PANAMJAS
Pan-American Journal of Aquatic Sciences

# Modeling transport and retention of *Engraulis anchoita* Hubbs & Marini, 1935 (Clupeiformes, Engraulidae) early life stages along the Central Southwestern Atlantic Continental Shelf

ANA C. VAZ[1], CAROLINA E. PARADA[2], ELBIO D. PALMA[3], JOSÉ H. MUELBERT[4] & EDMO J. D. CAMPOS[5]

[1]*Dept. of Oceanography, Univ. of Hawaii, 1000 Pope Rd, Honolulu, HI 96822, USA - vaz@hawaii.edu*
[2]*School of Fisheries, Univ. Washington, Seatle, WA 98195, USA*
[3]*Dept. Fisica, Univ. Nacional del Sur, Av. Alem 1253 (8000), B. Blanca, ARG*
[4]*Fundação Univ. Federal do Rio Grande (FURG), Cx. Postal, 474 , Rio Grande, RS, 96201-900, Brazil.*
[5]*Inst. Oceanográfico, Univ. de São Paulo, Praça. do Oceanográfico, 191, São Paulo, SP, 05508-120, Brazil – edmo@io.usp.br*

**Abstract.** Recruitment of pelagic fish is the result of a group of processes that affect their entire life cycle. Most of the variability in pelagic fish natural mortality is thought to occur during the early life stages of development, and to be related to environmental factors. The central Southwestern Atlantic Continental Shelf is one of the most productive fishing sites in the western South Atlantic, but the processes involving the circulation in this area and its influence on eggs and larvae transport and retention are still poorly understood. The use of coupled physical-biological models to investigate fish early life history is relatively common. This work presents results of such a model applied to anchoita (*Engraulis anchoita*). The model is alternatively coupled to two surface velocity fields: the Ekman surface velocities computed from wind stress data, and the output of a three dimensional hydrodynamic numerical model. It is used to compute larval retention over the shelf. The results show that taking into account only Ekman velocities does not explain the seasonal and spatial spawning patterns observed in the region. Retention values with the experiments forced with output of the hydrodynamical model better match the observations. Our results suggest that the density driven circulation, induced by freshwater discharges of the Patos Lagoon and the la Plata River, and intrusions produced by the variability of the boundary currents (Brazil and Malvinas Currents) are efficient mechanisms of larval retention, especially due to the formation of recirculation cells that trap the organisms in coastal areas.

**Keywords:** Anchoita, retention and transport of fish eggs and larvae, individual based model, Southwestern Atlantic Continental Shelf.

**Resumo. Modelagem do transporte e retenção dos estágios iniciais da *Engraulis anchoita* Hubbs & Marini, 1935 (Clupeiformes, Engraulidae) na plataforma continental do Atlântico Sudoeste.** O Recrutamento de peixes pelágicos é o resultado de um grupo de processos que afetam todo o seu ciclo de vida. Assume-se que a maior parte das variações na mortalidade natural de peixes pelágicos ocorre durante os estágios iniciais de seu desenvolvimento e que seja relacionada a fatores ambientais. A parte central da plataforma continental do Atlântico sudoeste é um dos sítios pesqueiros mais produtivos na parte ocidental do Atlântico Sul, mas os processos envolvendo a circulação nessa área e sua influência no transporte de larvas e ovos são ainda muito pouco conhecidos. O uso de modelos físico-biológicos na investigação da história inicial da vida de peixes é relativamente comum. Este trabalho apresenta resultados de um modelo desse tipo aplicado à anchoíta (*Engraulis anchoita*). O modelo é forçado alternativamente por dois campos de velocidade: a velocidade superficial de Ekman, computada de dados da tensão de cisalhamento do vento, e saídas de um modelo numérico hidrodinâmico tri-dimensional. O modelo acoplado é usado para computar a retenção larval sobre a plataforma. Os resultados mostram que somente a velocidade de Ekman não explica os padrões sazonais e espaciais de reprodução observados na região. Valores de retenção obtidos com o modelo forçado com saídas do modelo hidrodinâmico são comparados aos observados. Os resultados sugerem também que a circulação gerada por gradientes de densidade resultantes das descargas de água doce do Rio da Prata e da Lagoa dos Patos, e as intrusões de águas das correntes de contorno oeste (Brasil e Malvinas), são mecanismos eficientes de retenção larval, especialmente devido à formação de células de recirculação que aprisionam os organismos em áreas costeiras.

**Palavras-chave:** Anchoíta, retenção e transporte de ovos e larvas de peixes, modelo baseado no indivíduo, plataforma continental do Atlântico Sudoeste.

## Introduction

The recruitment of pelagic fish is the result of several processes that affect their entire life cycle, although most of the variability in mortality rates occurs during the initial stages of development, probably associated to environmental factors (Bakun 1996, Bailey *et al*. 2005). Recruitment success forecast for fishery stocks based on empirical relationships (Megrey *et al*. 1995) that correlate environmental factors with abundance changes do not show good results, highlighting the complexity of the problem (Bailey *et al*. 2005). The need for improving the knowledge in this area lead to an increased development of more reliable alternatives, capable to explore the intricate ecological processes involved (Bailey *et al*. 2005).

Hydrodynamic and biological models coupling techniques have been applied in several studies of fish early life history (Parada *et al*. 2003, Mullon *et al*. 2002). Usually, in such models, the early life stages of fish are represented by passive particles that confront environmental conditions provided by hydrodynamic models (Huggett *et al*. 2003, Ådlandsvik *et al*. 2004, Sentchev & Korotenko 2004, Lyne & Thresher 1994). Individual-based models (IBMs) coupled to hydrodynamic models represent an alternative to the aforementioned empirical relationships for studying early life history of fish (DeAngelis & Gross 1992, Grimm & Railsback 2005). IBMs treat individuals as unique and discrete entities, with particular attributes such as size and weight that change during their life cycle and according to environmental conditions. These models allow a spatial representation and integration of environmental, biological and ecological data (Grimm 1999, Huggett *et al*. 2003), and constitute useful tools to investigate fish early life history and recruitment variability.

The central southwestern Atlantic Continental Shelf (SWAS) is one of the most important fishing sites in the southwestern Atlantic (Garcia *et al.* 2001), where about 6500 fishermen are temporally or continually in activity (Reis & D'Incao 2000, Haimovici *et al*. 1996). The documented ichthyoplanktonic community in this area is composed by 88 distinct fish species, distributed in 48 families (Sinque & Muelbert 1997). Despite the ecological and economical importance of the SWAS fisheries, the influence of physical mechanisms on eggs and larvae survival in the region is still poorly understood.

