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CEPHALOPOD BIOLOGY AND EVOLUTION

The São Paulo shelf (SE Brazil) as a nursery ground for *Doryteuthis plei* (Blainville, 1823) (Cephalopoda, Loliginidae) paralarvae: a Lagrangian particle-tracking Individual-Based Model approach

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Abstract The São Paulo shelf ranges from ~23°S to 25°S, comprising nearly 622 km of shoreline. This region sustains historical landings of the tropical arrow squid *Doryteuthis plei*. As in other coleoid cephalopods, the broodstock dies following spawning and the continuance of the population relies exclusively upon the survival of the paralarvae, which are very sensitive to oceanographic conditions. As a first step towards the understanding of paralarval transport, the shelf area was evaluated in terms of retention/dispersion potential. A Lagrangian particle-tracking Individual-Based Model was set up using a 3D Princeton Ocean Model model forced with in situ data obtained from July 2009 to July 2011. Neutrally buoyant particles were released every first day of every month in the model, and tracked for 30 days. The retention potential was high for particles released from the bottom all over the study area from the coast to the shelf break (200 m isobath). Offshore losses showed a marked seasonality. Regarding inshore losses, the percentage of particles beached was constant year round and smaller than offshore losses, being higher south of 24°S. Simulation results seem to agree with present knowledge of the reproductive behaviour of the species in the region.

Keywords Larval dispersal · Squid · Hydrodynamics · Modelling · SW Atlantic · Retention

Introduction

The tropical arrow squid *Doryteuthis* (formerly *Loligo*) *plei* (Blainville, 1823) is regarded as an important component of the marine trophic web off southern Brazil (Gasalla et al., 2010). In addition, the species sustain an important trawl fishery industry on the inner shelf and a seasonal artisanal fishery (using a number of fishing practices, including beach seining, bottom trawling, lift-netting, hand-jigging and fish-trapping) close inshore, mostly around coastal islands, between Rio de Janeiro and Santa Catarina States (Costa & Haimovici, 1990; Perez, 2002; Gasalla, 2004; Martins & Perez, 2007). Records of commercial exploitation

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of *D. plei* off the São Paulo coast dates back to the late 1950s, and landings have increased two orders of magnitude between 1959 and 1999 (Gasalla et al., 2005). Artisanal catches attain high economic and social importance during summer months on the northern São Paulo coast, where fishers catch squid mostly by hand-jigging around coastal islands (Gasalla, 2004; Postuma & Gasalla, 2010). Whereas the biology and ecology of adult squid is relatively well studied off southern Brazil (e.g. Perez et al., 2002; Martins et al., 2006; Martins & Perez, 2007; Rodrigues & Gasalla, 2008; Gasalla et al., 2010; Postuma & Gasalla, 2010), there is little knowledge on their planktonic early life stages (i.e. paralarvae; Young & Harman, 1988) in the region (Martins & Perez, 2006).

Because of the typically short life span (≤1 year) of loliginid squid, the recruitment is dependent exclusively on the survival of paralarvae (Agnew et al., 2000), which in turn is influenced by food availability, the physical environment and predation (Martins, 2009). This squid early life history–environment link is usually quite obvious and reflected directly in the fishery yields, as good or poor annual catches often follow years of good and bad environmental conditions, respectively (Vidal et al., 2002; Roberts, 2005; Roberts & Mullon, 2010). In other words, recruitment success or failure echoes the environmental conditions experienced by the paralarvae. As a result, both physical (temperature) and biological (paralarval abundance) environmental variables have been found to be reliable proxies for forecasting the recruitment (Sakurai et al., 2000; Agnew et al., 2002; Roberts, 2005; Zeidberg et al., 2006). Importantly, larval transport has been identified to be an essential ingredient for the recruitment, as current patterns can transport and retain the offspring in suitable or unsuitable environments for their post-hatching survival, growth and development (Martins, 2009).

In recent years, computer-based biophysical modelling techniques have been developed and applied to a number of fish and invertebrate species to clarify larval transport mechanisms in open ocean, shelf and inshore ecosystems (Cowen et al., 2006; North et al., 2008; Kitagawa et al., 2010; Watson et al., 2010). Among these, coupling of Lagrangian particle-tracking Individual-Based Models (IBMs) and 3D hydrodynamic models have been used to model the transport of small pelagic fish eggs and larvae, and squid paralarvae (e.g. Mullon et al., 2003; Huggett et al., 2003; Miller et al., 2006; Parada et al., 2008; Roberts & Mullon, 2010; Huret et al., 2010; Martins et al., 2010a). In areas where fine-scale information on circulation patterns and larval distribution/abundance is poor, the biophysical modelling approach can be used as a useful tool to investigate potential larval dispersal patterns (Roberts & Mullon, 2010) and therefore delineate hypotheses that can be surveyed in the field (Lett et al., 2010). In addition, this approach also allows for the identification of potential nursery and spawning grounds (Martins, 2009).

