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Effect of retention processes on the recruitment of tropical arrow squid (*Doryteuthis pleii*): An individual-based modeling case study in southeastern Brazil

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ABSTRACT

Squid recruitment depends on paralarvae survival, as the parental stock dies following reproduction. Therefore, the biotic and abiotic environmental conditions experienced by paralarvae control recruitment strength. To benefit from the favorable environments (i.e. nursery grounds) in the dynamic pelagic domain, paralarvae rely on passive retention by currents to remain in suitable nursery habitat. To evaluate the retention conditions for tropical arrow squid (*Doryteuthis pleii*) paralarvae off the South Brazil Bight (SBB, 22–29 °S), we ran a series of particle-tracking Individual-Based Models (IBM) coupled to a 3D Princeton Ocean Model (POM). We forced the hydrodynamic model with observed satellite data obtained from January 2000 to December 2010. The IBM-POM models considered two transport scenarios: (1) passive Lagrangian transport and (2) Diel Vertical Migration (DVM). The results show a high retention on actual and putative nursery grounds that could retain paralarvae in a suitable environment for survival, growth, and ultimately to recruit to the adult population. Moreover, model outputs showed high correlation between autumn-winter retention indexes and spring-summer commercial and artisanal landings in the following year. Considering the nine-month post-hatching lifespan of the species, autumn-winter retention indexes potentially provide forthcoming adult biomass predictions.

1. Introduction

Because of their short life-span and semelparity, squid population survival depends on their recruitment success (Agnew et al., 2000). This results mostly from density-independent factors that influence paralarvae survival (Roberts, 2005), although density-dependent factors such as seasonal population fecundity (Boavida-Portugal et al., 2010) and stock size (Agnew et al., 2000) may also play a role in paralarvae population abundance. Paralarvae survival is controlled primarily by the environmental conditions experienced in the planktonic phase of ontogeny, including physical variables such as current patterns (i.e. direction and velocity), salinity, temperature, pH, and dissolved oxygen (Roberts, 2005; Pecl and Jackson, 2008); adequate food availability and quality to fuel their fast metabolism and ensure further development (Vidal et al., 2005); and ecologic interactions like predation and competition, that may impact directly on mortality rates (Steer et al., 2003; Villanueva and Norman, 2008).

Squid paralarvae ecology is similar to that of fish larvae and other meroplankters, inasmuch as they must be within favorable environments in time and space. These environments must meet suitable physical and ecological conditions to ensure paralarvae survival and growth (Martins et al., 2014a, b). Such environments are commonly referred to as “nursery grounds” (Beck et al., 2003). In the dynamic pelagic domain, nursery grounds conditions result from the temporal and spatial overlap of three physical mechanisms: (1) nutrient enrichment, (2) concentration of larval food, and (3) local retention of eggs and larvae—a scenario that is known as the “ocean triad” or, more often, “Bakun’s triad”, in reference to the first proponent of this phenomenon (Bakun, 1996).

Thus, paralarvae should be under the Bakun’s triad influence in time and space to ensure survivorship during the so-called “critical period” (Vecchione, 1981; Vidal et al., 2002). The critical period can be defined as a variable, mostly temperature-dependent, stretch of time during which paralarvae are prone to starvation, because yolk absorption is directly dependent on the environmental temperature (Vidal et al., 2002; Martins et al., 2010). During this phase, paralarvae must improve

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their predatory skills to acquire enough food to survive the period after yolk absorption (Vidal et al., 2005). This encourages further development and growth that will lead to the abandonment of planktonic habits over time and ultimately to the recruitment of young squid to the adult population (Martins et al., 2010). Considering how critical retention in nursery grounds is for paralarvae at the recruitment stage (Roberts, 2005, Martins et al., 2010, Martins et al., 2014a, b) and that several biological and physical environmental variables have been used to predict adult biomass (Agnew et al., 2000; Zeidberg et al., 2006), we hypothesized that retention conditions could be used to predict recruitment strength.

Albeit relatively competent swimmers since hatching, early paralarvae are, as most marine larvae at this stage (e.g. Chia et al., 1984; Clark et al., 2005), unable to swim against a current, and thus behave almost like passive drifters (Vidal et al., 2018). Therefore, biophysical interactions, such as species-specific behavioral selective use of vertically stratified currents is a mechanism often used to enhance retention in nursery grounds (Otero et al., 2016; Roura et al., 2016). For instance, it seems that early *Octopus vulgaris* paralarvae may use diel vertical migration (DVM) to remain close to the coast in northwest Iberian upwelling system, a strategy also observed in other meroplankters elsewhere (e.g. Otero et al., 2016).