The circulation over the area is mainly driven by three factors: wind, freshwater discharges from the Patos Lagoon and from the la Plata River, and the proximity of the Brazil Malvinas Confluence. The Brazil Malvinas Confluence is formed by the convergence of the cold and relatively fresh water of the Malvinas Current (MC) that flows northward and the warm and salty water of the Brazil Current (BC) flowing southward. Usually at 38°S the BC and the MC separate from the coast and turn their flow eastward (Zavialov *et al*. 1998). It is believed that this separation zone presents a latitudinal seasonal variability, and also that during summer the BC might be the major current affecting the circulation over the shelf, while during winter the MC would play this role (Olson *et al*. 1988, Souza & Robinson 2004). The wind driven circulation also shows a seasonal variability, being oriented southwards during spring and summer, and northward during autumn and winter. The flow oriented northward is also strengthened during autumn and winter when the freshwater discharges from the la Plata River and from the Patos Lagoon reach their maximum values (Moller *et al*. 1991, Pereira 1989, Piola *et al*. 2005).

Despite preliminary results obtained in a few studies (Bakun & Parrish 1991, Lima & Castello 1995, Busoli 2001, Soares 2003), the influence of the circulation on the distribution of eggs and larvae in the region is not well understood. Previous studies based on field sampling and conceptual dynamical models suggested that the Ekman transport towards the coast in winter and spring is a mechanism responsible for egg and larval retention close to the shore (Lima & Castello 1995). Baroclinic residual currents produced by freshwater discharges have also been suggested to control ichthyoplankton retention by favoring the accumulation of passive substances such as plankton, eggs and larvae (Busoli 2001, Soares 2003).

This study represents the first attempt to present results of a modeling work taking into account the circulation patterns of the SWAS region and the larval transport of the anchoita *Engraulis anchoita* Hubbs & Marini, 1935 (Clupeiformes, Engraulidae). Anchoita is a small pelagic fish that presents high biomass values over the entire area. It is seldom exploited, but represents a viable commercial alternative for the region, given the decline of demersal fishery. Besides, it is an important component of the regional ecosystem, supplying food source for valuable fish stocks (Bakun & Parrish 1991, Lima & Castello 1995).

The anchoita spawning pattern presents a large seasonal variability over the study area. According to Sanchez & Ciechomski (1995), Castello (1997) and Sinque & Muelbert (1997), during the austral winter, spring and early summer (from July to December), the highest concentrations of spawning adults and of eggs and larvae are observed in the southern Brazilian Shelf and Uruguayan Shelf areas. During the months of October, November and May, high spawning activity is observed along the Northern Argentinean Shelf. Considering the whole area, the highest spawning of anchoita occurs from May to November (Weiss & Souza 1997, Hubold 1982, Lima & Castello 1995, Sanchez & Ciechomski 1995).

The present study involves the development of an IBM for the early life stages of anchoita and its coupling with two different surface velocity fields to simulate transport and retention of eggs and larvae. The first velocity field is generated by the wind driven Ekman surface velocities, and represents an idealized forcing. The second one is the output of a 3D hydrodynamic model that simulates more accurately the local velocity fields. The value of these modeling experiments is to improve understanding about processes underlying favorable conditions for transport and retention of anchoita in the SWAS region, using a series of simulations that include an increased level of complexity on the physical features represented.

## Materials and Methods

*Individual-based model of anchoita early life stages*

The IBM developed for anchoita simulates spawning, hatching, growth and transport of anchoita eggs and larvae, until the larvae reach the postflexion stage (10 mm). Preflexion and flexion anchoita larvae in the region are at highest densities in the mixed layer, especially in the upper 25 meters stratum (Matsuura & Kitahara 1995). In this work, it was assumed that the velocity in the mixed layer was homogeneous and approximately equal to the surface velocity. Therefore, only surface velocity fields were used as inputs to the particle-tracking algorithm embedded in the IBM.

The spawning area of anchoita was defined in the model as the continental shelf area extending from 31°S to 38°S between the 20 and 200 m isobaths. This region was subdivided into four subareas (Fig. 1) as follows: 1) the southern Brazilian Shelf (SBS) from 31°S to 33.5°S, 2) the Uruguayan Shelf (US) from 33.5°S to 35°S, 3) the la Plata River Region (LPR) from 35°S to 36°S and 4) the northern Argentinean Shelf (NAS) from 36°S to 38°S. This division takes into account both oceanographic features and the anchoita spawning behavior, and facilitates the comprehension of the dominant retention mechanisms operating in the different subareas, the origin of the retained larvae and the seasonal variability in the retention processes.

In the IBM simulations, eggs were released randomly within the spawning areas. Hatching depended on sea surface temperature (SST), according to the relation obtained by Ciechomski & Sanchez (1984): $\log Y = 2.449 - 0.042X$, where $Y$ is the age of hatching, in hours, and $X$ is the temperature in degrees Celsius. The SST considered here, characterized by large seasonal variability, was based on the analysis of Piola *et al.* (2000). The resulting hatching times were 1.5 days in summer and spring and 3 days in autumn and winter. The larvae size at hatch time was 2.718 mm, and larval growth was calculated by the following relation (Ekau 1998):

$$Lt = a*\exp(b*[1 - \exp(-c*t)]) \qquad (1)$$

where $a$, $b$, and $c$ are constants (a=2.18, b=3.102, c=0.041), $Lt$ is larval total length (centimeters) at time $t$ (days). The larvae were tracked during the most critical phase of their development, *i.e.*, when they are without motion capability and their movement is only due to the transport by currents. This phase extends until they reach about 10 mm in size. Then they are able to swim on their own, and can keep themselves in appropriate areas for their development, called hereafter nursery areas. In the IBM once larvae reached 10 mm their positions were stored, they were removed from the simulation and a new spawning event occurred.