Thus, the objective of the present study was to evaluate the role of the São Paulo shelf (henceforth referred to as SP shelf) as a nursery ground for *D. plei* paralarvae using a coupled Lagrangian particle-tracking IBM–3D Princeton Ocean Model (POM) hydrodynamic model on the basis of retention/dispersal patterns identified according to the model. The outputs are discussed under the light of regional patterns of circulation and productivity and the potential of population connectivity through larval drift.

Methods

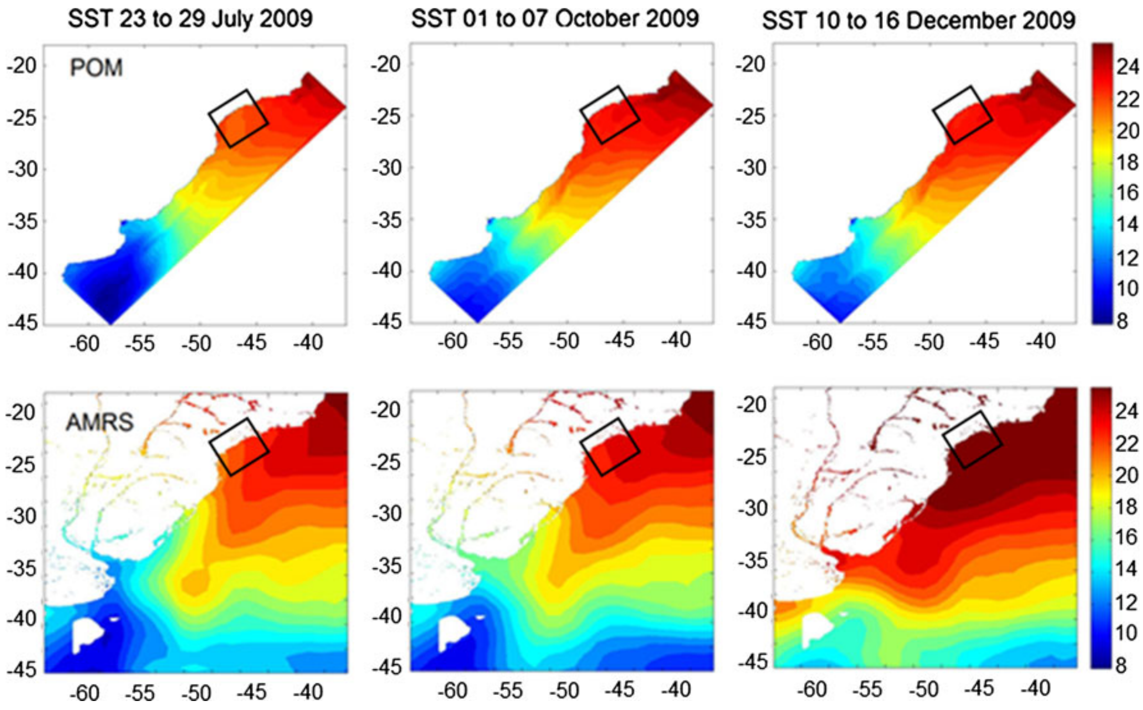
Hydrodynamic model

Due to the availability and appropriated spatial and temporal coverage, we used an implementation of the POM (Mellor, 1998) to obtain the hydrodynamic fields for the dispersal simulations. The model code is in the public domain, and the version used in the present study was also employed by Camargo & Harari (2003) and Harari & Camargo (2003) for estuarine areas. POM is a primitive equation hydrodynamic model based on Boussinesq assumption and hydrostatic approximation, with three-dimensional, non-linear equations written in flux form. A second-order turbulent closure scheme is used to compute the coefficients of vertical viscosity and diffusion, with equations for the turbulent kinetic energy and the length scale of turbulence. The horizontal viscosity and diffusion are parameterised using the Smagorinsky scheme. The grid (Fig. 1) has a resolution of 1/12 (∼8 km on the horizontal dimension) with 22 sigma levels (bottom following) and covers the area between 22°S and 42°S, encompassing 102 × 357 grid points. The grid is rotated ∼45° clockwise relative to N–S direction to follow the orientation of the coast in the region. The model runs from July 2009 to July 2011, resulting in nearly 2 years of simulations, and was forced with in situ wind data obtained from the Global Forecast System (GFS) 1° × 1° analysis available four times daily. A comparison between weekly averaged, model-generated sea surface temperature (SST) and in situ satellite-measured SST data showed a good agreement, indicating that the model reasonably reproduced the behaviour of the ocean (Fig. 1).

Lagrangian experiments

Very little data is available on the distribution of *D. plei* paralarvae off southern Brazil. The little information available accounts for their nearshore occurrence around Santa Catarina Island (Martins & Perez, 2006) as well as on the continental shelf between São Paulo and Rio de Janeiro (Araújo et al., 2011; Araújo, 2013). Published data on their abundance, vertical distribution, buoyancy, swimming ability, resistance to starvation, feeding behaviour, lethal temperature and growth is still not available. Because of this, it would be extremely difficult (and certainly unrealistic) to portray *D. plei* paralarvae in the IBM. Hence, as a first step towards investigating the role of regional circulation in the larval transport, the model was set up as a Lagrangian particle-tracking IBM with the main focus on investigating the potential dispersal and retention of paralarvae within the study area according to the modelled regional circulation.