Other physical mechanisms, acting associated or independent of larval behavior, also contribute to larval retention. For example, the “sticky waters” phenomenon (i.e. increased water residence time around islands, reefs and other subsurface obstacles), may enhance local retention (Zeidberg and Hamner, 2002). Other examples include concentration of eggs and larvae along abrupt density gradients, such as pycnoclines and oceanographic fronts, and entrapment within current gyres, eddies and meanders (Bradbury and Snelgrove, 2001; Vidal et al., 2010; Somarakis et al., 2019). Regardless of the mechanism, retention seems to have important implications to the recruitment in fish, cephalopods and other marine invertebrates (Morgan et al., 2009; Otero et al., 2016; Somarakis et al., 2019).

Studies on the role of larval transport and retention on recruitment are relatively frequent for benthic/demersal fish and, to a lesser degree, invertebrate species (e.g. Swearer et al., 2019). On the other hand, similar efforts towards cephalopods are less common (Otero et al., 2016). Nonetheless, field sampling, satellite imagery-derived retention indexes, and genetics have been used to clarify the role of larval retention on cephalopod recruitment (Semmens et al., 2007; Roura et al., 2019). More recently, Martins el al. (2014b) and Downey-Breedt et al. (2016) investigated the role of retention on chokka squid *Loligo reynaudii* recruitment off South Africa using computer-based biophysical modelling.

The tropical arrow squid *Doryteuthis pleii* is widely distributed and commercially fished along the so-called South Brazil Bight (SBB, 22–28.5 °S; Lopes et al., 2006) by both artisanal and commercial fleets (Perez, 2002; Martins and Juanicó, 2018). Catches are concentrated during austral spring-summer, when dense schools of spawning squid are common on the shelf and nearshore (Perez, 2002). Artisanal fishing targets nearshore areas, where squid are typically caught with homemade jigs (“zangarilhos”), although other fishing gears may also be employed (Costa and Haimovici, 1990; Martins and Perez, 2007). Commercial double-rig and pair-trawlers target squid that aggregates on 15–45 m sandy bottoms on the continental shelf (Perez, 2002). As in other loliginid fisheries, tropical arrow squid landings present high interannual variability, sometimes with landings varying up to 400 tons between consecutive years (Instituto de Pesca, 2017). Such catch fluctuation may reflect recruitment strength, which in turn depend on the survival of paralarvae (Roberts, 2005).

Nonetheless, except for some data on paralarvae distribution (Martins and Perez, 2006; Araújo and Gasalla, 2018), tropical arrow squid early life story is poorly known off southeastern Brazil. Spawning have never been recorded in Brazil until 2010, when egg capsules, embryos and newly hatched paralarvae of the species were described for the first time (Gasalla et al., 2011). Thus far, egg masses have been only found in nearshore areas (6–20 m deep) on São Paulo State north coast (23.2–24.0 °S). Underwater surveys conducted during summer months showed that egg masses are sparsely aggregated, and are laid on sandy bottoms in sheltered bays (unpublished data).

Given that recruitment likely depends on paralarval retention at nursery grounds, and retention can potentially be modelled using a hydrodynamic model (e.g. Martins et al., 2014a, b) we developed such a biophysical model, based on particle-tracking Individual-Based Models (IBMs) coupled to a 3D Princeton Ocean Model (POM), and then investigated the utility of the model output to forecast fishery success.

2. Material and methods

2.1. Study area

The study area lies on the South Brazil Bight (SBB), encompassing coastal and shelf areas between southern Rio de Janeiro and northern São Paulo States. The regional coastline is oriented in the NE-SW direction, and includes two large islands (Ilha Grande – IG, and São Sebastião Island – SSI), several islets and rocky reefs, rocky shores, oceanic sandy beaches, a number of rivulets and a wide estuarine system close to the northernmost part of the study area (Fig. 1).

The IG is separated by a narrow constriction from the continent, and thus the inner embayment is split in two well defined bays. The western bay is connected to the adjacent ocean by a large channel (~17 km wide), and has low influence of continental runoff. On the other hand, the eastern bay is connected to both the ocean and a wide estuarine system (Sepetiba Bay), and is strongly influenced by estuarine outflow. A remarkable feature of the local circulation is the non-tidal, quasi-steady clockwise flow around the island (Signorini, 1980a, b).

The SSI, the largest oceanic island off Brazil, comprises a prominent regional feature, acting as a barrier to the coastal currents that flow along the inner shelf, driving different hydrological, sedimentary and primary production conditions on the southwest and northeast sectors of the adjacent shelf (Mahiques et al., 2004).

Overall, the coastal currents in the region are mainly driven by the winds, presenting bidirectional motions approximately parallel to the local isobaths at all levels (Castro, 1996). The predominant northerly winds drive southeastward coastal currents, with flow reversals (i.e. northeastward currents) occurring associated to southerly frontal systems (cold fronts), which are more frequent during austral autumn-winter (Dottori and Castro, 2009). Circulation inside the many bights and bays along the regional coast, however, may also be influenced by other forcing factors, such as tides and density-driven flows (Signorini, 1980a; Siegle et al., 2018).