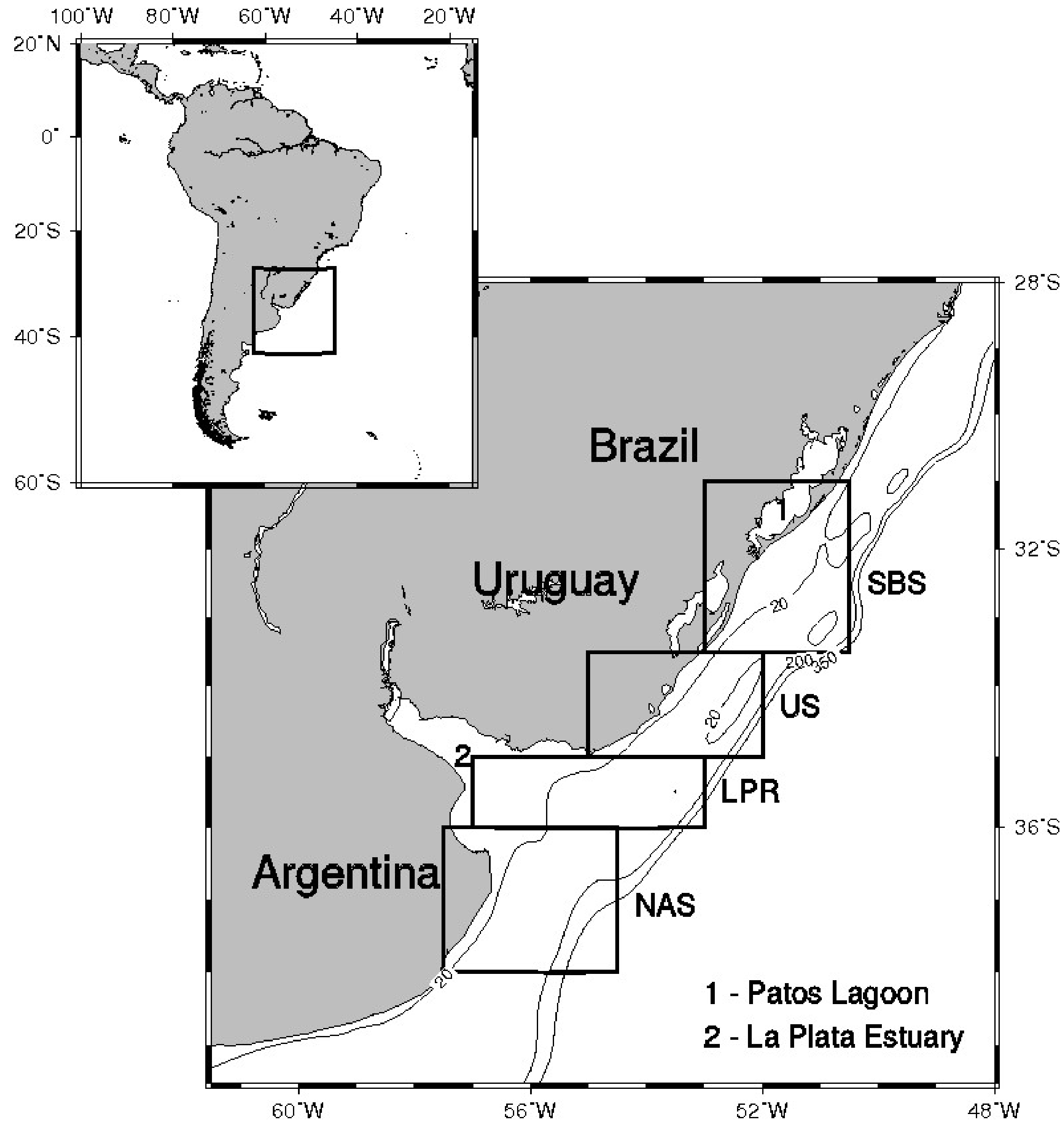


**Figure 1:** The study area comprises the continental shelf between 39°S and 30°S. Squares represent the subareas used in the model: SBS: Southern Brazilian Shelf, US: Uruguayan Shelf, LPR: La Plata River Region, NAS: Northern Argentinean Shelf.

In this study, the nursery area was defined as the surface area contained in the continental shelf between the 20 and 350 meters isobaths and from 31°S to 38°S, with the same latitudinal subdivisions as for the spawning areas. Larvae retention in the model was considered successful when 10 mm larvae were in a nursery area, whether the larvae where released or transported there.

We used a fourth order Runge-Kutta spatial integration scheme for the computation of particle advection (Press *et al.* 1994, Sebastião & Soares 1995). A random walk component was added to the model to account for turbulent movements influencing eggs and larvae displacements (van Dop & Nieuwstadt 1985, Thomson 1986, Dutkiewicz *et al*. 1993). The time step used in the IBM was 12 hours, and both velocity input fields data were available every 3 days.

The number of released eggs in both simulations was much lower than the natural values, as concentrations larger than $10^4$ eggs $m^2$ have been registered *in situ* (Sanchez & Ciechomski 1995). This number was determined by computational constraints, so our results are expressed as proportions that we will use to perform comparisons in the next sections.

*Surface velocity fields used to force the model*

Two sets of surface velocity fields were used to force the IBM: (i) the wind driven Ekman velocities, which represent an idealized forcing, and (ii) the surface layer from a 3D hydrodynamic model that simulates the complexity of the regional velocity fields forced by winds, tides, freshwater discharges and western boundary currents. The objective of the first experiment was to compute the larval drift pattern when the IBM was forced only with the Ekman velocities, in order to assess the importance of the wind driven circulation on larval transport and retention. The turbulence effect on displacement was not considered in this case, because the currents generated only by the wind presented low magnitudes and would have resulted in low turbulence. The Ekman surface velocity was calculated from the classical equations, forced by a mean monthly wind stress field. This field was obtained from the European Center for Medium Range Forecast (ECMWF) and compiled by Trenberth *et al*. (1990), with a resolution of 1/12 degree.

The hydrodynamic model employed was the Princeton Ocean Model (POM). The model was set up on a curvilinear horizontal grid covering a domain from 55°S to 20°S and 70°W to 40°W. This grid had an average resolution of 7.5 Km in the alongshore direction, 10 Km in the cross shore direction and 25 vertical sigma levels. The model, which included a realistic representation of the bottom topography, was initialized with climatological mean values of temperature and salinity and forced with the same ECMWF winds. The inflows and outflows of the Malvinas and Brazil Currents were obtained from the Parallel Ocean Climate Model (POCM4B) (Tokmakian 1996) and prescribed at the model open boundaries. The amplitude and phase of the principal tidal constituents were from the Oregon State University TPXO.5 tidal model (Egbert *et al*. 1994). The model was also forced with the monthly mean river discharges of the la Plata River and the Patos Lagoon. The model was spin up for an initial 3 year period followed by an additional 1 year run for analysis. A more comprehensive description of the experiments conducted with the hydrodynamic model can be found in Palma *et al*. (2004).

## Results & Discussion

*IBM forced with Ekman surface velocities*

The results from the first set of experiments, where IBM is forced with the Ekman surface velocities (Fig. 2) showed that during the whole year the retention values are very high, always near 1, for the four nursery areas considered. During May, June, November and December, slightly lower values are registered.

The high retention values obtained in this experiment are possibly related to two reasons: (1) the Ekman transport that forces the IBM is directed towards the coast during most of the year, and (2) the low magnitude of the surface currents generated based uniquely on the wind stress prevents a quick larval drift towards the open sea, in situations where the currents are directed offshore.