A Lagrangian particle-tracking IBM tool (*Ichthyop*, version 3.0b) was used to track neutrally buoyant particles released near the bottom all over the SP shelf (Fig. 2). Because this IBM tool was not originally developed to work with POM outputs, the latter was modified to emulate original ROMS outputs which *Ichthyop* can deal with. The modification code was written using Matlab by the second author. Overall, 10,000 particles ("virtual paralarvae") were released every first day of every month during the hydrodynamic model time duration (2 years) and tracked for 30 days. All those particles that crossed the 200 m depth contour (shelf break) at an age of 20 days were considered lost from the ecosystem, because survival of paralarvae depends on their remaining on the productive shelf ecosystem, particularly during the critical period (the so-called "no net growth phase", Vidal et al., 2005), when paralarvae are extremely


SST 23 to 29 July 2009

SST 01 to 07 October 2009

SST 10 to 16 December 2009

Fig. 1 POM domain with a comparison between average modelled SST (*upper panel*) and in situ satellite-measured SST data (*lower panel*) for three different periods. The study area is *boxed* susceptible to starvation. The SP shelf was further divided into two broad release subareas by a perpendicular transect off Santos (24°S), from the coast to the shelf break (200 m), in order to access latitudinal differences in dispersal/retention patterns (Fig. 2). The number of particles released in each subarea was proportional to their surface area.

The 20 days "deadline" was initially chosen because it was assumed to be the end of the planktonic stage of *D. plei* paralarvae. The species inhabits an environment considerably warmer than other loliginid species (e.g. the California market squid *D. opalescens,* the planktonic stage of which lasts ~40 days in colder waters; Yang et al., 1986). Thus, it is expected that the onset of independence of water currents by *D. plei* paralarvae would occur considerably sooner due to their faster growth, since the Pelagic Larval Duration (PLD) tends to be shorter in higher water temperatures (Moreno et al., 2012).

The same experiment protocol was applied for inshore losses, and this was estimated from the number of particles that hit the coastline ("beached" particles). Other criteria analysed included inter-area exchange (i.e. how many particles were retained in each subarea and exchanged between the two areas) and losses to the northern and southern boundaries of the study area. In all cases, the percentage of lost particles in accordance with each of the four criteria was examined by year, months and subareas to access the retention conditions on the SP shelf. In addition, the losses to the north and south of the study area were also quantified. A flow chart depicting the three stages of the modelling process for the Lagrangian transport experiment is shown in Fig. 3.

A Chi-squared (χ^2) test to examine whether apparent peaks of lost particles relative to areas, seasons and years were statistically significant ($P < 0.05$) was performed for each one of the four criteria chosen following Miller et al. (2006). In short, the results obtained were compared to a uniform distribution (equal to the mean rate of percentage of particle losses). If a significant departure was found, then an a posteriori test was applied to identify which variable (month or year) was causing the differences. The "noisy" variable was removed and the test was repeated. If the result of the test was then found to be non-significant, it was assumed that the removed variable was responsible for the departure found. A simple 2×2 Chi-squared test was employed in the case of release areas.

Results

General patterns of offshore and inshore losses

Overall, the losses to the open sea (particles crossing the 200 m isobath—offshore losses) and to the coast (beached—inshore losses) were found to be very low

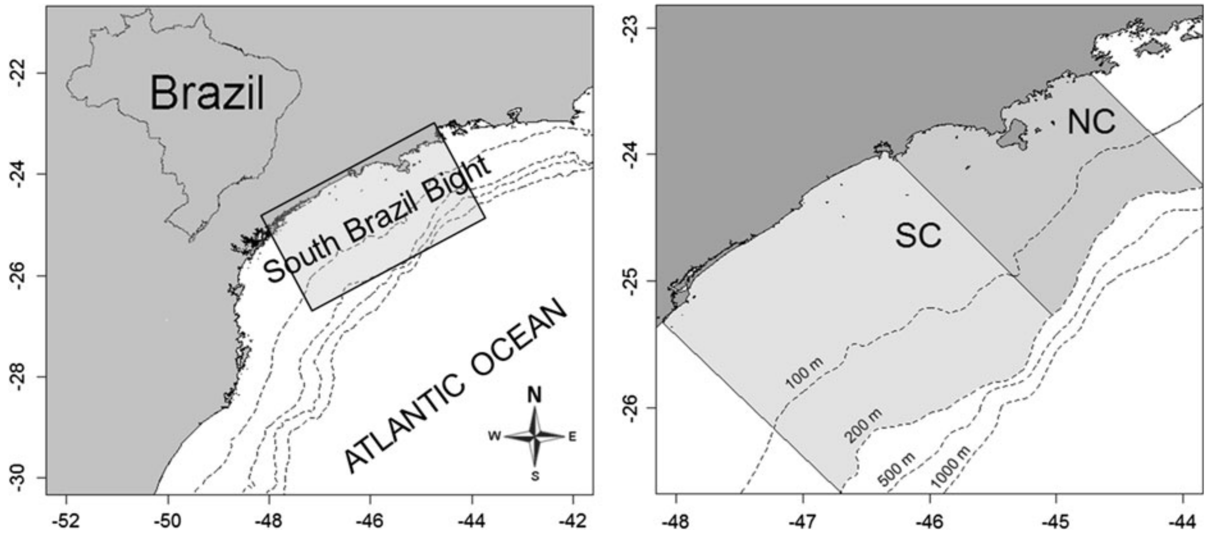


Fig. 2 Study area. The *rectangle* in the *inset* shows the approximate location of the study area on the southeastern coast of Brazil. North Coast (NC) and South Coast (SC) are the broad divisions (subareas) used in the inshore and offshore loss experiments

