

Enrichment, concentration and retention processes in relation to anchovy (*Engraulis ringens*) eggs and larvae distributions in the northern Humboldt upwelling ecosystem[☆]

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Abstract

A Lagrangian model is used to simulate and quantify in the northern Humboldt upwelling ecosystem the processes of enrichment, concentration and retention, identified by Bakun [Bakun, A., 1996. Patterns in the ocean. Ocean processes and marine population dynamics. University of California Sea Grant, California, USA, in cooperation with Centro de Investigaciones Biológicas de Noroeste, La Paz, Baja California Sur, Mexico, 323 pp.] as being important for the survival and recruitment of early life stages of pelagic fish. The method relies on tracking the positions of particles within water velocity fields generated by a three-dimensional hydrodynamic model. Simple criteria for considering particles as participating to enrichment, concentration or retention are used to derive indices of the three processes. We analyse the spatial distribution of and seasonal variability in these indices. The results are discussed in relation to anchovy (*Engraulis ringens*) eggs and larvae distributions off Peru, and to a comparable study conducted in the southern Benguela upwelling ecosystem.

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1. Introduction

An increasing number of studies stress the influence that mesoscale hydrodynamic structures have on the dy-

namics of fish early life stages in eastern boundary current upwelling systems. For example, Logerwell and Smith (2001) found an association between offshore sardine survival and the presence of mesoscale eddies in the California Current upwelling system. Rodríguez et al. (1999, 2001, 2004) showed that retention and dispersion due to mesoscale features influenced the horizontal distribution of fish eggs and larvae in the northern Canary Current upwelling system. Castro and Hernández (2000) and Rodríguez-Graña and Castro (2003) argued that mesoscale filaments and plumes influence the composition of the ichthyoplankton community in the southern Humboldt Current upwelling system. Hutchings et al.

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(2002) mentioned the impacts of mesoscale activity on fish reproductive patterns in the Benguela Current upwelling system.

Nowadays hydrodynamic models produce realistic water circulation simulations at the regional scale. These simulations are increasingly used in connection with individual-based models of fish early life stages dynamics (Werner et al., 2001). Such “coupled” models have been used to study how water circulation affects transport of fish eggs and larvae (Quinlan et al., 1999; Allain et al., 2003; Huggett et al., 2003; Skogen et al., 2003; Ådlandsvik et al., 2004; Thorpe et al., 2004), their retention (Stenevik et al., 2003; Santos et al., 2004) or both (Voss et al., 1999; Hannah et al., 2000; Hinrichsen et al., 2001a,b, 2003, 2005; Miller et al., in press). The effects of water temperature on growth and mortality of ichthyoplankton (Miller et al., 1998; Bartsch and Coombs, 2001; Brickman et al., 2001; Pedersen et al., 2001; Mullon et al., 2003) and of water density on their vertical displacement (Hinckley et al., 1996; Hinckley, 1999; Parada et al., 2003) have also been considered in these models.

The success of recent coupled models attests that they are good tools for studying how biological and physical processes, and their interactions, affect the dynamics of fish early life stages. These works are, however, difficult to compare as they concern different species in various locations, and rely on different hydrodynamic models operating at various spatial and temporal scales. Considering coupled models within a generic framework would help this comparison. A step in this direction was achieved with the method proposed by Lett et al. (in press), which couples a hydrodynamic model and a Lagrangian particle-tracking model within the framework of Bakun’s fundamental triad processes (Bakun, 1996). Bakun proposed an integrated theory of how the physical environment may influence the recruitment of marine populations having pelagic early life stages, based on three fundamental processes, enrichment, concentration and retention. Enrichment and concentration processes lead to areas where there is enough food that is sufficiently aggregated for larvae to feed, and retention processes enable them to stay in these favourable areas.

A first application was designed to study the spatial and seasonal variability of enrichment and retention in the southern Benguela upwelling system, and discussed regarding the reproductive strategies of anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*) off South Africa (Lett et al., in press). Here we use the same methodology to study Bakun’s fundamental triad processes in the northern Humboldt upwelling system in relation to anchovy (*Engraulis ringens*) eggs and larvae distributions off Peru, and we compare the results of the two studies.

2. Methods

2.1. Anchovy eggs and larvae distributions

Between 1964 and 2003, 132 surveys were carried out by the Instituto del Mar del Perú (IMARPE) to assess anchovy (and other species) abundance. Ichthyoplankton samples were taken with Hensen nets of 0.33 m² mouth area and 300 µm mesh size, by vertical hauls between 0 and 50 m. The samples were fixed in 2% formaldehyde buffered with borax. Einarsson and Rojas de Mendiola (1963) was used for the taxonomy determination. Eggs and larvae were removed from the samples for counting. When their abundance was too high (more than 500 approx.), they were counted in only half or quarter of the entire sample and subsequently raised accordingly. This extensive dataset is under analysis at IMARPE and a comprehensive description of it will be presented in more detail in a forthcoming paper.

2.2. The hydrodynamic model

The ocean model is the Regional Oceanic Modeling System (ROMS). The reader is referred to Shchepetkin and McWilliams (2005) for a complete description of the model. ROMS solves the Primitive Equations in an Earth-centered rotating environment, based on the Boussinesq approximation and hydrostatic vertical momentum balance. ROMS is discretized in coastline- and terrain-following curvilinear coordinates. The model grid, forcing, initial and boundary conditions are built using the ROMSTOOLS package (Penven, 2003). To encompass the whole Peru Upwelling System, the grid extends from 20°S to 3°N and from 90°W to 70°W at a resolution of 1/9° (i.e., 10 km). The grid contains 192 by 256 points and 32 vertical levels.