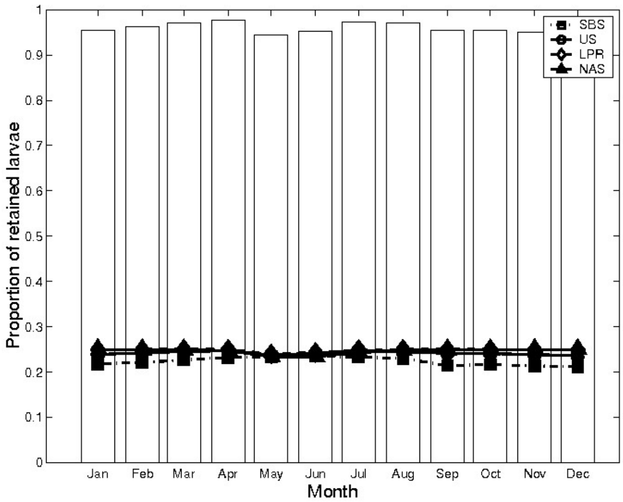


**Figure 2:** Seasonal distribution of the proportion of retained larvae obtained in the IBM forced with Ekman surface velocities. The lines represent the proportion of retained larvae per nursery area (SBS, US, LPR and NAS).

*IBM forced with POM surface output*

The patterns of simulated retention within the entire study area are shown in Figure 3. Retention within specific spawning areas and the transport among them are represented in Figure 4. In Figure 3 the bars represent the proportion of retained larvae over the entire study area per month. The lines indicate the proportion of larvae retained in each retention area (SBS, US, LPR and NAS) per month. In Figure 4, the bars depict the proportion of the total retained larvae per month in the areas SBS (A), US (B), LPR (C) and NAS (D). The lines represent the proportion of larvae retained per spawning area (SBS, US, LPR and NAS). A clear seasonal tendency could be observed in the retention patterns obtained when the IBM was forced with the POM surface output (Fig. 3). The retention values were lowest in the beginning of summer, increasing with the upcoming of autumn, reaching the highest values during this season. In winter the proportion of retained larvae is slightly reduced, but it still high and nearly constant until the coming of spring, when it decreases. A two-fold increase from the smallest to the highest values of retention was obtained, from ~0.35 in December and January to ~0.70 in May and June. The curves in Figures 3 and 4 also show some other intriguing patterns in the simulated data. Larger values of retention occur in winter time (Figs. 3 and 4A). The retention curves present a possible bimodal behavior with peaks around April and August (Figs. 4B, C and D). The transport seems to be northward in May-June (Figs. 4A, B and C) and southward during the summer (Figs. 4C and D). This suggests a possible match/mismatch of the simulated patterns with circulation and spawning patterns, which we are investigating as part of ongoing work.

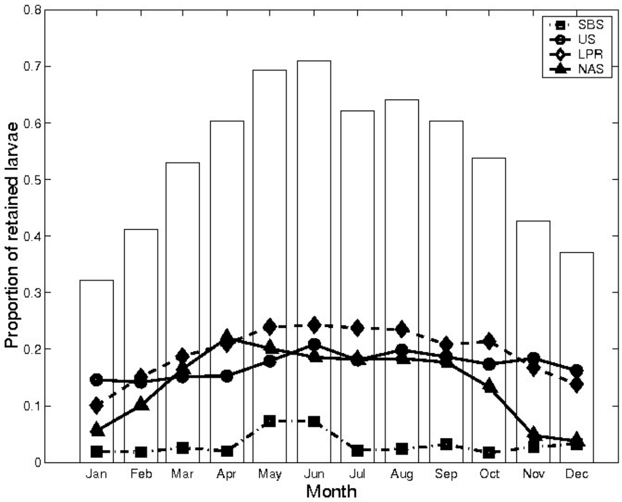


**Figure 3:** Seasonal distribution of the proportion of retained larvae obtained in the IBM forced with the POM hydrodynamic model output. The bars represent the proportion of retained larvae over the entire study area per month. The lines represent the larvae retained percentage per retention area (SBS,US,LPR and NAS) per month.

The influence of the seasonality of the circulation on retention is very clear. As stated in the Introduction, the major forcing factors of the system are the Brazil-Malvinas Confluence, wind and the river discharges. The months of autumn and winter are the ones with the largest amount of larvae in the nursery areas. The peak in larvae concentration coincides with the larger occurrence of winds from the southern quadrant, whose effect is added upon that of the density gradient and the strong influence of the MC, resulting in an intensification of the current towards northeast. This current helps transporting eggs from one nursery area to another one northwards and keeping them near the coast (Figs. 5B and C). During these seasons, the near shore currents in the US area show very low velocities. This helps the formation of an important center for larval retention over this area. The existence of such an area with weak residual currents, and its probable biological importance, have already been reported by Soares (2003). The larvae that hatched in US and LPR are the major beneficiaries of this lower hydrodynamic zone, showing the least dispersion along the year.

Inside the la Plata estuary, the formation of an anticyclonic gyre (Fig. 5C) can be observed especially during the late winter and early spring, foment by the wind system and the larger river discharge. This kind of feature has been reported several times as an important mechanism for larval retention (Bakun *et al.* 1974, Busoli 2001, Bartsch & Coombs 2004) in other systems. Zooplankton distribution studies within the la Plata estuary reported the occurrence of anchoita eggs and larvae (Berasategui *et al.* 2004), which can confirm the importance of the estuarine recirculation cell in larval transport and retention in coastal areas. However, it is important to highlight that although the larvae are retained, it is not possible to assure whether or not they are going to find appropriate conditions to survive in such environment, given that the salinity within the estuary can vary from 0 to 30 psu (Giberto *et al.* 2004).

The months of spring and summer were the ones with the smallest retention values. In January and December, almost 65% of the total larvae were dispersed outside the retention area. During these months, the BC increases its influence on the circulation over the continental shelf. Added to this strong southward flow, there is also the influence of wind blowing from the northeast and generating a southward current along the shore. A large share of the larvae are carried towards the Confluence and/or south of the study area (Figures 5A and D). The lower values of river discharges registered during these months do not favor the generation and propagation of an estuarine plume strong enough to surpass the northeast winds effect on the surface currents.

The NAS and LPR areas (Figures 4B and C) present the highest values of retention during the entire year. Even considering some biases of the modeling experiment that can contribute to this result, such as the location of the LPR on the middle of the study area (thereof receiving larvae from both extremes areas) and the fact that the NAS is the largest of the four areas (and the larger the area, the more likely the particles are to stay within it), we believe that this result is still relevant, especially comparing to the very low retention rates registered for the SBS area.