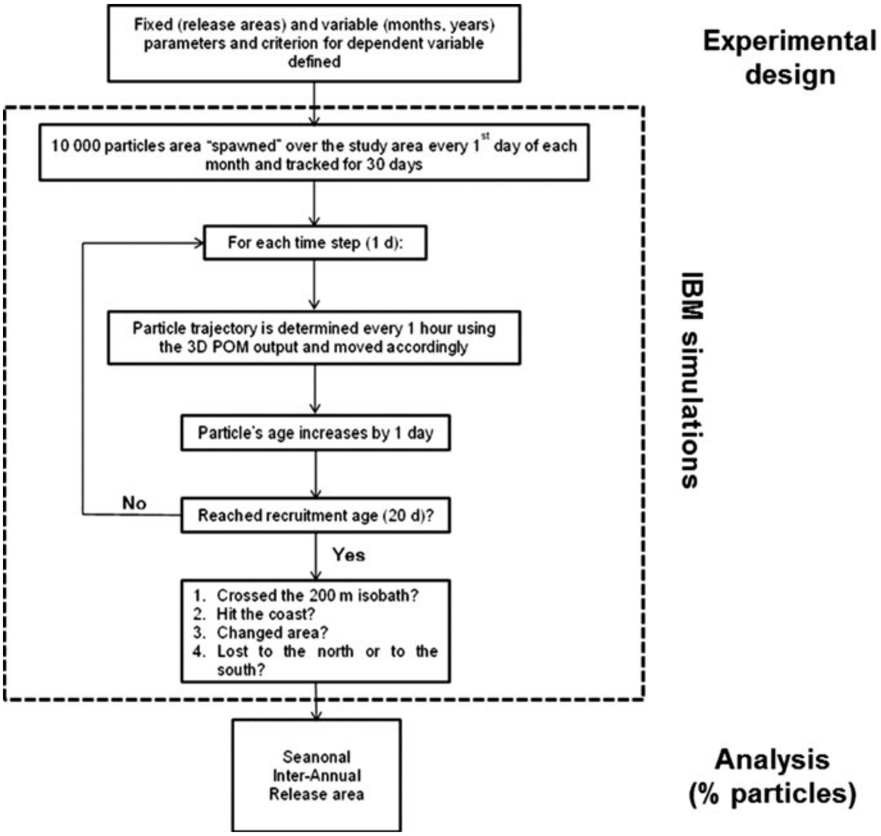


Fig. 3 Flow chart depicting the three stages of the modelling process for the Lagrangian transport experiment

on the SP shelf, never surpassing 8 and 0.4%, respectively (Fig. 4). This means that the SP shelf is extremely retentive on the basis of modelled circulation patterns. Accordingly, dispersal is low and restricted within the shelf.

Offshore losses presented a marked seasonal signal, with a strong and statistically significant peak in July (Fig. 4). However, this peak seems to be the result of a circulation anomaly detected in July 2009 (data not shown). This anomaly in our model is not unexpected, since the second semester of 2009 experienced an El Niño episode particularly strongly (NOAA, 2012). July 2009 was also the rainiest July in the region for decades (R. Camargo, pers. comm). This is also evidenced by the higher offshore losses signal detected in 2002, which was nearly 1.5 times greater than the remaining years (Fig. 4). There was no discernible difference between the release areas (Fig. 4).

Inshore losses, by contrast, showed no seasonality or inter-annual differences (Fig. 4). However, in terms of release areas, losses were much higher on the southern coast (Fig. 4).

Retention on each subarea and exportation between subareas

Retention in each release area was very high, being slightly higher on the south coast. The same pattern was detected in terms of exportation (i.e. there were slightly more particles being exported from the south coast to the north coast than the other way around) (Fig. 5). No seasonal or annual pattern was detected when each subarea was analysed separately (Figs. 6, 7), with retention always >90% regardless of the release area, and exportation varying between 2% from the north coast to the south (Fig. 6) and between 3.5 and 4.5% from the south coast to the north (Fig. 7). However, a weak seasonal signal appears to be discernible for exportation from the south coast to the north coast, with values generally lower during June and July than the rest of the year (Fig. 7).

