)</td>
<td></td>
</tr>
<tr>
<td>Northern Humboldt</td>
<td>Off central Peru (6–</td>
<td>Main peak in</td>
<td>Winter</td>
</tr>
<tr>
<td>(Anchovy</td>
<td>14°S) over the</td>
<td>shelf, no field data</td>
<td></td>
</tr>
<tr>
<td>Engraulis</td>
<td>continental shelf, o</td>
<td>of 4′S</td>
<td></td>
</tr>
<tr>
<td>ringens</td>
<td>0–50 m, mostly</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>concentrated in</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>the surface layer</td>
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</tr>
<tr>
<td></td>
<td>(0–30 m) (Ayón,</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2004)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Southern Humboldt</td>
<td>Off Peru–Chile border</td>
<td>Winter in both</td>
<td>Winter in</td>
</tr>
<tr>
<td>(Anchovy</td>
<td>(18–22°S) and off</td>
<td>areas</td>
<td></td>
</tr>
<tr>
<td>Engraulis</td>
<td>central Chile (33–40°S)</td>
<td>(Parrish et al.,</td>
<td></td>
</tr>
<tr>
<td>ringens</td>
<td>(Castro and Hernández,</td>
<td>1983)</td>
<td></td>
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<tr>
<td></td>
<td>2000; Cubillos et al.,</td>
<td></td>
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<tr>
<td></td>
<td>2007)</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>Off Northern Chile:</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>0–50 m (Morales et al.</td>
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<tr>
<td></td>
<td>1996) (no published</td>
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<tr>
<td></td>
<td>data off central</td>
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<td>Chile)</td>
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### Table 2

<table>
<thead>
<tr>
<th>Region (species)</th>
<th>Spawning pattern</th>
<th>Selective constraint</th>
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<th>Non-dispersion</th>
<th>Shelf retention and non-dispersion</th>
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<td>Partial for</td>
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<td>Yes for sardine</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Partial for anchovy</td>
<td>anchovy</td>
<td></td>
<td>Yes for sardine</td>
</tr>
<tr>
<td></td>
<td>Vertical</td>
<td>Yes for sardine</td>
<td>Yes for sardine</td>
<td>No</td>
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<tr>
<td></td>
<td></td>
<td>Yes for anchovy</td>
<td>Yes for sardine</td>
<td>Yes</td>
<td>Yes for sardine</td>
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<td></td>
<td>Seasonal</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>No for anchovy</td>
<td>Yes for sardine</td>
<td></td>
<td>Yes for sardine</td>
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<tr>
<td>Northern Humboldt</td>
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<td>Partial</td>
<td>No</td>
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</tr>
<tr>
<td></td>
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<td>Yes</td>
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<tr>
<td></td>
<td>Seasonal</td>
<td>No</td>
<td>Partial</td>
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<tr>
<td>Southern Humboldt</td>
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<td>Partial</td>
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<td></td>
<td>Vertical</td>
<td>12 °C (low intensity)</td>
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<tr>
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<td>Seasonal</td>
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<td>14 °C</td>
<td>Partial</td>
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</table>

### 4.2. Northern Humboldt Current System

Unlike the two other systems studied here, the maximum upwelling favourable winds in the northern Humboldt Current system occur during winter (Parrish et al., 1983). With the shelf retention selective constraint alone, the vertical spawning pattern selected was between 25 and 50 m (Fig. 3a). At this depth, shelf retention is maximum in summer because individuals remain below the shallow stratified surface Ekman layer (Bakun, 1987; Brochier et al., 2008a). As reported in Table 1, anchovy (E. ringens) off Peru spawn mainly over the central shelf (Parrish et al., 1983), close to the surface (Ayón, 2004) and in winter. With the retention constraint alone, the selected spawning area (6 to 12 m, Fig. 3a) obtained corresponded well with observations but the seasonal (summer) and vertical (sub-surface) patterns did not match observed patterns (Table 2). When applying the non-dispersion constraint in isolation the model selected vertical spawning pattern agreed with observations but the horizontal and seasonal patterns did partially only (Fig. 3b). Finally, the simultaneous use of both constraints allowed for a comparable selection of spawning area and season but only partially for depth distribution, in the major spawning area (6–12°S) (Fig. 3c). The model also selected for spawning in the Bay of Guayaquil (2–4°S) during late austral summer (March–April) and in surface layers (Fig. 3c). There are no ich-
thyopelagic data available in this area. However, temperatures in this bay usually exceed 22 °C and this may be too warm for anchovy spawning to occur there, although results from Gutiérrez et al. (2008) suggest that adult anchovy have no preference for temperatures between 14–23 °C.

Although the ENSO was taken into account in the hydrodynamic input, the strong 1997–1998 El Niño event, in particular, it did not have any significant effect on our results. In fact, other modelling studies have indicated that shelf retention increased during the 97–98 ENSO event (Brochier, 2009; Colas et al., 2008). The dramatic effect of this phenomenon on the anchovy population (Cubillos and Arcos, 2002) may therefore be due to other factors such as the strong temperature anomaly, the diminution of enrichment and the subsequent reduction in phytoplankton production (Enfield, 1988; Halpern, 2002).