As a first approach, we concentrate on the mean circulation and the seasonal cycle, leaving aside the inter-annual variability. The model is forced by COADS ocean surface monthly climatology for the heat and fresh water fluxes, and by a monthly climatology derived from QuikSCAT satellite scatterometer data for the wind stress. The three lateral open boundaries are forced using a climatology derived from the OCCAM global ocean model (Saunders et al., 1999). The model solution reaches a statistical equilibrium after a spinup of about 2 years. A complete description of the model configuration, analysis and validation is given by Penven et al. (2005). The average behaviour of the model and its variability has been checked against observed data and the close comparison between model output and observations provides confidence in the reliability of the model output to

reproduce the average circulation, seasonal cycle and mesoscale dynamics for the Peru Current System (Penven et al., 2005). A snapshot of the simulated sea surface currents and temperature is shown in Fig. 1.

Outputs of the hydrodynamic simulations were averaged every 2 days and archived for use by offline modelling tools such as the Lagrangian model (see below). Preliminary tests of sampling frequencies show that 2-day averages retain a satisfactory representation of the hydrodynamics (F. Colas, IMARPE, pers. com.).

2.3. The Lagrangian model

The Lagrangian model makes use of water velocity fields generated by the hydrodynamic model to transport passive individuals that are called particles. Transport of particles relies only on advection (or drift) as no diffusion term is introduced. Linear interpolations in time and space of the velocity fields are performed 15 times within 2-day timesteps. In these conditions, the “well-mixed condition test”, stating that an initially uniform distribution of particles maintains its uniform distribution (Brickman and Smith, 2002), was visually estimated as being satisfied. A simulation consists in releasing a large number of these particles (500 000), tracking them and then using a criterion (see below) to consider them as participating to enrichment, concentration or retention, depending on the process under study. Simulations are repeated periodically in time for 4 years (named Y11 to Y14). Results of the

simulations are then averaged over time to study the spatial variability of the processes, or averaged over space to focus on seasonal variability. Five sets of simulations were performed that principally differ in the spatial distribution of particles release according to the process studied (Table 1). Henceforth we call these sets of simulations experiments.

2.4. Enrichment, concentration and retention

The criteria used for particles to be considered as participating to enrichment, concentration or retention, are similar to those used by Lett et al. (in press) but with parameter values re-evaluated according to the study area and the biology of the species. Several studies suggest that the development time of anchovy eggs off Peru is about 2 days at temperatures around 16 °C, close to the central range of temperature observed in situ during the spawning season (see, e.g., Santander and Sandoval de Castillo, 1973; Ware et al., 1980; Santander, 1987). Muck et al. (1989) showed that the length of first-feeding anchovy larvae is 3–4 mm. Considering a length at hatching of 2 mm and a growth rate of 1.4 cm/month (Palomares et al., 1987), this length corresponds to 2–4-day-old larvae. A similar estimation is obtained using the growth curves estimated for anchovy larvae off central Chile (Castro and Hernández, 2000). In experimental conditions at 18 °C, Ware et al. (1980) reported that first-feeding began on average 4.4 days after hatching. They also mentioned that larvae had to feed before 5–6 days otherwise they would die of starvation. First-feeding larvae feed principally on phytoplankton, but increasingly on micro-zooplankton as they grow (Ware et al., 1980; Muck et al., 1989). They swim actively half of the time (Ware et al., 1980), but at such low speeds compared to typical speeds of horizontal current that they can be considered as passive (Walsh et al., 1980). Active behaviours like vertical migration or swimming are therefore not taken into account. In the simulations we decided to apply the retention criterion after 8 days of passive transport. According to the studies above, this can be considered as the critical time when larvae have to feed but are not able to swim efficiently in the horizontal plane. Main currents and undercurrents off Peru flow at velocities of 5–40 cm s⁻¹ (Penven et al., 2005), if we exclude cape effects, particularly around Cabo Blanco (4.16°S, 81.15°W). Areas characterized by lower flow velocities can be considered as potential retention areas for fish eggs and larvae. Therefore, we considered particles to be retained when they were less than 27.65 km (the distance covered during 8 days at a velocity of 4 cm s⁻¹) away from their release point. This criterion also preserves particles travelling at speeds

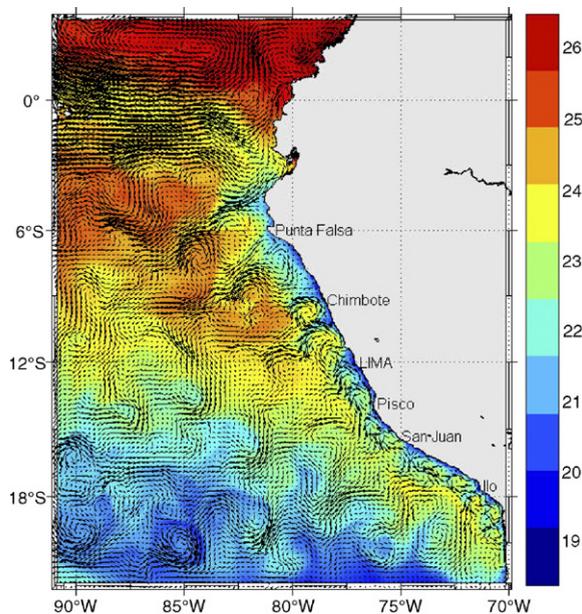


Fig. 1. Sea temperature (°C) and currents at the surface simulated by the hydrodynamic model for day 8 of year Y12.