Exportation from SP shelf towards the north

Losses beyond the SP shelf boundaries set in the present study occurred only to the north, never exceeding 9% of

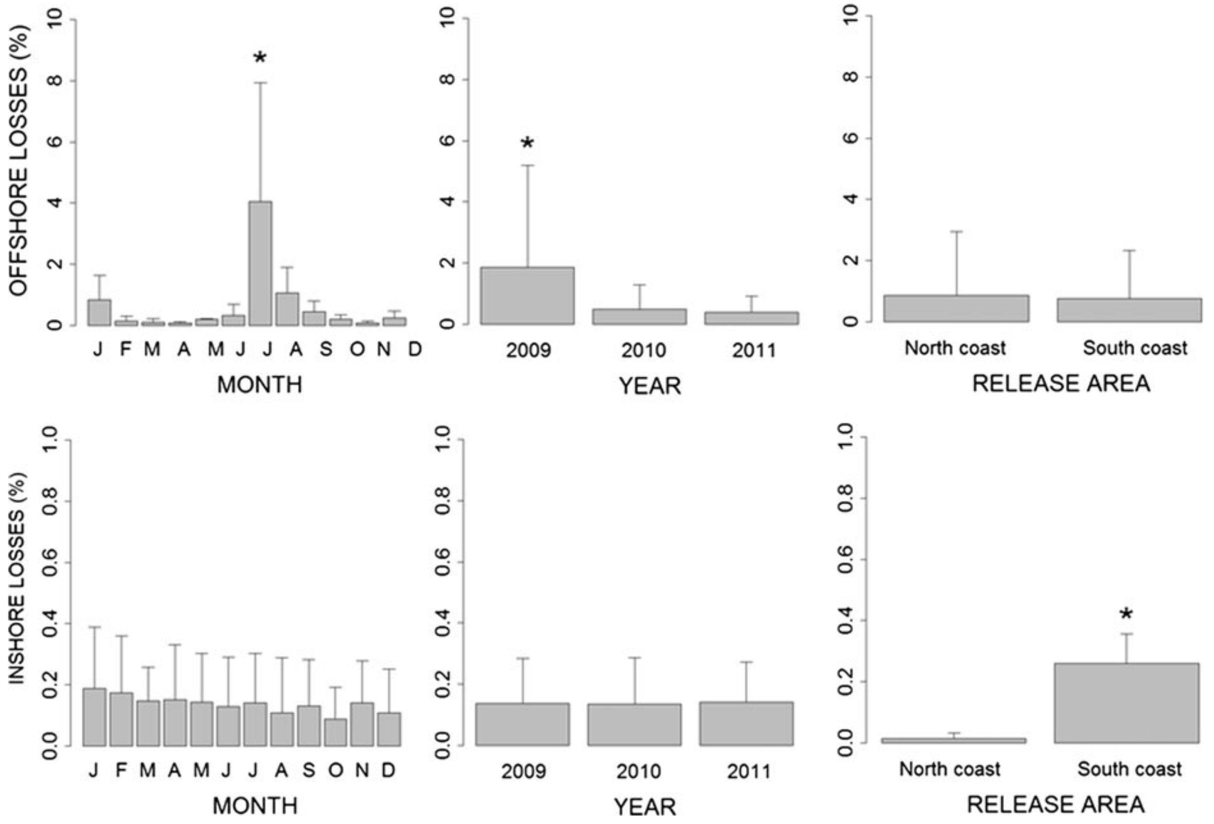
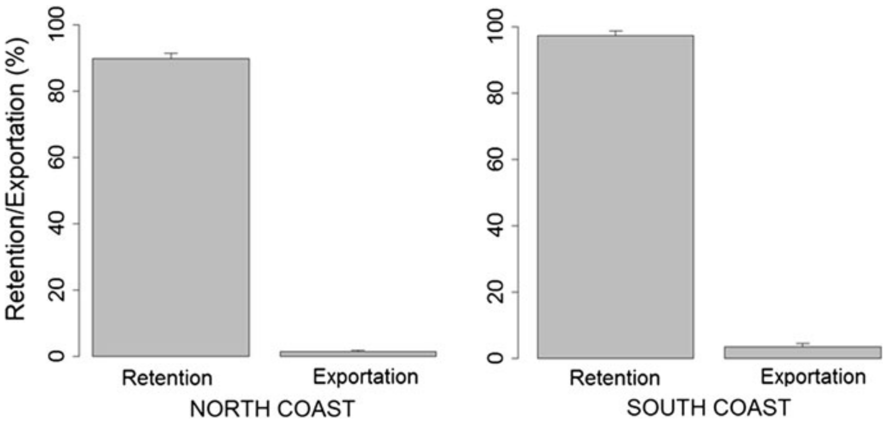


Fig. 4 Modelled results for percentages of particles lost from the SP shelf ecosystem. *Upper panel* particles that crossed over the 200 m depth contour (offshore losses). *Lower panel* particles beached (inshore losses). *Vertical bars* show the standard deviation. Note the different *y*-axis for each panel. The *asterisks* denote significant differences (Chi-squared test)

Fig. 5 Modelled results for percentages of particles retained on each subarea and exported between the two subareas of the SP shelf ecosystem. *Vertical bars* show the standard deviation



the particles originally seeded. There was a visible seasonal pattern, with exportation generally lower during the austral winter (June to August) and higher during the rest of the year, peaking during April–May (Fig. 8). No annual pattern could be identified (Fig. 8).