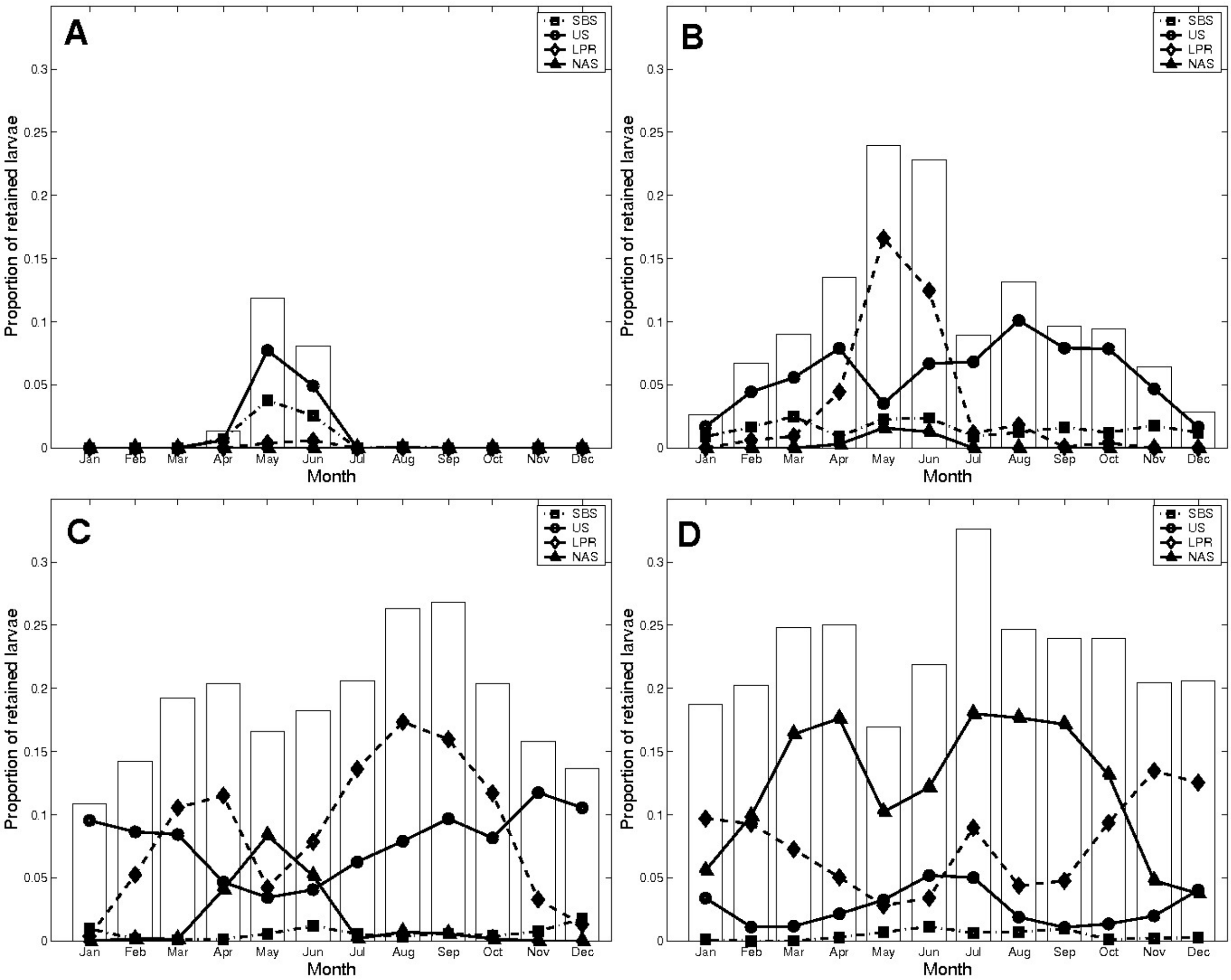


**Figure 4:** Seasonal distribution of the proportion of retained larvae per month, in the areas (A) Southern Brazilian Shelf; (B) Uruguayan Shelf; (C) La Plata River Region e (D) Northern Argentinean Shelf. The lines represents the larvae retained percentage per spawning area (SBS, US, LPR and NAS). Experiment using the POM output.

For each area a different retention mechanism can be highlighted. For the NAS it is a combination of the wind driven circulation and the seasonal changes of the Brazil-Malvinas Confluence. For the LPR area, the high retention registered brings out again the importance of the circulation governed by river discharges in the creation of environments which are favorable to larvae retention, which can be confirmed by the retention observed over the US area. The SBS (Figure 4A) on the other hand presents the lowest retention.

In the experiment forced only with Ekman surface velocity, the lowest retention values are registered in May and June, when the constant passage of frontal systems results in predominantly southerly winds (Moller *et al.* 1991). During these months, the Ekman surface velocities are directed towards the coast in all areas and this could explain the lower retention values, because one of the assumptions adopted in the model states coastal areas with depths below 20 meters were not considered anchoita nursery areas. This assumption is based on the fact that there are no available data of anchoita eggs and larva occurrence in these shallow depths that could clarify their role in the anchoita development. However, as these areas are very productive, it is possible that they could constitute a highly favorable environment for anchoita development. The coastal boundary condition employed by the IBM established that whenever a larva reached the coast (depth equal or above 0 meters) it was eliminated from the simulation. The lowest retention values were registered for the SBS and were related to the surface currents caused by the Ekman drift, which are directed towards the ocean almost all year long. These results are not satisfactory in order to explain the larval transport and retention patterns observed for the anchoita. Ekman surface velocities are not appropriate to represent the hydrodynamic activity of the study area.

The results obtained with the IBM forced with POM output seem to represent better the behavior of anchoita eggs and larvae in their environment. Information of eggs and larvae distribution, both seasonally and geographically, is largely available only for the NAS. For the SBS and US, the available sampling data came from a limited number of surveys (none of these regions was sampled more than twice in a season) and did not cover the entire area. However, in spite of this limitation, the available sampling data could be compared with the IBM results.

With respect to the seasonality, as indicated earlier, Sinque & Muelbert (1997) found that on the SBS and northern US the highest larvae abundance during late spring and summer months, when larvae concentrations reached values of about 200 larvae/m$^{-2}$. During winter and early spring, the concentration was lower, less than 20 larvae/m$^{-2}$. These values are well represented by the IBM (Figs. 4A-B, 5A). During autumn the largest larval retention, both for the sampled and modeled data, occurred in the southern Brazilian and northern Uruguayan areas (Figs. 4A-B, 5B), In winter and spring the presence of larvae was registered over all the continental shelf of US and SBS, which was not observed in the IBM output.