4.3. Southern Humboldt Current system

In the southern Humboldt Current system, the continental shelf is very narrow along most of the coast: the distance from the coast to the 1500 m isobath (the value we chose for our definition of the “shelf”) ranges from 10 km to 75 km offshore for central Chile and from 10 km to 30 km offshore for northern Chile. As reported in Table 1, spawning of anchovy (E. ringens) off Chile peaks in austral winter (Parrish et al., 1983) and the areas where anchovy spawning occurs most often are off the Peru–Chile border (18–22°S) and off central Chile (33–40°S) (Castro and Hernández, 2000; Cubillos et al., 2007). This corresponds well with the horizontal and seasonal spawning patterns obtained with the shelf retention selective constraint alone, however the vertical pattern of spawning did not totally match the observations (Fig. 4a, Table 2).

In the wide bay formed between the southern Peru and northern Chile regions there is a little wind seasonality and minimal offshore transport (Bakun and Parrish, 1982; Morales et al., 1996), which explains the emerging spawning in this area with the shelf retention selective criterion, despite the narrow shelf. Off central Chile upwelling favourable winds are maximum during summer. The area off central Chile has a wider shelf, but early life stage survival in this area may be compromised by low temperature, ranging from 10 to 12 °C during the winter spawning season (Cubillos et al., 2007). Tarifeño et al. (2008) found temperature optima ranges of 12–15 °C and 15–18 °C for anchovy distributed off central and northern Chile, respectively. In addition, larval hatching did not occur at temperatures below 8 °C in central Chile. In our results, most of the spawning occurred off central Chile for lethal temperature of 10 °C and 12 °C but for 14 °C the main spawning area changed to northern Chile.

Lluch-Belda et al. (1989) showed that during periods of low abundance, sardine spawning grounds are restricted to northern Chile while during periods of high abundance, spawning occurs both in northern and central Chile. This may imply that the area off northern Chile is a more permanent and successful nursery than the area off central Chile. Nevertheless, anchovy populations from central Chile can compensate for their low larval growth rates by increasing their initial egg and hatch size (Llanos-Rivera and Castro, 2004; Llanos-Rivera and Castro, 2006). The central Chile area was not selected when a combination of shelf retention and non-dispersion selective constraints was used, even without the temperature limitation. The northern Chile area was still selected but the selected seasonal spawning peak shifted to summer (Fig. 4c), which does not match observations (Tables 1 and 2).

4.4. Conclusions and Perspectives

We obtained the best agreement between spawning patterns selected in the model and observed patterns using the retention constraint alone for sardine in the central Canary Current, for anchovy in the southern Humboldt Current systems, and using a combination of the retention and non-dispersion constraints in the northern Humboldt Current system, still for anchovy (Table 2). Additional simulations in the northern Humboldt (not shown) indicated that limiting spawning to the surface layer only did not influence the selected spawning patterns. In addition, our results suggest that, similarly to that in the southern Benguela (Mullon et al., 2002), larval lethal temperature affected the selected patterns in the southern Humboldt, but not in the central Canary and northern Humboldt. Spawning areas off central Chile and in the southern Benguela are located at relatively high latitudes (33–40°S and 34–35°S, respectively) and are therefore characterized by lower water temperatures. It does seem likely that the anchovy spawning strategy off central Chile is mainly driven by the need for shelf retention, which is maximum in winter, when water temperatures are lower.

Although the proxies used led to interesting results, it is important to highlight the risks of errors inherent to our choice. Indeed, the shelf retention criterion assumes a static prey field for larvae, while the actual offshore extent of the upwelled, plankton-rich waters is related to meso-scale current and upwelling dynamics, ranging from a very coastal area or oppositely far away from the continental slope. Nonetheless, even if larvae can find enough food to survive offshore, their fate remains uncertain. Similarly, the non-dispersion criterion may favour ichthyoplankton catch in very laminar flow, that not necessarily corresponds to plankton-rich waters. Finally, recent studies suggest that in non-upwelling regions, the retention area resulting in good recruitment may not be restricted to the shelf (Trigoien et al., 2008). Indeed, the predator field may coincide with the larval prey field so that growing in these waters may not always benefit to the overall recruitment. In the case of a detrimental predation pressure vs food supply ratio over the continental shelf, the shelf retention criterion would not be pertinent. However, field observations showed that being in a growing favourable area may be more important for larval survival than avoiding predation (Pepin et al., 2003), which is in agreement with the “bigger is better” hypothesis (Bailey and Houde, 1989; Miller et al., 1988).

Natal homing to specific locations and at particular times to spawn remains an hypothesis for small pelagic fish species, although there are some indications that this may occur (see our introduction). In the southern Benguela, regular spawning patterns for anchovy are observed in restricted areas, and do not seem to be related to environmental changes (Hutchings, 2001; van der Lin- gen et al., 2001). This is not necessary the rule in other upwelling regions, especially in the northern Humboldt where spawning time and location are highly variable. An alternative to the natal homing is “environmental homing” driven by imprinting of environmental cues during individuals early life. In that picture, spawning occurs in areas with similar environmental conditions (moving target) instead of fixed locations. Preliminary results indicate that an evolutionary model including environmental homing strategy allows for the selection of realistic anchovy spawning patterns in the northern Humboldt (Brochier, 2009).

In future, this modelling approach could be used to investigate the interplay between climate change and changes in pelagic fish spawning patterns and strategies (Lett et al., 2009). To do so, hydrodynamic simulations run under climatic change scenarios are needed. Such simulations are currently being developed (Goubanova et al., 2008).

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Engraulis ringens

Engraulis encrasicolus


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