Table 1
Definition of initial conditions for the five experiments performed

Experiment	Process	Spatial distribution of release		Time of release	
		Horizontal	Vertical (m)	Day	Year
1	Enrichment	Whole domain	100–300	0, 15, 30, ..., 345	Y11–Y14
2	Enrichment	Coastal domain 1	100–300	0, 15, 30, ..., 345	Y11–Y14
3	Retention	Whole domain	0–100	0, 15, 30, ..., 345	Y11–Y14
4	Retention	Coastal domain 2	0–100	0, 15, 30, ..., 345	Y11–Y14
5	Concentration	Coastal domain 2	0–30	0, 15, 30, ..., 345	Y11–Y14

500 000 particles were released in each simulation. The coastal domains used in experiments number 2, 4 and 5 are delimited by the coast, the isobath 1000 m, latitude 4°S and 18°S (domain 1) or 6°S and 14°S (domain 2) on the east, west, north and south boundaries, respectively. Coastal domain 1 corresponds to the area of most intense coastal enrichment as determined in experiment 1 (see Results section). Coastal domain 2 is the zone where most anchovy eggs and larvae were found (see Results section).

higher than 4 cm s^{-1} but being transported back by recirculation features to be counted as retained. Following the criterion used by Lett et al. (in press), particles upwelled to the first 30 m below the sea surface within 60 days of transport were considered as participating to enrichment. As they were released at a depth between 100 m and 300 m and typical upwelling vertical velocity in the region is of the order of 0.1 mm s^{-1} (or 10 m day^{-1}), even particles subjected to lower vertical velocities could be upwelled within 60 days. We did not use any criteria to study the concentration process but only tracked particles through time in order to identify areas where they were more likely to be transported. Table 2 gives a summary characterisation of enrichment, retention and concentration areas, and of the way they are identified in the simulations.

3. Results

3.1. Anchovy eggs and larvae distributions

Though some anchovy eggs and larvae were collected all along the Peruvian coast, they were mainly found between Punta Falsa and Pisco (6°S–14°S) (IMARPE, unpublished data). Within this area, most eggs were found in the northern sector, from 6°S to 9°S (Fig. 2a), and this is even more marked for larvae (Fig. 2b). The majority of eggs and larvae were collected within the 50 m isobath. Size of the sampled larvae was in a range 2–15 mm, with a mode at 4 mm.

3.2. Enrichment

Results generated by experiment 1 (see Table 1 for the definition of initial conditions) showed that three main areas of enrichment are found in the whole domain: one is a large area in the south-western corner of the domain; another one is a smaller zone along the equator; the last

but most intense zone of enrichment is a narrow coastal strip found from 4°S to 18°S (figure not shown). Offshore upwelling was only present during May–October. It was clearly due to upward velocity fields associated with eddies, but the identification of the processes responsible for its location and seasonal pattern requires further investigation. Coastal upwelling was present throughout the year but also showed strong seasonal variability (see below). This experiment revealed that most particles upwelled at the coast had been released close to the coast and essentially within the 1000 m isobath (results not shown).

We used these first results to design a simulation experiment focusing on the main coastal upwelling area, by defining a restricted zone for the release of particles (experiment 2, see Table 1). Fig. 3 shows the number of particles upwelled averaged over simulations repeated every 15 days from year Y11 to Y14. There is a significant number of upwelled particles almost all along the defined coastal domain, but higher values are obtained between Punta Falsa (6°S) and Pisco (14°S) than further north or south.

Table 2

Summary characterisation of enrichment, retention and concentration areas (in brackets is the restricted characterisation used in the context of this work), and of the way they are identified in the simulations

Process	Characterisation	Identification in the simulations
Enrichment	Areas where primary production occurs (here where upwelling occurs)	Counting the number of particles upwelled to the 30 m depth level
Retention	Areas where larvae are trapped (here where they stay in the vicinity of their spawning location)	Comparing the distance travelled by particles to a threshold value
Concentration	Areas where larvae food accumulate	Tracking particles through time