Some differences between model and data were observed. In the SBS area eggs and larvae flux directed northward was identified during the months of October 1987 and September 1988 (Busoli 2001),

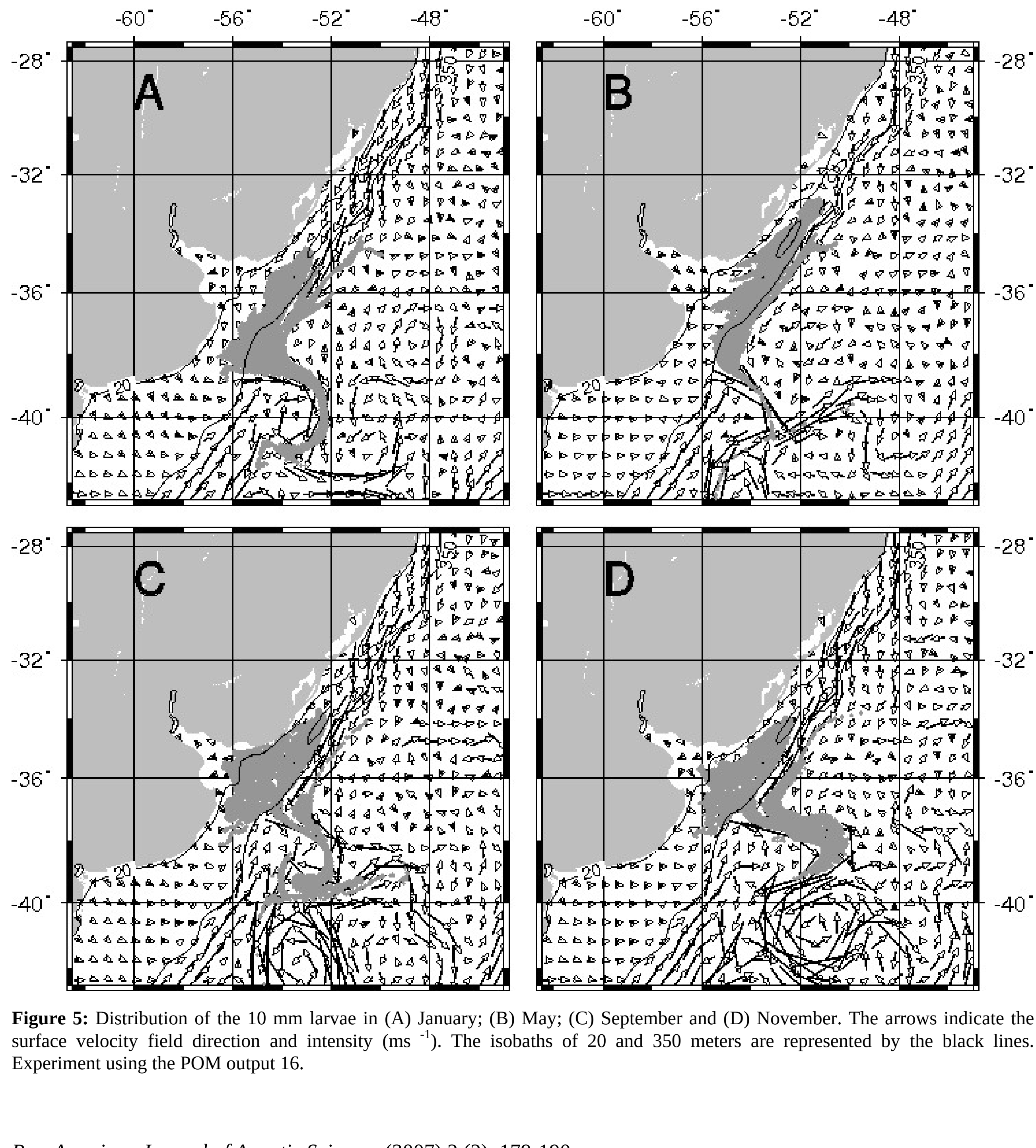


**Figure 5:** Distribution of the 10 mm larvae in (A) January; (B) May; (C) September and (D) November. The arrows indicate the surface velocity field direction and intensity (ms $^{-1}$). The isobaths of 20 and 350 meters are represented by the black lines. Experiment using the POM output 16.

which was not observed in the IBM results. One hypothesis that could explain this difference is that during 1987/1998 years a La Niña event occurred that is related with the strengthen of the southerly winds, and consequently northward currents, over the study region (Piola *et al*. 2005). The IBM was forced with mean seasonal winds and freshwater discharges, and was therefore not able to reproduce this event. On the other hand, the freshwater discharge was pointed out by the author as playing an important role on the larval retention in this region, and this mechanism and its relevance for the successful larval retention was observed in the results.

Sanchez & Ciechomski (1995) assigned that along the northern Argentinean Coast a large amount of eggs and larvae are retained, especially during spring and summer, and that part of the larvae hatched in this region during winter and autumn is advected northwards to complete their development in warmer waters. This situation is well represented by the IBM, as the NAS area does not show a pronounced seasonality in the proportion of retained larvae. However, the results present a seasonality considering the origin of the retained larvae over this area, which does not agree with the conclusions reached by Sanchez & Ciechomski (1995) work. In summer the majority of the larvae registered in the NAS were transported from the LPR, whereas in the rest of the year they were mainly released in the NAS and retained there (Fig. 4D). One reason for these differences could be that larvae in this study are only until they reach a size of 10 mm, and it is likely that bigger larvae look for warmer places to complete their development. High turbulent and cold environment found in this region during the winter could present additional benefits for the larval retention and development, which are not known so far. This leads to the open question that requires future investigation on the area: when and where can the best conditions for the development of anchoita larvae be found?

The most outstanding differences between model results and observation concern the SBS. The main causes for these differences could be that small scale circulation patterns, such as gyres and currents, that are largely present in this area due to the Patos Lagoon discharge, and local and remote wind effect, are not well represented by the hydrodynamic model, due to a too coarse spatial resolution. Also, the observed patterns reflect the seasonal spawning variability of the anchoita, while the IBM investigates the larval retention pattern that occurs due to physical aspects, not taking into account biological aspects concerning the anchoita reproduction and/or environmental pressure effects that may be acting upon the spawning stock.

The highest spawning of anchoita in the Southwestern Atlantic Continental Shelf occurs during autumn, winter and spring (Weiss & Souza 1997, Hubold 1982, Lima & Castello 1995, Sanchez & Ciechomski 1995), which are the seasons when the IBM results exhibited the overall highest retention pattern (Fig. 3). This reflects that the occurrence of circulation favorable for retention plays an important role in the anchoita spawning strategy.