2.2. Hydrodynamic model

The hydrodynamic model used was the Princeton Ocean Model (POM; Mellor, 1998). This model resolves the primitive hydrodynamic equations based on Boussinesq assumption and hydrostatic approximation, with three dimensional, non-linear equations written in flux form. A built-in second moment turbulent closure scheme was used to compute the coefficients of vertical viscosity and diffusion with equations for the turbulent kinetic energy and the length scale of turbulence (Mellor and Yamada, 1982). The horizontal viscosity and diffusion coefficients were parameterized using Smagorinsky scheme (Blumberg and Mellor, 1987). The version used in the present study was originally developed for estuarine areas (Camargo and Harari, 2003; Harari and Camargo, 2003).

The model grid has a 1 km resolution in the horizontal dimension with 22 bottom following sigma-levels, and covers the area between 22.5° and 29 °S that encompasses 290 × 940 grid points (Fig. 2). The grid was rotated ~45° clockwise relative to the N–S direction to follow the coast orientation in the region. We opted for this fine grid

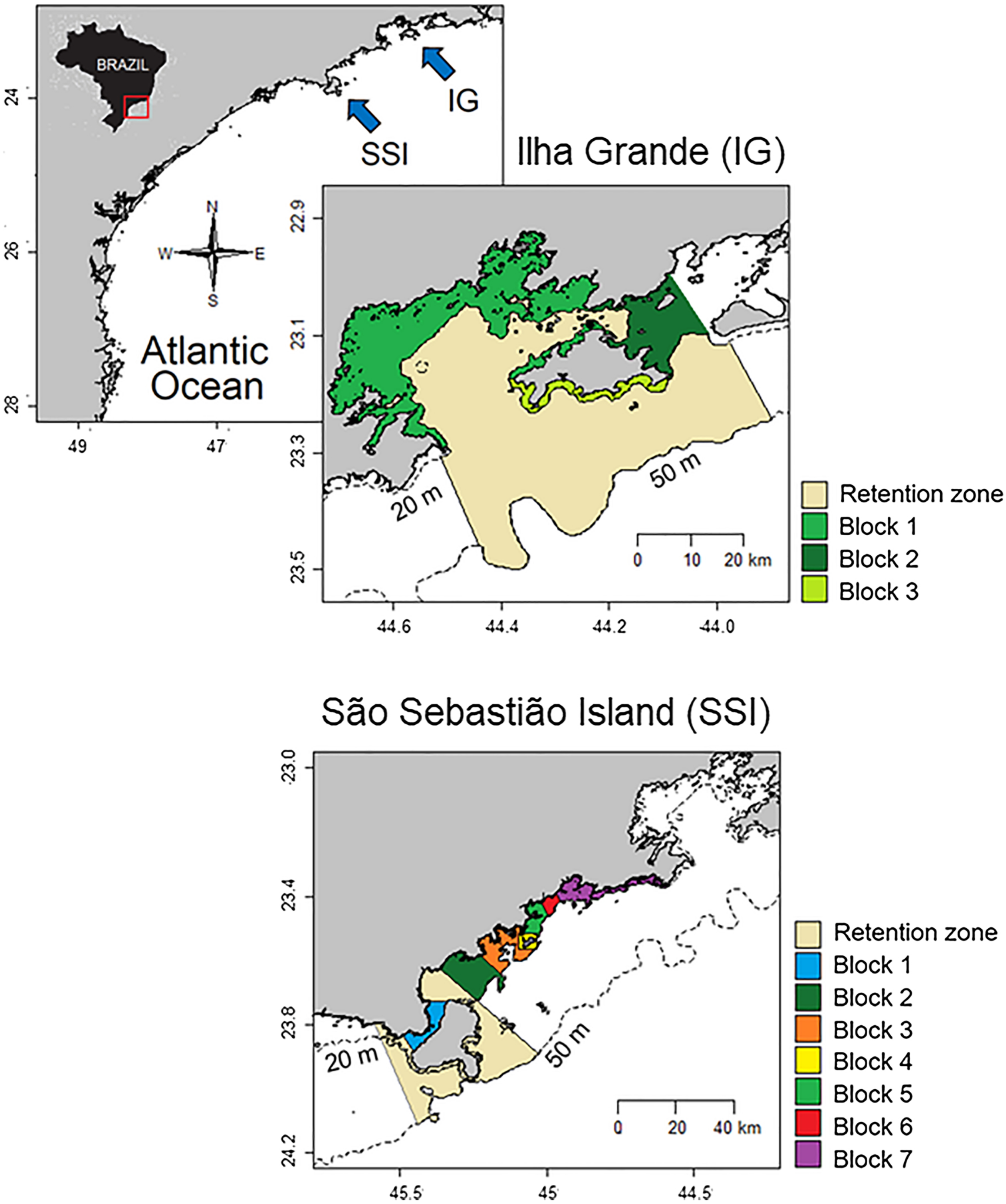

Fig. 1. Study area. The retention zones selected for numerical experiments are shown along with their release blocks. The bathymetric limits for retention zones and release blocks are 0–50 m and 0–20 m, respectively. Note that all release blocks overlap with the retention zone around Ilha Grande, and release block 1 overlaps with the retention zone around SSI. The arrows in the inset indicates the location of Ilha Grande (IG) and São Sebastião Island (SSI) on the South Brazil Bight (SBB). The relative position of South Brazil Bight (SBB) is boxed in red. The 20 and 50 m isobaths are showed. Latitude and longitude are decimal transformed (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

configuration because tropical arrow squid eggs are found near the shore in very shallow areas (Gasalla et al., 2011). Therefore, a hydrodynamic model able to resolve small-scale current patterns close to shore was necessary for our modeling approach (Fig. 3).