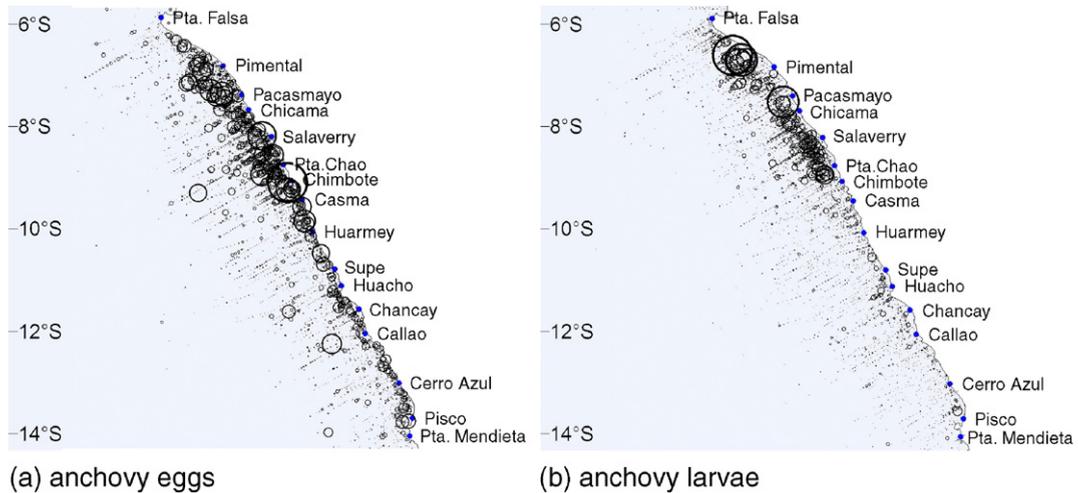


Fig. 2. Composite distribution maps for (a) eggs and (b) larvae of anchovy collected during surveys conducted by the Instituto del Mar del Perú over the period 1970–2003 (IMARPE, unpublished data). The zone shown is a focus on the main anchovy spawning area. Circles radius are proportional to numbers, with the biggest circle corresponding to (a) 74 496 eggs/m² and (b) 29 680 larvae/m².

3.3. Retention

On the map showing the proportion of retained particles averaged over simulations repeated every 15 days from year Y11 to Y14 over the whole domain of the model (experiment 3, Fig. 4a), one can see three main areas of low retention. The first one is a band following the south coast off the 1000 m isobath (label 1 in Fig. 4a). It connects to a second band located approximately at 4°S (label 2). The third area is a band located at the equator (label 3). Along these three bands, less than 10% of the released particles are retained. Low retention in these areas is due to the Peru Coastal Current, the South Equatorial Current and the Equatorial Current flowing at the surface, and to the Peru–Chile Under Current, the South Equatorial Under Current and the Equatorial Under Current that flow already at around 50 m depth (Penven et al., 2005). All these currents flow at velocities of 5 cm s⁻¹ or more (Penven et al., 2005). There are also three principal zones of enhanced retention. One is located in the western part of the domain (label 4 in Fig. 4a). A second one is a band along the southern border of the domain (label 5). These two zones correspond to areas where flow velocities are generally low. Finally, high values of retention are noticed almost all along the coast within the 200 m isobath, where more than 50% of particles are retained in many places. The map displayed in Fig. 4a is the average of 96 individual maps, one of these being displayed in Fig. 4b. The patterns described above for the average map can be detected on most individual maps. But those also reveal a complex pattern of smaller scale structures of high and low retention, particularly in the

southern part of the domain, which correspond well to the mesoscale structures observed in the hydrodynamic simulations. In particular, all the “discs” seen in the south in Fig. 4b, with a small core red area surrounded by blue, are eddies (see Fig. 1). There is high variability in the spatial location of the structures from one individual map to another, but we observed a clear trend for westward displacement with time.

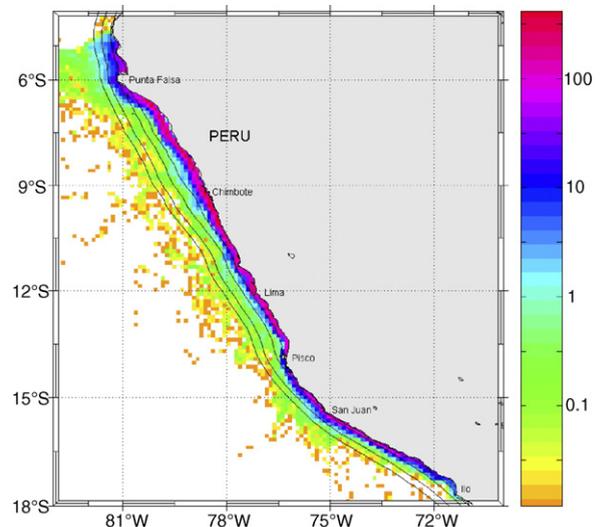


Fig. 3. Enrichment in the coastal domain (results from experiment 2, see Table 1 for the definition of initial conditions). The values shown are the number of particles released at depth 100–300 m that are upwelled within 60 days of transport (i.e., that reach a depth of 30 m), averaged over simulations repeated every 15 days from year Y11 to Y14. The isobaths drawn are 100, 200, 500 and 1000 m. Note the use of a logarithmic colour scale.