Discussion

SP shelf as *D. plei* paralarvae nursery ground

Overall, our results suggest that spawning on the SP shelf is conducive for the survival and growth of *D.*

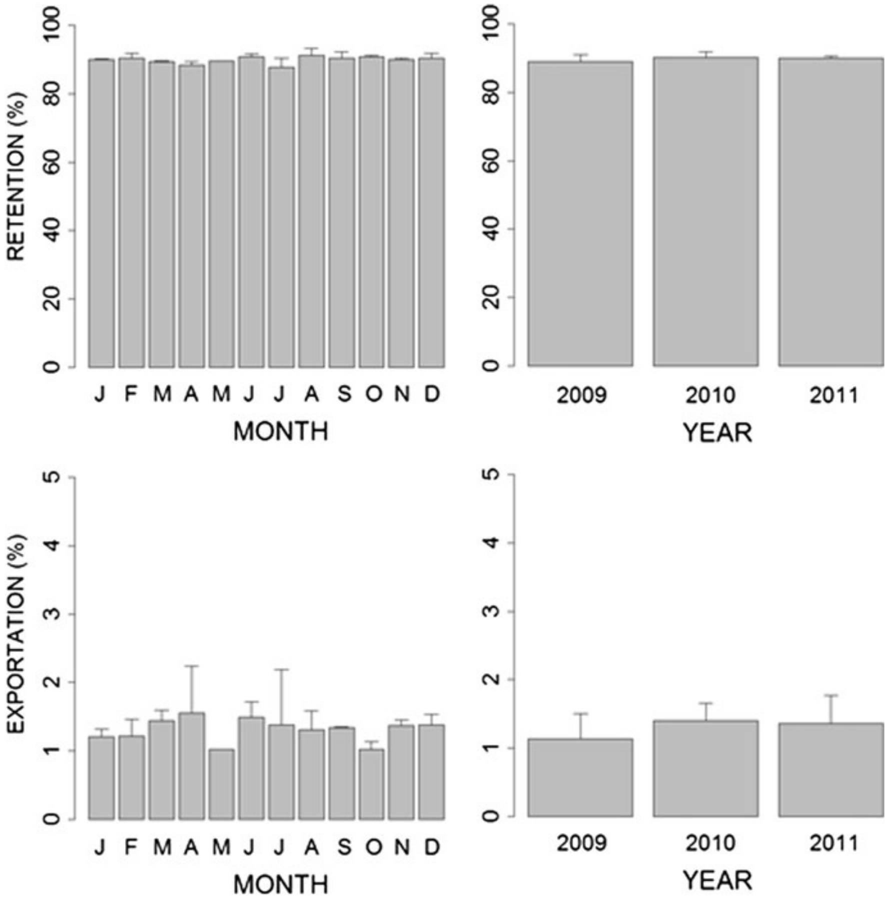


Fig. 6 Modelled seasonal and annual results for percentages of particles retained and exported from the North Coast subarea of the SP shelf ecosystem. *Vertical bars* show the standard deviation. Note the different *y*-axis for each panel

plei paralarvae on the basis of circulation patterns in the model. Potential losses towards both the open sea and the shore were found to be very low, which means that paralarvae hatched on any bottom on the shelf suitable for egg laying would likely be retained within the shelf ecosystem, where the physical and biological conditions are presumably conductive for post-hatching survival. Importantly, these modelled results agree and seem to reproduce to a great extent previous inferences on the behaviour of currents on the Southeastern Brazilian Bight (SBB, Matsuura, 1986; where the SP shelf is nested), where retention of plankters overwhelms dispersal (and thus removal from the ecosystem) due to a general cyclonic geostrophic circulation pattern, except at the northernmost (22°S) and southernmost (29°S) extremes, where seasonal wind-driven upwelling is likely to flush floating biological material (i.e. zoo and phytoplankton) out to the open sea due to offshore-directed Ekman transport (Bakun & Parrish, 1991).

It is important to bear in mind that, whereas spawning squid can be found in the region throughout the year (Rodrigues & Gasalla, 2008), the oceanographic conditions on the shelf may not be optimal for paralarval survival year round. This is because productivity peaks during spring–summer months, when cold and nutrient-rich South Atlantic Central Water (SACW) penetrates the shelf bringing nutrients to the euphotic zone (Matsuura, 1986). This, coupled with the aforementioned retention mechanisms and the stability of the water column due to low wind mixing (Bakun & Parrish, 1990, 1991) results in a would-be “optimal environmental window” (sensu Cury & Roy, 1989), when the triad of enrichment, productivity and concentration overlaps in time and space and becomes conducive to planktonic larvae feeding and thus improving survival (Bakun, 1996). In the winter, the SACW retracts to the slope and wind mixing homogenises the water column, decreasing overall productivity (Matsuura, 1986). Thus, environmental

Fig. 7 Modelled seasonal and annual results for percentages of particles retained and exported from the South Coast subarea of the SP shelf ecosystem. *Vertical bars* show the standard deviation. Note the different *y*-axis for each panel