## Conclusion

For a long time, it was believed that the occurrence of favorable conditions for an Ekman transport towards the coast was the main cause for the anchoita spawning patterns in the central southwestern Atlantic Continental Shelf. The effects of the freshwater discharge and of the penetration of subantarctic water on larval retention were considered as less important, acting indirectly on the vertical stabilization of the water column and on the nutrient enrichment (Bakun & Parrish 1991, Lima & Castello 1995). Our results suggest that the wind driven associated Ekman transport alone is not enough to explain patterns of anchovy spawning observed in the study area (Sanchez & Ciechomski 1995, Castello 1997, Sinque & Muelbert 1997). The retention patterns obtained with the IBM using surface velocities from the POM output matched the observed spawning patterns more. Values of retention over the shelf were larger in autumn and in winter than in spring and in summer. An intense larval transport was obtained along the shelf, northwards during autumn and southwards during summer. The present IBM therefore provides an improvement in the knowledge of general dispersion patterns of ichthyoplankton (particularly anchoita) in the study area.

The above results obtained with the POM model output suggest that the importance of continental water discharge and the penetration of cold currents are not confined to the creation of a stratified environment, or with an increase in the availability of food supply. The baroclinic circulation induced by the la Plata River and by the Patos Lagoon discharges is an efficient mechanism for organism retention, acting by the formation of recirculation cells and by weak currents near the estuarine mouth. This study also provides new information on the role that the Brazil Malvinas Confluence may play in the success of anchoita larval retention in the area. The model results show that seasonal circulation patterns induced by the boundary currents modify the eggs and larvae retention. They also suggest that the circulation patterns which favor the eggs and larvae retention play an important role in the anchoita spawning strategy. However, future studies should help understanding further the factors influencing anchoita early life history, including other relevant processes than those investigated here, such as food availability, predation, occurrence of suitable temperature and salinity levels, among others.

## Acknowledgments

This research is part of Project LAPLATA, supported by FAPESP (grant 2004/01950-3), by the Inter-American Institute for Global Change Research (IAI), through project SACC (CRN-061), and by the NICOP Program of the U.S. Offce of Naval Research (Grant N00014-02-1-0295). The first author was supported by a scholarship from the Conselho Nacional de Desenvolvimento Científico e Tecnológico-CNPq (Brazil). The last version of the manuscript was greatly enhanced by the most constructive comments and suggestions from the anonymous reviewers.

## References

Ådlandsvik, B., Gundersen, A. C., Nedreaas, J. K. H., Stene, A. & Albert, O. T. 2004. Modeling the advection and diffusion of eggs and larvae of Greenland halibut (*Reinhardtius hippoglossoides*) in the north-east Arctic. **Fisheries Oceanography**, 13: 403-415.

Bailey, K. M., Ciannelli, L., Bond, N. A., Belgrano, A. & Stenseth, N. Chr. 2005. Recruitment of walleye pollock in a physically and biologically complex ecosystem: A new perspective. **Progress in Oceanography**, 67(12): 24-42.

Bakun, A., McLain, D. R. & Mayo, F. 1974. The mean annual cycle of coastal upwelling off western North America as observed form surface measurements. **Fisheries Bulletin U.S.**, 72: 843-844.

Bakun, A. & Parrish, R. H., 1991. Comparative studies of coastal pelagic fish reproductive habitats: the anchovy (*Engraulis anchoita*) of the southwestern Atlantic. **ICES Journal of Marine Science**, 48: 343-361.

Bakun, A. 1996. **Patterns in the Ocean. Ocean Processes and marine population dynamics**. La Paz, California Sea Grant College System, National Oceanic and Atmospheric Administration in cooperation with Centro de Investigaciones Biologicas del Noroeste. 323 p.

Bartsch, J. & Coombs, S. H. 2004. An individual-based model of the early life history of mackerel (*Scomber scombrus*) in the eastern North Atlantic, simulating transport, growth and mortality. **Fisheries Oceanography**, 13(6): 365-379.

Berasategui, A. D., Acha, E. M. & Fernandez Araoz, N. C. 2004. Spatial patterns of ichthyoplankton assemblages in the Rio de la Plata Estuary (Argentina - Uruguay). **Estuarine, Coastal and Shelf Science**, 60: 599-610.

Busoli, R. O. 2001. Transporte e retenção de ovos e larvas de *Engraulis anchoita* na plataforma continental sul do Brasil. **MSc. Thesis**, Fundação Universidade Federal do Rio Grande, Rio Grande, Brazil. 100 p.

Castello, J. P. 1997. A anchoita (*Engraulis anchoita*, Engraulididae, Pisces) no Sul do Brasil. **PhD. Thesis**, Fundação Universidade Federal de Rio Grande, Brazil, 80 p

Ciechomski, J. D. & Sanchez, R. P. 1984. Field estimates of embryonic mortality of Southwest Atlantic anchovy *Engraulis anchoita*. **Meeresforshung**, 30(3): 172-187.

De Angelis, D. L. & Gross, L. J. 1992. **Individual-based models and approaches in ecology: populations, communities and ecosystems**. Chapman and Hall, New York, NY. 552 p.

Dutkiewicz, S., Griffa, A. & Olson, D. B. 1993. Particle diffusion in a meandering jet. **Journal of Geophysical Research**, 98(C9): 16487-16500.

Egbert, G. D., Bennett, A. F., & Foreman, M. G. G. 1994. TOPEX/POSEIDON tides estimated using a global inverse model. **Journal of Geophysical Research**, 99(C12): 24,821-24,852.

Ekau, W. 1998. Comparative growth analysis of *Engraulis anchoita* from southern Brazil. **Archive of Fishery and Marine Research**, 46(1): 117.

Garcia, A. M., Vieira, J. P. & Winemiller, K. O. 2001. Dynamics of the shallow-water fish assemblage of the Patos Lagoon estuary (Brazil) during cold and warm ENSO episodes. **Journal of Fish Biology,** 59(5): 1218-1238.

Giberto, D. A., Bremec, C. S., Acha, E. M. & Mianzan, H. 2004. Large-scale spatial patterns of benthic assemblages in the SW Atlantic: the Rio de la Plata estuary and adjacent shelf waters. **Estuarine and Shelf Science**, 61: 1-13.

Grimm, V. 1999. Ten years of individual-based modeling in ecology: what have we learned and what could we learn in the future? **Ecological Modeling**, 115: 129-148.

Grimm, V. & Railsback, S. F. 2005. **Individual-based modeling and ecology**. Princeton, Princeton University Press. 480 p.

Haimovici, M., Castello, J. P. & Vooren, C. M. 1997. Fisheries, pp. 183-196. *In*: Seeliger, U., Odebrecht, C. & Castello, J. P. (Eds.). **Subtropical convergence environments: the coast and sea in the southwestern Atlantic**. Springer Verlag, Berlin, 308 p.

Hubold, G. 1982. Fish spawning in the Southwest Atlantic in austral winter/spring 1977 and autumn 1978. **Atlântica**, 5(2): 59.