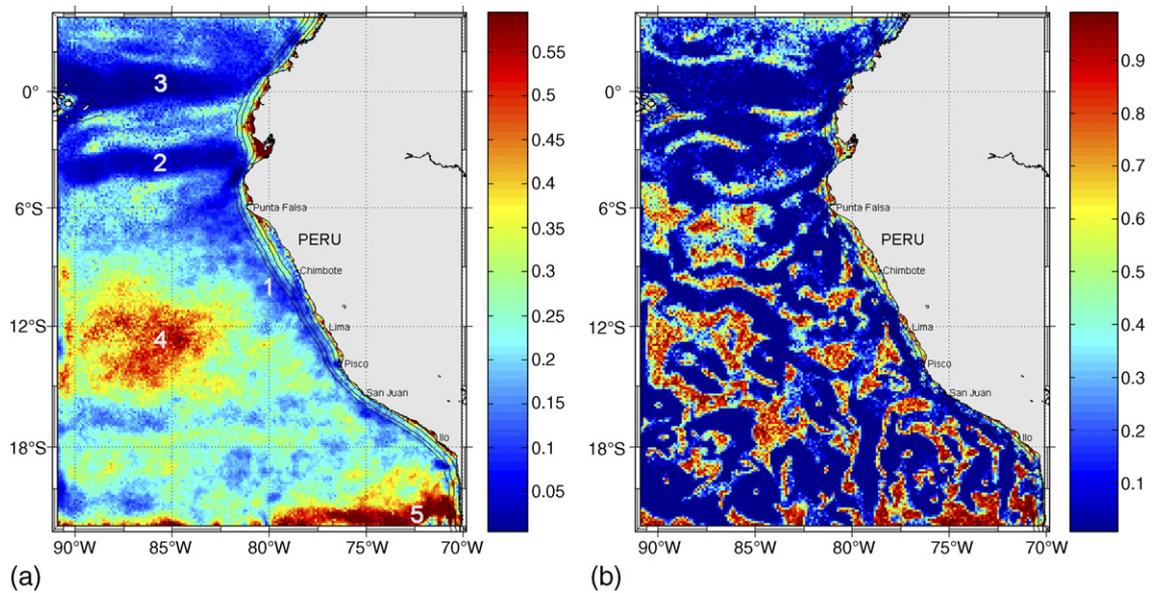


Fig. 4. Retention in the whole domain (results from experiment 3, see Table 1 for the definition of initial conditions). The values shown are the proportion of particles released at depth 0–100 m that are retained after 8 days of transport (i.e., are less than 27.65 km away from their release point), (a) averaged over the 96 simulations starting every 15 days from year Y11 to Y14 (b) for the simulation starting at day 0 of year Y12. Note the different ranges of the colour scales. Labels in figure (a) indicate some of the areas of low (1–3) or high (4–5) retention and are related to comments in the text.

Experiment 4 (see Table 1), focusing on retention within the main spawning area of anchovy between Punta Falsa and Pisco (6°S–14°S), reveals that retention is high north of Chimbote both close to the surface (0–30 m, Fig. 5a) and deeper (not shown). Retention is lower south of Chimbote close to the surface (Fig. 5a),

and there is an area around 10°S where retention is low both close to the surface (Fig. 5a) and deeper (not shown). For increasing durations of transport (and associated longer distances of travel using the threshold velocity of 4 cm s^{-1} as retention criterion), enhanced retention close to the surface switches from the inshore

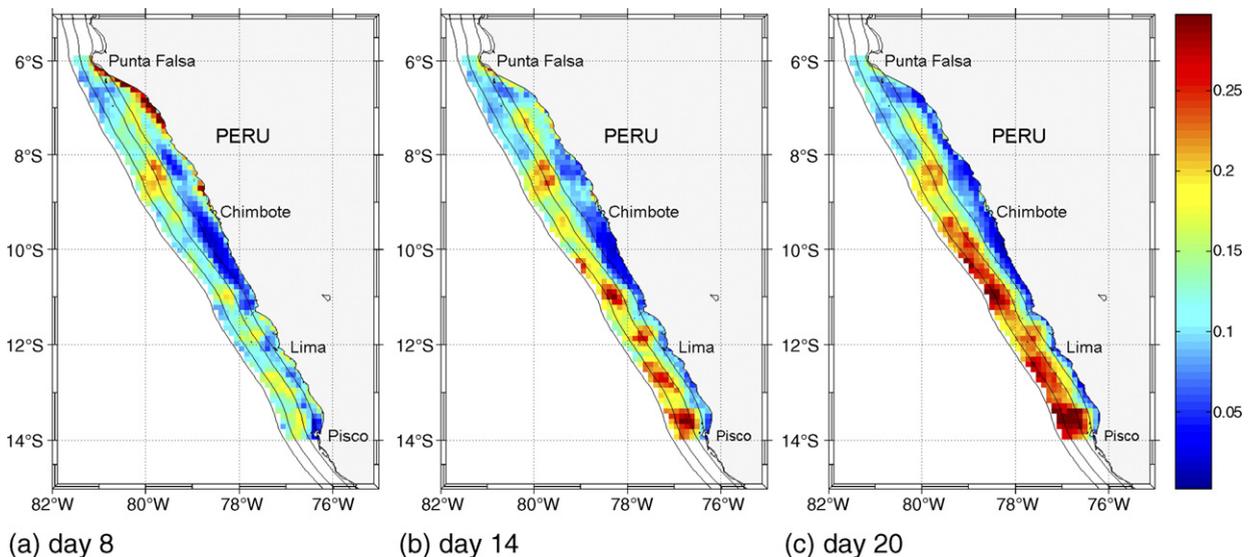


Fig. 5. Retention in the coastal domain (results from experiment 4, see Table 1 for the definition of initial conditions). The values shown are the proportion of particles released at depth 0–30 m that are retained after (a) 8, (b) 14 and (c) 20 days of transport, averaged over simulations repeated every 15 days from year Y11 to Y14.