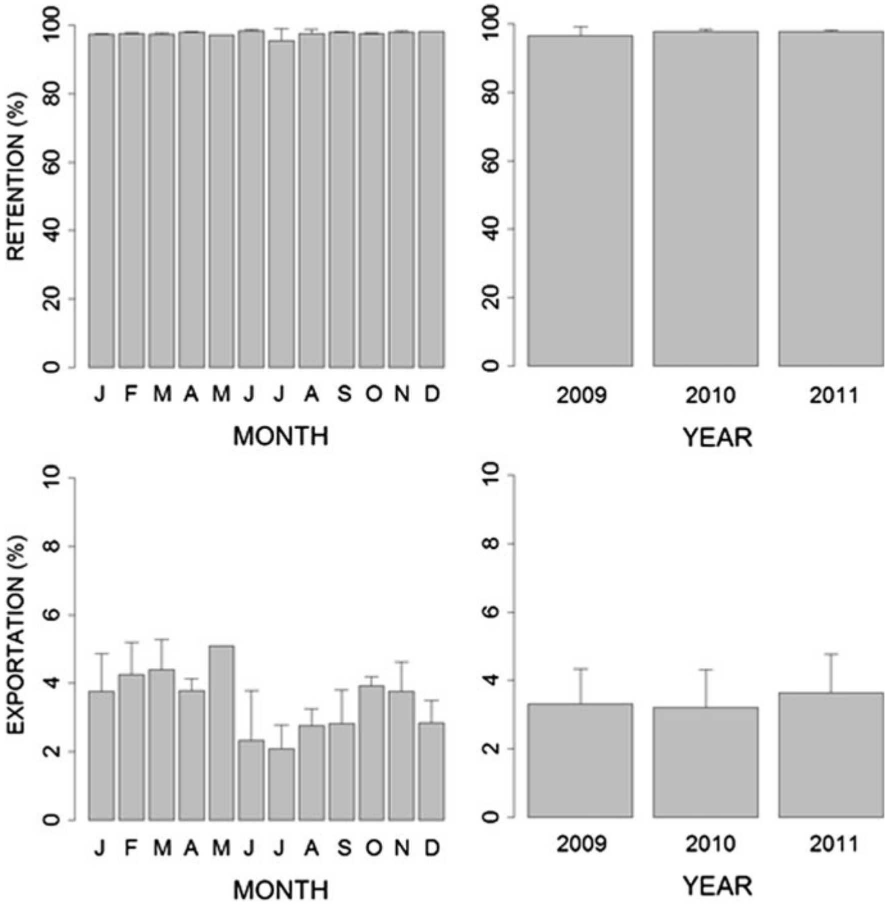
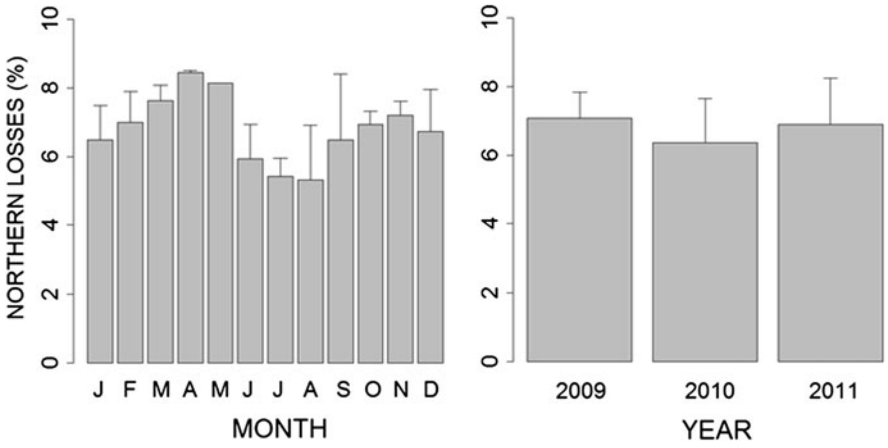


Fig. 8 Modelled seasonal and annual results for percentages of particles exported from the northern boundary of the SP shelf ecosystem towards the north. *Vertical bars* show the standard deviation



conditions at this time of year become poorer for the energetically demanding paralarvae which need plenty of food to fuel their high metabolism (Martins et al., 2010b). However, winter spawning squid may lay larger eggs (Boavida-Portugal et al., 2010) and the embryogenesis taking place in low temperatures tends to produce larger paralarvae which hatch with more yolk and are more resistant to starvation (Martins et al., 2010b). Nevertheless, our model showed that potential losses to the ocean and to the shore were highest during winter, which would translate to the worst time of the year for spawning.

An interesting pattern that also emerges from the modelling is that there was no exchange of virtual paralarvae from the southern SP shelf limit set in the model (Cananéia, ~25°18′S) toward the south. This implies poor population connectivity through larval drift from the SP shelf to the southern sector of the SBB shelf. In contrast, there was some larval drift towards the north at the northernmost geographic limit of the model (Ubatuba, ~23°22′S). These results, although limited to the SP shelf, raise interesting questions, as adult *D. plei* populations seem to display discernible morphotypes both alongshore (i.e. along the SBB; Juanicó-Rivero, 1979) and cross shore (Martins & Perez, 2007; Rodrigues & Gasalla, 2008). Whether or not these morphological variations can be related to putative latitudinal and bathymetric patterns of larval dispersal and retention that would lead to phylogeographic boundaries is still open to question, and modelling *D. plei* larval transport throughout the whole SBB, coupled with genetic studies of adult morphotypes on both alongshore and cross shore bases, should be pursued to explore this hypothesis.