The model ran from January 2000 to December 2010 and resulted in 11 years of simulations. However, only outputs from 2002 to 2010 were used in our study to allow for two years of spin up for statistical equilibrium (Martins et al., 2014b). The model was forced by winds and salt/heat fluxes from NCEP/CFSR (Saha et al., 2010) and considered the monthly temperature and salinity fields provided by the Simple Ocean Data Assimilation (SODA; http://www.atmos.umd.edu/~ocean/data.html) as a reference. We employed results from a coarse grid based on the same setup to represent the high portion of shelf circulation driven by tides and surges. This coarse grid covered the entire South Atlantic with 0.5° spatial resolution and included the tidal potential generator explicitly (Camargo and Harari, 2003).

2.3. Modeling approach and experiments

We ran a suite of coupled POM–particle-tracking Individual-Based

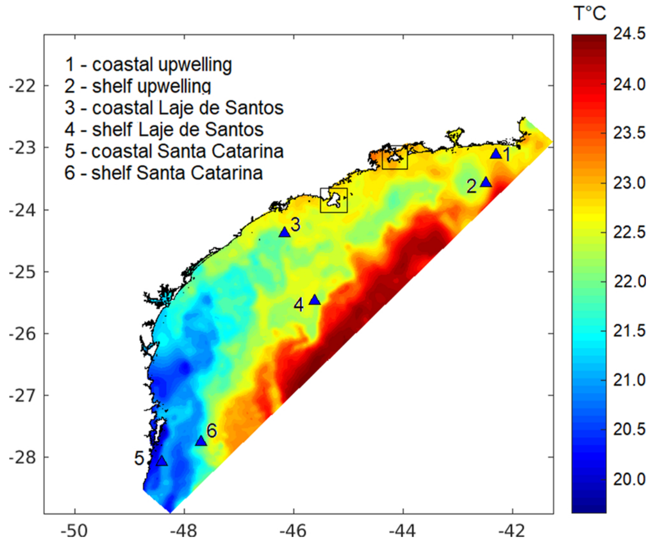

Fig. 2. Princeton Ocean Model (POM) domain showing a *snapshot* of sea surface temperature modeled from climatological data (daily averaged data as for 01 June 2006). Note that the domain includes the whole SSB. The locations of Ilha Grande (IG) and São Sebastião Island (SSI) are boxed.

Model (IBM) simulations with the public domain Ichthyop® software (version 3.0b). This tool allowed virtual particles representing tropical arrow squid paralarvae to be tracked in space and time using offline hydrodynamic model outputs under different transport scenarios (Lett et al., 2008). In all cases, the 4th order Runge-Kutta transport scheme was adopted because it resolved better the particle trajectories near physical obstacles such as islands and reefs (Lacroix et al., 2009). Before the simulations, POM outputs were converted to Regional Ocean Modeling System (ROMS) format to be compatible with the particle-tracking tool (Martins et al., 2014a). The details of each performed simulation are given below.

2.3.1. *A priori identification of tropical arrow squid paralarvae nursery grounds (model retention zones) and spawning grounds (model release blocks)*

The areas selected for the present modeling approach are depicted in Fig. 1. We assumed that model retention zones and release blocks corresponded to real-life nursery and spawning grounds, respectively. Nursery grounds (= model retention zones) referred to the zones where paralarvae may be retained and benefit from a favorable environment for survival and growth. Spawning grounds (= model release blocks) encompassed the benthic environment where eggs are laid and paralarvae hatch, since environmental conditions in these sites optimize loliginid embryonic development (Roberts and Sauer, 1994; Roberts, 2005).