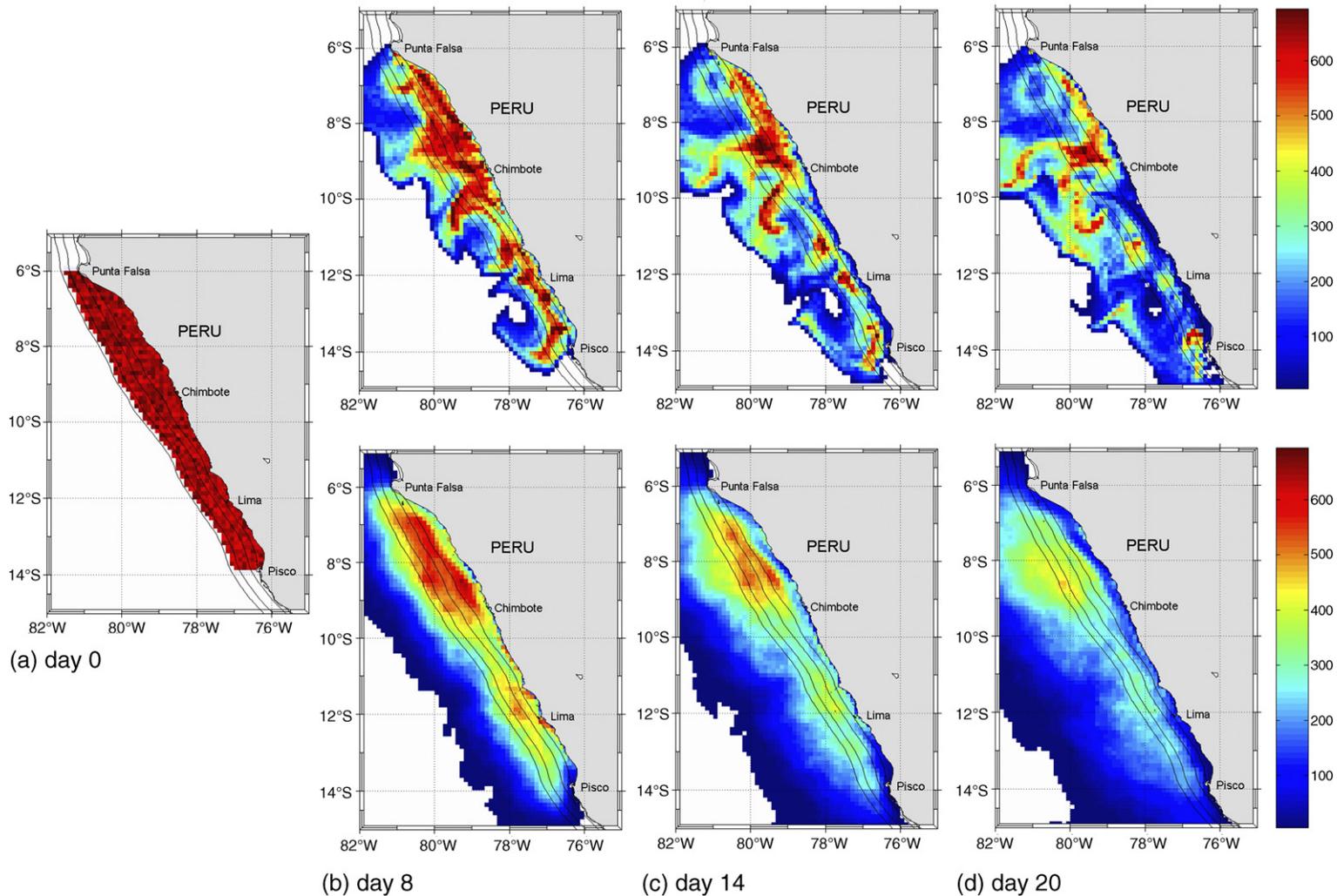


Fig. 6. Concentration in the coastal domain (results from experiment 5, see Table 1 for the definition of initial conditions). The number of particles at a depth between 0 and 30 m is shown (a) initially and after (b) 8, (c) 14 and (d) 20 days of transport for the simulation starting at day 0 of year Y11 (first row) and averaged over the 96 simulations starting every 15 days from year Y11 to Y14 (second row).

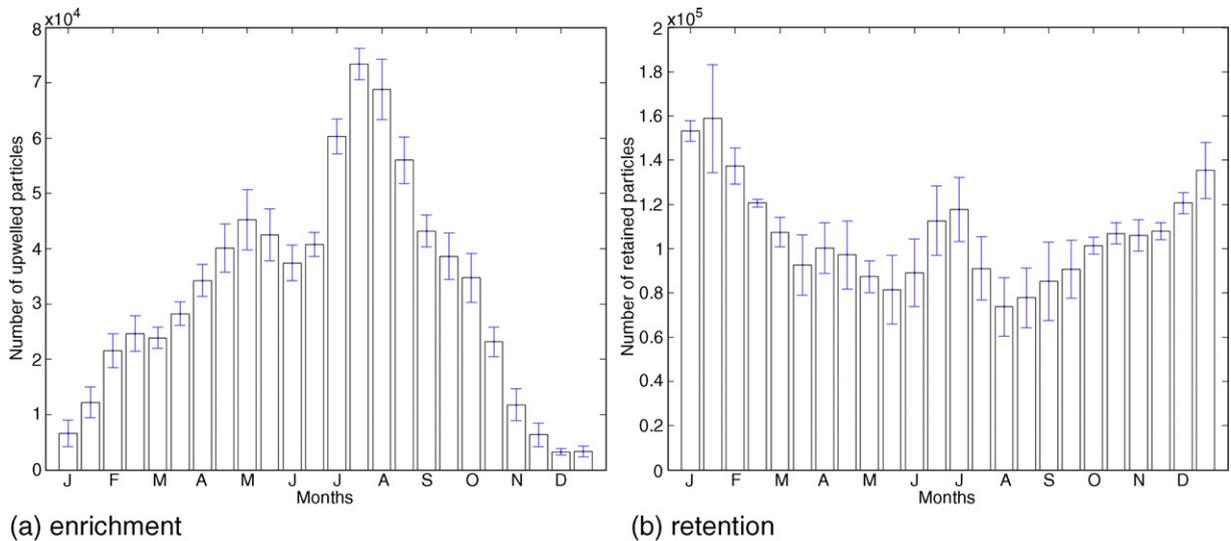


Fig. 7. Seasonal variability in the number of (a) upwelled particles in experiment 2 (b) retained particles in experiment 4. Particles are summed over the domain and over depth 0–100 m for retention. The yearly means and standard deviations are shown.

northern part to the offshore southern part of the coastal domain (Fig. 5).