Huggett, J., Fréon, P., Mullon, C. & Penven, P. 2003. Modeling the transport success of anchovy *Engraulis encrasicolus* eggs and larvae in the southern Benguela: the effect of spatio-temporal spawning patterns. **Marine Ecology Progress Series**, 250: 247-262.

Letcher, B. H., Rice, J. A., Crowder, L. B. & Rose, K. A. 1996. Variability in survival of larval fish: disentangling components with a generalized individual based model. **Canadian Journal of Fisheries and Aquatic Sciences**, 53: 787-801.

Lima, I. & Castello, J. P. 1995. Distribution and abundance of Southwest Atlantic anchovy spawners (*Engraulis anchoita*) in relation to oceanographic processes on the southern Brazilian shelf. **Fish Oceanography**, 4(1): 1-16.

Lyne, D. V. & Thresher, R. E. 1994. Dispersal and advection of *Macruronus novaezealandiae* (Gadiformes: Merlucciidae) larvae off Tasmania: Simulations of the effects of physical forcing on larval distribution. Pp. 109-136. *In*: Sammarco, P. W. & M. L. Heron (Eds.). **The Biophysics of marine larval dispersal. American Geophysical Union**. Washington, American Geophysical Union. 352 p.

Matsuura, Y. & Kitahara, E. M. 1995. Horizontal and vertical distribution of anchovy (*Engraulis anchoita*) eggs and larvae off Cape Santa Marta Grande in southern Brazil. **Archive of Fishery and Marine Research**, 42(3): 239-250.

Megrey, B. A., Bograd, S. J., Rugen, W. C., Hollowed, A. B., Stabeno, P. J., Macklin, S. A., Shumacher, J. D. & Ingraham, W. J. 1995. An exploratory analysis of associations between biotic and abiotic factors and year class strength of Gulf of Alaska walleye pollock (*Theragra chalcogramma*). pp. 227-243. *In*: Beamish, R. J. (Ed.). **Climate change and northern fish populations**. Canadian Special Publication of Fisheries and Aquatic Sciences no. 121. 768 p.

Moller, O. O., Paim, P. S. G. & Soares, I. D. 1991. Effects and mechanisms of water circulation in the Patos Lagoon Estuary. **Bulletin Institute Géologique**, 49: 15-21.

Mullon, C., Cury, P. & Penven, P. 2002. Evolutionary individual-based model for the recruitment of anchovy (*Engraulis capensis*) in the southern Benguela. **Canadian Journal of Fisheries and Aquatic Sciences**, 59: 910-922

Olson, D. B., Podesta, G. P., Evans, R. H. & Brown, O. B. 1988. Temporal variations in the separation of Brazil and Malvinas Currents. **Deep Sea Research**, 35: 1971-1990.

Palma, E. D., Matano, R. P. & Piola, A., 2004. A comparison of the circulation patterns over the Southwestern Atlantic Shelf driven by different wind stress climatologies. **Geophysical Research Letters**, 31(24): L24202

Parada, C., Van Der Lingen, C. D., Mullon, C. & Penven, P. 2003. Modeling the effect of buoyancy on the transport of anchovy (*Engraulis capensis*) eggs from spawning to nursery grounds in the southern Benguela: an IBM approach. **Fisheries Oceanography**, 12(3): 170-184.

Pereira, C. S. 1989. Seasonal variability in the coastal circulation on the Brazilian continental shelf (29S 35S). **Continental Shelf Research**, 9(3): 285-299.

Piola, A. R., Campos, E. J. D., Moller Jr., O. O., Charo, M. & Martinez, C. 2000. The subtropical shelf front off eastern South America. **Journal of Geophysical Research**, 105 (C3) 6566-6578.

Piola, A. R., Matano, R. P., Palma, E. D., Möller Jr., O. O. & Campos, E. J. D. 2005. The influence of the Plata River discharge on the western South Atlantic shelf. **Geophysical Research Letters**, 32: L01603.

Press, W. H., Vetterling, W. T., Teukolsky, S. A. & Flannery, B. P. 1994. **Numerical recipes in Fortran. The art of scientific computing**. Cambridge, Cambridge University Press. 722 p.

Reis, E. G. & D'Incao, F. 2000. The present status of artisanal fisheries of extreme Southern Brazil: an effort towards community-based management. **Ocean and Coastal Management**, 43: 585-595.

Sanchez, R. P & Ciechomski, J. D. 1995. Spawning and nursery grounds of pelagic fish species in the sea-shelf off Argentina and adjacent areas. **Scientia Marina**, 59(34): 455-478.

Sebastiao, P. & Soares, C. G. 1995. Modeling the fate of oil spills at sea. **Spill Science & Technology Bulletin**, 2: 121-131.

Sentchev, A. & Korotenko, K. 2004. Stratification and tidal current effects on larval transport in the eastern English Channel: Observations and 3D modeling. **Environmental Fluid Mechanics**, 4: 305-331.

Sinque, C. & Muelbert, J. H. 1997. Ichthyoplankton. Pp. 120-123. *In*: Seeliger, U., Odebrecht, C. & Castello, J. P. (Eds.). **Subtropical convergence environments: the coast and sea in the southwestern Atlantic**. Springer Verlag, Berlin, 308 p.

Soares, I. D. 2003. The southern Brazilian shelf buouancy driven currents. **PhD. Thesis**. University of Miami, Miami, USA, 100 p.

Souza, R. B. & Robinson, I. S. 2004. Lagrangian and satellite observations of the Brazilian Coastal Current. **Continental Shelf Research**, 24:241-262.

Thomson, D. J. 1986. A random walk model of dispersion in turbulent flows and its application to dispersion in a valley. **Quarterly journal of the Royal Meteorological Society**, 112: 511-530.

Trenberth, K. E., Large, W. G. & Olson, J. G. 1990. The mean annual cycle in global wind stress. **Journal of Physical Oceanography**, 20: 1742-1760.

Tokmakian, R. 1996. Comparisons of Time Series from Two Global Models with Tide-Gauge Data. **Geophysical Research Letters**, 23: 3759-3762.

van Dop, H. & Nieuwstadt, F. T. M. 1985. Random walk models for particle displacements in inhomogeneous unsteady turbulent flows. **Physics of Fluids**, 28(6): 1639-1653.

Weiss, G. & Souza, J. A. F. 1977. Desova invernal de *Engraulis anchoita* na costa sul do Brasil em 1970 e 1976. **Atlântica**, 2(2): 5-24.

Zavialov, P. O., Ghisolfi, R. D. & Garcia, C. A. E. 1998. An inverse model for seasonal circulation over the southern Brazilian shelf: near surface velocity from the heat budget. **Journal of Geophysical Research**, 28: 545-562.

Received July 2007
Accepted August 2007
Published online October 2007