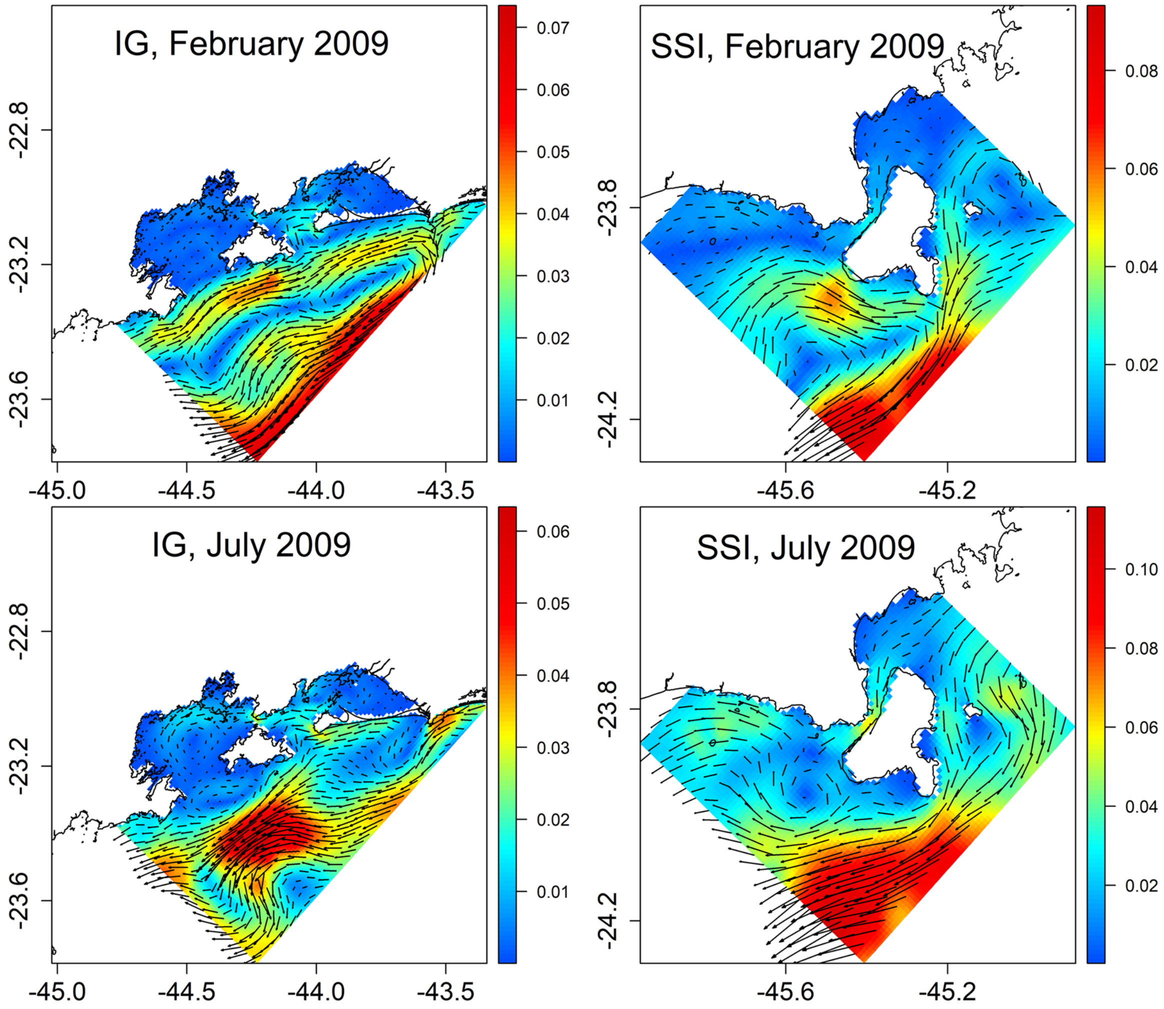

Fig. 3. Comparison between summer (top maps) and winter (bottom maps) depth-averaged currents (m s^{-1}) POM outputs for Ilha Grande (IG) and São Sebastião Island SSI).