3.4. Concentration

Particles initially uniformly distributed along the coast tend to be advected offshore. But a large proportion of them are retained in the vicinity of their release point or transported together within mesoscale structures, so that their distribution becomes rapidly heterogeneous (Fig. 6, first row). Nonetheless, it is more correct to consider that these areas of mesoscale activity provide less dispersion than concentration (see the discussion on that topic). These figures are derived from a particular simulation, i.e., for a specific day and year of particles release. When simulations are repeated for other times of release (experiment 5, see Table 1), similar patterns are observed, though areas of retention or of non-dispersion may be located at different places. The analysis of the averaged pattern (Fig. 6, second row) shows that particles tend to “concentrate” in the northern part of the coastal domain.

3.5. Seasonal variability

The number of upwelled particles in the coastal domain displays seasonal variations of more than an order of magnitude ($0.5\text{--}7.5 \times 10^4$, Fig. 7a). The distribution shows a peak in July–August and a trough in November–January. The number of retained particles shows an opposite seasonal pattern (except for a small increase in June–July), and varies only by one fold ($0.8\text{--}1.6 \times 10^5$, Fig. 7b).

4. Discussion

Ekman transport computed from summaries of maritime reports appears to be strongest off Peru in austral winter, July–September, and weakest in summer, December–February (Bakun, 1987). This is in line with results obtained from satellite measurements (Carr and Kearns, 2003). Our simulations are in agreement with these results as the number of upwelled particles was shown to be highest in winter and lowest in summer (Fig. 7a). The order of magnitude of increase in this number is high when compared to results of Bakun (1987), but those of Carr and Kearns (2003) suggest that Ekman transport shows a particularly high seasonal variability from 5°S to 15°S , an area that corresponds well to our coastal domain. In addition, satellite data revealed that Ekman transport off Peru is significantly stronger from 5°S to 15°S than further south (Carr and Kearns, 2003; Thomas et al., 2004). This is consistent with the results we obtained (Fig. 3) where coastal upwelling is maximum between Punta Falsa (6°S) and Pisco (14°S). Primary production appears to be also higher in this area (Thomas et al., 2001; Carr and Kearns, 2003). Historical modelling results suggested that primary production off Peru was also highest in austral winter (Chavez et al., 1989; Mendo et al., 1989), but remote sensing data revealed that it actually peaks in summer (Thomas et al., 2001; Carr and Kearns, 2003; Montecino et al., in press). Our enrichment index peaks in winter, and the 6 month lag between the two peaks is by far too long to reflect the growth of phytoplankton population in response to increased nutrients. This discrepancy between the seasonality of enrichment and primary production in the

northern Humboldt Current system is believed to be caused by maximum upwelling occurring in winter, a season of low solar radiation because of cloud cover (Bakun, 1987; Montecino et al., in press). This was not taken into account in our simulations, which appear to give a satisfactory representation of spatial and seasonal variability of the upwelling process, but not of the seasonal trend of the whole enrichment process. The next step of the present team work will be to couple the hydrodynamic model to a productivity (NPZD) model in order to take into account the effect of solar radiation on productivity.

Anchovy egg production usually displays a bimodal seasonal distribution, with peaks in January–March and August–October (Mendelssohn and Mendo, 1987; Peña et al., 1989; Senocak et al., 1989) despite some interannual variability. Vélez et al. (2005) found a similar seasonal pattern for the density of anchovy larvae sampled through the year 2000 near Pisco. As pointed out by Muck (1989), anchovy may tend to avoid spawning during the months of high variability in temperature. Anchovies recruit at about 3 months (Palomares et al., 1987). The first peak in egg production, which also corresponds to a peak in parent biomass, seems therefore to contribute to the May–August peak generally observed in recruitment (Mendelssohn and Mendo, 1987). The second peak, however, would correspond to a period of low parent biomass and recruitment 3 months later (Mendelssohn and Mendo, 1987). Different hypotheses have been suggested to explain this unexpected situation (that may also partly be due to biased data as anchovies are more dispersed in winter than in summer and therefore less accessible to surveys or fishing, A. Bertrand, IRD, pers. comm.). The reproductive strategy adopted by anchovy for the second peak of reproduction could be to make use of energy stored as fat during austral summer, as suggested by fat content data (Tsukayama, 1989), and utilise it a few months later for gonad production (a similar strategy was observed in Venezuela for *Sardinella aurita*, Fréon et al., 1997). Whether or not the two spawning peaks are related to two genetically different anchovy (sub)populations remains an open question (Mathisen, 1989). Repeated El Niño events may have favoured the selection of a bet-hedging spawning strategy (Slatkin, 1974) rather than spawning only during the normally favourable period (Mendelssohn and Mendo, 1987; Ñiquen and Bouchon, 2004). Buitrón and Perea (2000) showed that anchovy responded to the 1997/98 El Niño event by a delayed spawning season. Our simulation results support the belief that spawning in austral summer provides better conditions than spawning in winter as far as retention is concerned. Compared to the annual mean, the number of retained particles increased (resp. decreased) by around 30% at the time of the first

(resp. second) peak of anchovy spawning (Fig. 7b). The relative amplitude of these variations is similar to that reported by Pauly (1987) for recruitment.