PLD and implications for retention/dispersal

Because of the lack of data on *D. plei* paralarvae PLD, we have an age of 20 days as criterion for the end of this phase. Whereas further studies are necessary to clarify the PLD in *D. plei* paralarvae, perhaps using an analysis of accretion pattern (i.e. difference of the thickness of growth rings during the would-be pelagic phase) on statoliths of adult squid (e.g. Moreno et al., 2012), preliminary ageing readings in statoliths of juvenile squid of ~30 mm in dorsal mantle length (ML) showed 78 growth rings (Tanaka et al., 2011). Assuming that these are laid daily with a resulting linear growth rate of 0.39 mm day^{-1}, a 1.2 mm ML newly hatched *D. plei* paralarva would reach approximately 6 mm ML in 13 days, which is the size at which they would be able to school and presumably swim against a current, at least under experimental conditions (Vidal et al., 2009). Thus, the PLD period used in this study (20 days) may be considered reasonable within the modelling approach context and the apparently fast growth of *D. plei* paralarvae.

Limitations of the simulations

There were a number of limitations in the modelling approach adopted in the present study, and these must be recognised when interpreting the simulation results. First, our model considers passive Lagrangian transport only, and therefore only represents the role of modelled circulation for the virtual paralarvae released on the SP shelf. The incorporation of biological characteristics such as buoyancy, vertical migration behaviour and growth in larval transport IBM–3D hydrodynamic models developed for a number of species have led to mixed results, from being particularly important to having no effect at all on the larval trajectories in the models applied (e.g. Hare et al., 1999; North et al., 2008; Martins et al., 2010a). Whichever effect holds for modelling *D. plei* larval transport on the SP shelf is still unknown, and this issue must clearly be assessed by incorporating biological traits into the virtual paralarvae in future studies.

A second limitation is that little is still known about the locations and spatial structure of *D. plei* egg beds on the SP shelf, and a more accurate analysis should consider this factor. This was preliminarily addressed to a limited degree in the present study by dividing the shelf into two broad release subareas, but this is unlikely to reasonably capture the variability of transport trajectories within the shelf. For instance, larval transport IBM studies of chokka squid (*Loligo reynaudii* d'Orbigny, 1839) paralarvae off the South African eastern coast, where the location of the spawning grounds is well known (Sauer et al., 1992; Roberts et al., 2012) showed that the release areas were the most important explanatory variable in the models (Martins, 2009; Martins et al., 2010a). Furthermore, dispersal and retention patterns changed cross shore, with the former being important for paralarvae released on the mid-shelf and the latter important for those released inshore.

Finally, one last important limitation that must be observed is that the duration of the simulations (2 years) was too short to allow for meaningful interannual interpretations. Future modelling studies using longer time series should be developed to adequately address this question. Notwithstanding the latter, it must be stressed that the present model used in situ wind field data, and thus reproduced the shelf circulation patterns almost realistically. This is an important achievement, because circulation on the SP shelf is largely wind-driven (Mazzini, 2009) and most 3D hydrodynamic models available are normally forced with averaged environmental data that may not reproduce the variability in the circulation patterns in detail (R. Camargo, pers. comm). This is an important issue because recruitment strength variability in loliginid squid has been found to readily respond to interannual oceanographic anomalies (e.g. Roberts, 2005), some of which may not be reproducible in the hydrodynamic models if one uses averaged data.

Conclusions

Our model results suggest that the SP shelf would be an "almost perfect" nursery ground for *D. plei* paralarvae if circulation-driven dispersion and retention alone are considered. While extrapolation of these findings to reality can be questionable, they do appear to fit present knowledge on *D. plei* reproductive biology off the São Paulo coast. For instance, dense schools of spawning adults concentrate (and become available to artisanal hand-jigging fishery) around coastal islands off São Paulo's northern coast during the summer (Postuma & Gasalla, 2010). In this situation, model results showed low regional inshore losses and the risk of offshore losses is lower than during the rest of the year. These dense coastal concentrations of spawning adults have not been hitherto reported on the south coast where the model showed a higher risk to inshore losses than the northern coast, which supports our present results, at least as far as coastally spawning squid are concerned.

This study represents the first step towards a better understanding of the role of the larval transport on *D. plei* recruitment. However, this work should be refined. For the first time ever, *D. plei* egg capsules were found in the wild, off the northern São Paulo coast (Gasalla et al., 2011). Because these were observed in very shallow waters (6–20 m deep), a refined IBM model using a fine scale model grid, also including biological variables such as growth, body density and vertical migration (e.g. Roberts & Mullon, 2010; Martins et al., 2010a), should be used to adequately capture nearshore circulation patterns and the interactions with the biologically mediated vertical position that would be of relevance to paralarval transport.

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