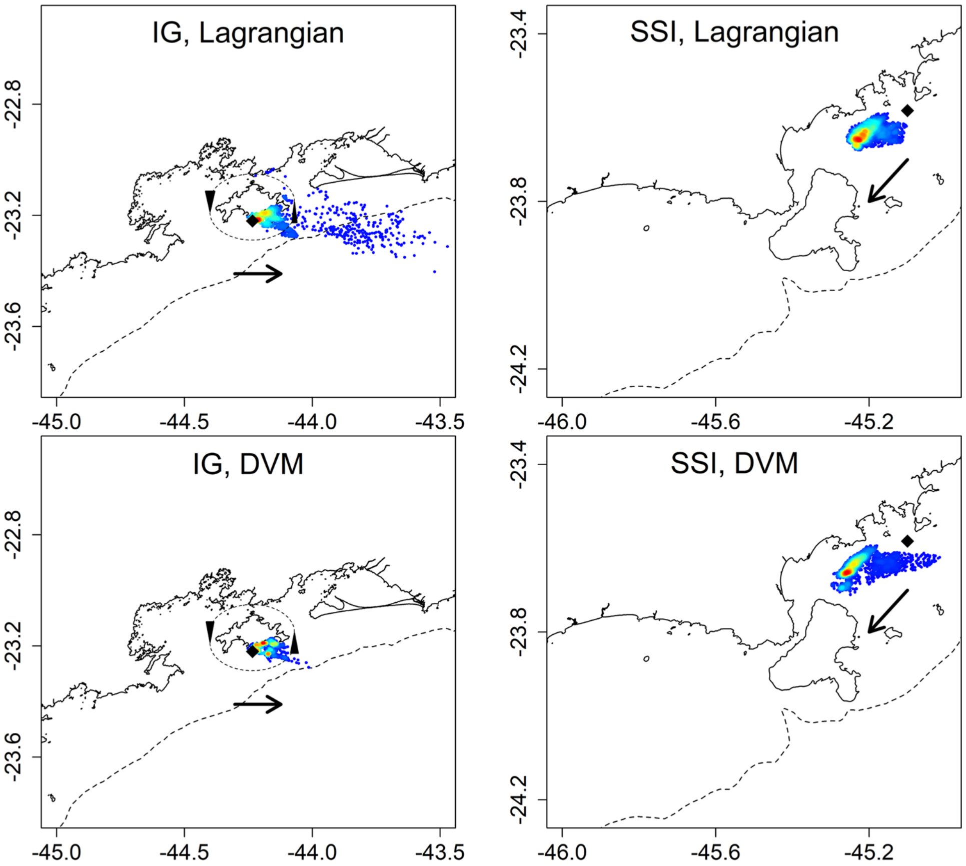

Fig. 4. Examples of 30 d dispersal (1000 virtual paralarvae released and tracked in each scenario). Top panels: Lagrangian transport. Bottom panels: DVM transport. Thick black arrows represent the local predominant coastal current directions as resolved by our POM model for February 2009. Thin dashed black arrows around Ilha Grande (IG) represent the clockwise flow around this island. Black diamonds represent the release points. The 50 m isobath is showed.

Selected retention zones were bound by the coastline and the 50 m isobath because historical research cruises conducted off SBB have seldom found tropical arrow squid paralarvae beyond this depth (Araújo, 2013). Release blocks were confined to the inshore between the coastline and the 20 m isobath, as egg masses have been found on 6–20 m soft bottoms (Gasalla et al., 2011). In addition, spawning squid are rarely caught beyond 20 m deep bottoms (Postuma and Gasalla, 2014), suggesting that the bulk of spawning takes place nearshore. Release blocks may or may not overlap with the retention zones, depending on the region (Fig. 1).

2.3.2. *Ilha Grande (IG)*

We selected the Ilha Grande (IG) surroundings (Fig. 1) for our IBM modeling approach because of its importance as both artisanal and commercial squid fishing grounds (Begossi, 2001; Gasalla et al., 2005). These areas included one putative retention zone and three release blocks. Two out of three selected release blocks were located within the island's bay (representing the western and eastern parts of the bay), while the other spread along the rocky shores on the seaward face of the island. These release blocks were selected because they are representative of three broad regions around this island (Signorini, 1980a, b). In all cases, release blocks overlapped with the retention zone.

2.3.3. *São Sebastião Island (SSI)*

We selected the São Sebastião Island (SSI) surroundings (Fig. 1) for our modeling experiments because SSI comprises one of the most important and traditional *D. pleii* artisanal fishing grounds off southeastern Brazil (Gasalla, 2004).The area around the island was considered an actual retention zone in our model because all *Doryteuthis pleii* life stages have been recorded there (Gasalla et al., 2012). Release blocks were located between São Sebastião (23.7 °S) and Ubatuba (23.3 °S). In total, seven release blocks were chosen and only the channel separating SSI from the adjacent continent (São Sebastião Channel) overlapped with the retention zone. Release blocks configuration was established to address the effect of release block distance on retention. No release blocks were set south of the island because artisanal squid fishing does not take place in this area (Leite and Gasalla, 2013), suggesting fewer or no spawning grounds in this region.

2.3.4. *Virtual paralarvae retention experiments*

We used modeled retention as an index of environmental suitability for tropical arrow squid paralarvae survival and growth in the wild. Virtual particles representing paralarvae (hereafter referred to as "virtual paralarvae") were treated as neutrally buoyant, and were released 0.1 m above the model seabed because loliginid paralarvae hatch from benthic eggs in the wild (Boletzky, 2003). The model did not include sources of mortality such as lethal temperatures, predation or losses from advection out of the shelf ecosystem, transport to inappropriate areas, or any other biological trait other than Diel Vertical Migration (DVM). This was due to the lack of data on any of these aspects for this species paralarvae, either in the wild or in aquaria. In addition, beached particles were flagged and not considered in the analysis.

Virtual paralarvae were released every first day of each month over successive years and were tracked for 30 d. We regarded paralarvae as "retained" if they were located within the nearest retention zone at this age. The 30 d age of retention was assumed because tropical arrow squid paralarvae would reach ~13 mm in dorsal mantle length (ML) at this age and may be fully able to school and hold a position against a current (sustained swimming), which represents the end of their pelagic larval duration (PLD). We based this assumption on laboratory rearing data for a congeneric species (i.e. *Doryteuthis opalescens*; Vidal et al., 2018) and aging readings from statoliths of squid as small as 30 mm ML and the resulting growth rate estimates (Martins et al., 2014a).