Composite distribution maps for eggs and larvae of anchovy showed higher concentrations between Punta Falsa and Pisco (6°S–14°S). Sampling was also more frequent there than further north or south and this may partly explain this result (A. Bertrand, IRD, pers. comm.). This area has already been identified as being characterized by more intense upwelling, higher nutrient concentrations and higher primary production (see above). Within this area, eggs, and particularly larvae, were mostly found in the north, from 6°S to 9°S (Fig. 2). A reason for this could be that this area provides enhanced retention for eggs and early larvae in the first days after spawning, particularly close to the surface, as suggested by our simulations (Fig. 5a). The northern part was also identified as an area of accumulation (Fig. 6), due to northward surface transport by the Peru Coastal Current. Though there is little information on vertical distribution of eggs and larvae off Peru so far, most anchovy eggs and larvae are believed to be found close to the surface. Mathisen (1989) showed that the depth distribution of anchovy during the spawning season is between 0 and 30 m, this shallow distribution being related to the depth of the minimum oxygen layer. Santander and Sandoval de Castillo (1973) historically reported larger concentrations of eggs around 30 m. IMARPE recently used a multinet for sampling five vertical layers (0–10 m, 10–25 m, 25–50 m, 50–75 m and 75–100 m), and preliminary results indicate larger concentrations of eggs and larvae around 20 m and 50 m, respectively. Due to the relatively small size of the mouth of the plankton net used for sampling and to its small mesh size (which limits the towing speed and induced bow wave favouring stemming), old larvae (>2 cm) are seldom caught. Other sampling gears provide information for fish with a minimum size of 3 cm (pelagic trawl) or 8 cm (purse-seine) of total length. As a result of this sampling gap, the exact location of the nursery area(s) is still unknown.

It can be argued that concentration as it is viewed in this work is not really concentration and, as we stated before, non-dispersion would be a more appropriate word. We still mainly used the word concentration as referring to the triad process that encompasses both non-dispersion and “real” concentration. Concentration is not possible in models with passive particles (Metaxas, 2001). In the real world, concentration occurring at physical barriers, for example, mainly results from density properties (e.g., concentration at sea surface, sea bottom, or pycnocline) or from sensitivity to environmental conditions (e.g., concentration at thermocline or halocline). Concentration

of zooplankton and fish larvae also occurs when animals try to maintain their depth by swimming against upwelling or downwelling (Genin, 2004; Genin et al., 2005). We did not take these processes into account, for the sake of simplicity and because there is little information available on them. We saw that non-dispersion can be due to collective transport within mesoscale structures (Fig. 6). This is believed to be important for spawning (Rodríguez et al., 2004), survival (Logerwell and Smith, 2001), and development of schooling (Hunter and Coyne, 1982).

It remains a challenge to understand the effects of El Niño events on anchovy recruitment. It is generally believed that anchovy larvae, being predominantly phytoplanktonic in their early stages, suffer more from El Niño induced reduction in primary production than sardine larvae, which feed mainly on zooplankton (Muck et al., 1989). Hence, during the three last strong El Niño events (1972/1973, 1982/1983 and 1997/1998) the biomass of anchovy off Peru decreased while that of sardine (*S. sagax*) tended to increase (Ñiquen and Bouchon, 2004). However, the way anchovy recovers after El Niño events is variable and better understood when analysed within an integrated context taking into account the combined effects of physical and biological processes operating at different spatial and temporal scales (Bertrand et al., 2004). The present study could not deal with this topic as the Peru configuration of the hydrodynamic model is currently forced using climatology. When realistic forcing is available we expect to investigate how the regional circulation, and consequently enrichment, concentration and retention, are affected by El Niño or La Niña events.

Using a Lagrangian model to track particles within water velocity fields generated by a hydrodynamic model enabled us to identify areas of enrichment, concentration and retention in the northern Humboldt upwelling system off Peru, and to match them with the observed distribution of anchovy (*E. ringens*) eggs and early larvae. In that way, the reasons of the adaptive spawning strategy of the species can be inferred. A coastal area of enhanced simulated enrichment was identified between Punta Falsa and Pisco (6°S–14°S), which corresponds to the zone where most anchovy eggs and early larvae are found. Why they are found mainly in the northern part of this zone (6°S–9°S) requires further investigation, our simulations suggesting that this sector could provide more retention and concentration. An area around 10°S where retention is particularly low also indicates that eggs and early larvae may be largely transported offshore there. Such correspondences between the ocean triad processes and spawning areas were not clear in a previous study conducted in the southern Benguela upwelling system off South Africa, where there was a spatial discrepancy between the major

spawning area of anchovy (*E. encrasicolus*) and sardine (*S. sagax*) located on the South African south coast and those of larger simulated enrichment and retention values that were on the west coast (Lett et al., in press). This stressed the importance of a transport process that had to be taken into account in South Africa to complement Bakun's fundamental triad. It does not seem to be so in Peru (at least not to the same extent), where it seems relevant to focus on the coastal domain between Punta Falsa and Pisco. A zoom on this domain, using the ROMS_AGRIF version of the ROMS model (Penven, 2003), would provide enhanced spatial resolution of the modelled hydrodynamics and may give new insights on the importance of enrichment, concentration and retention processes in relation to anchovy ichthyoplankton distribution.

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