In total, 25,000 virtual paralarvae were released randomly on the whole surface area of each selected release blocks. The number of virtual paralarvae released on each release block was proportional to the block area surface. The latter was not intended to represent a realistic number of paralarvae hatched, but rather chosen to ensure stability and robustness to the simulations (Miller, 2006). Model outputs were expressed as the percentage of released virtual paralarvae that were retained in each selected retention zone within the 30 d time frame.

2.3.5. Transport scenarios

We devised two transport scenarios according to the available information on tropical arrow squid larval transport:

Passive Lagrangian transport. This scenario represents the modeled transport of virtual paralarvae not controlling their trajectories. Therefore, it indicates the effect of local modeled circulation on retention or dispersal patterns. This means that virtual paralarvae were transported randomly both in the vertical and horizontal dimensions allowed by the advection scheme of the IBM tool. Lagrangian transport is exemplified in Fig. 4.

Diel Vertical Migration (DVM) transport. Because loliginid squid display Type-I DVM (Zeidberg and Hamner, 2002; Moreno et al., 2009), in this scenario the virtual paralarvae were transported into deeper waters during the day (07:00 AM to 07:00 PM) and shallower waters at night (07:00 PM to 07:00 AM). We assumed the 10–20 m vertical range as DVM interval of tropical arrow squid in our simulations based in empirical data (Araújo, 2013). The DVM behavior initiated at the beginning of the simulations, as squid paralarvae swim from the time of hatching, and vertical migration is observed in the wild (Zeidberg and Hamner, 2002; Boletzky, 2003). Paralarval transport in this case would be the net result of the interaction between the DVM behavior and the modeled circulation (Fig. 4).

2.3.6. Factors influencing the modeled retention of tropical arrow squid paralarvae

We conducted a sensitivity analysis to investigate the effect of release blocks, transport scenarios, months, and their interactions in modeled retention. This modeling was accomplished by fitting binomial Generalized Linear Models (GLMs) (Crawley, 2015).

The GLM was fitted only for the SSI, and included a proportional response variable vector combining the counts of retained vs. non-retained virtual paralarvae and three categorical explanatory variables (factors): *month* (seasonal effect, $n = 12$ levels), *area* (spatial effect, $n = 7$ levels), and *transport scenario* (Lagrangian vs. DVM transport effect, $n = 2$ levels). The factor *year* was excluded from this analysis to avoid the risk of Type-I error (Underwood, 1997). The selection of categorical explanatory variables and their retention or exclusion in the best fitted model was based on the Akaike Information Criterion (AIC) (Akaike, 1974), Bayesian Information Criterion (BIC) (Schwarz, 1978), and the total deviance explained.

Retention in the IG experiments was 100 % in Blocks 2 and 3 (see Results); therefore, statistical analysis was conducted to the overall and monthly effect of the transport scenarios on retention in Block 1, using the non-parametric Wilcoxon signed-rank test (Kloke and McKean, 2015).

2.3.7. Modeled retention vs. recruitment

To explore the correlation between retention and recruitment, we fitted simple linear regression models to seasonally averaged modeled retention and squid landing data. Both datasets were normally distributed (Shapiro–Wilk normality test, $p > 0.05$) (Zar, 2010). For simplicity, this approach was applied using only Lagrangian retention data. We did this exercise for spring-summer landings only because the bulk of tropical arrow squid is caught in that season (Perez, 2002).

We plotted averaged modeled retention data obtained in autumn-winter (April to September) against the landings recorded in the following spring-summer (October to March) in each nursery ground (model retention zones), under the assumption that the pots-hatching lifespan of tropical arrow squid inhabiting the South Brazil Bight is up to nine months (Perez et al., 2006). This implies that spring-summer spawning squid were born in the previous autumn-winter season. Two models were fitted: one including all dataset and a second one with outliers removed. We assumed as outliers (i.e. legitimately extreme observations) those data points that yielded residuals disproportionally far from the model fitted with the whole dataset.

Two types of landing data were employed: (1) data gathered from hand-jigging artisanal squid fisheries, and (2) data obtained from the commercial pair trawling fisheries. In both cases, the time series covered the period between 2003 and 2011. Landing data were obtained from the São Paulo Fishery Institute and Freire et al. (2015). Both datasets are publicly available from ProPesq® fishery statistical system (Instituto de Pesca, 2017; http://www.propesq.pesca.sp.gov.br/). Artisanal landing data for SSI were sourced from Postuma and Gasalla (2010).

2.3.8. Quantification of autumn-winter biological production

Considering that squid paralarvae must find plenty of food to avoid starvation (Vidal et al., 2005), we quantified the biological production in each retention zone during the autumn-winter of the modeled years. To accomplish this, we used seasonal satellite-sensed chlorophyll-*a* (Chla) concentration (mg m^{-3}) as a biological production index, since there is a tendency for phytoplankton accumulation in retention areas due increased water residence time (Graham and Largier, 1996). Satellite data were obtained from SeaWiFS (GIOVANNI database, NASA; Acker and Leptoukh, 2007), which runs twice a day with a resolution of 9 km. Local estimates were averaged for nursery grounds surface area, i.e. IG and SSI (Fig. 1). SeaWiFS data matched reasonably with near-shore Chla data measured in the same region and during the same period by the MODIS/Aqua ocean color sensor (Ciotti et al., 2010).

2.4. Modeled retention vs. biological production, and biological production vs. recruitment

To investigate the relationship between the modeled retention and biological production, and also between biological production and the recruitment index, we fitted simple linear regressions to the variables "Chla concentration vs. retention index" (intraseasonal: autumn-winter) and "spring-summer squid landings vs. autumn-winter averaged Chla concentration" (between consecutive years; i.e. Chla autumn-winter data of a given year against spring-summer squid landings in the following year). Model fitting and outlier removal criteria were the same described in item 2.3.7.

3. Results

3.1. Hydrodynamic model performance

We evaluated model performance by comparing POM-resolved sea surface temperature (SST) with actual satellite SST data (GHRSST: Group for High Resolution SST; https://sealevel.nasa.gov/missions/ghrsst) in six locations along the South Brazil Bight coast domain including coastal and offshore areas representative of (1) seasonal upwelling zones (Cabo Frio) and (2) typical regional neritic zones (Laje de Santos [~24.5 °S] and Santa Catarina shelf [~28.5 °S]) (Fig. 2).

Taylor diagrams (Taylor, 2001) were plotted for daily (January 01, 2002 to December 31, 2010), monthly (January 2002 to December 2010), and climatological monthly mean outputs (2002–2010) (Fig. 5). Results showed a good agreement between modeled and actual data with correlation coefficients ranging between 0.75 and nearly 1, low variability (normalized standard deviations ≤ 1 °C), and most root squared errors ≤ 0.5 °C (grey arcs) with points clustering close to the reference arc (black arc) (Fig. 3).

In addition, actual small scale oceanographic features were reproduced by our model, such as a winter cyclonic gyre in the southern

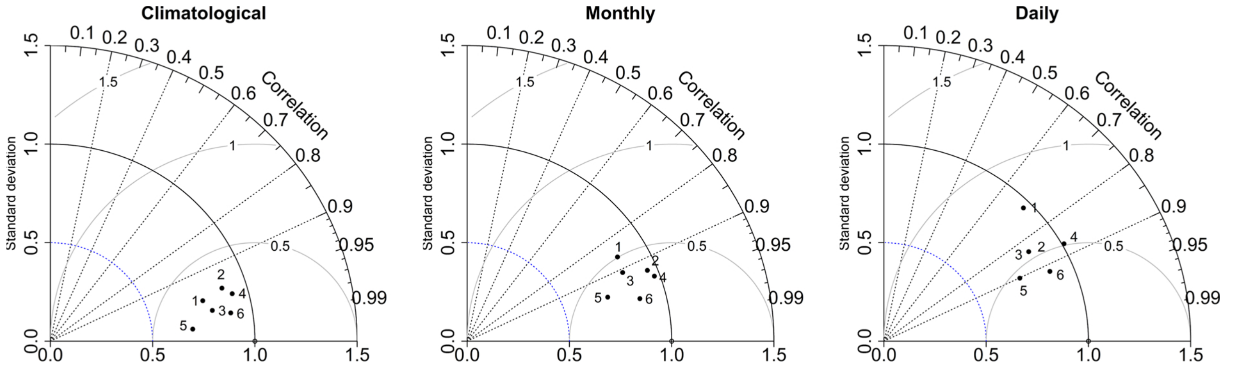

Fig. 5. Taylor diagrams of model performance. The diagram summarizes the normalized standard deviation and the correlation coefficient for each model point in Fig. 1. Note that the distance to unity at any given point is directly related to the root-mean-square error (RMSE). 1) Coastal upwelling, 2) Shelf upwelling, 3) Coastal Laje de Santos, 4) Shelf Laje de Santos, 5) Coastal Santa Catarina, 6) Shelf Santa Catarina.

part of channel between SSI and the continent (Castro, 1990) (Fig. 3). These assessments suggest that the POM model reasonably resolved the regional oceanographic patterns.

3.2. Modeled retention on the selected retention zones

3.2.1. Ilha Grande (IG)

Retention was very high around IG, with 100 % of virtual paralarvae released from the inner bays (Blocks 1 and 2) retained following 30 d of transport regardless of the transport scenario adopted. The block located on the seaward face of the island (Block 3) lost some particles beyond the 50 m isobath; however, retention in this block was also very high (average of 95.4 ± 1.59 SD % and 96.1 ± 1.79 SD % in the Lagrangian and DVM scenario, respectively) (Fig. 6).

Box-plots of seasonal retention patterns showed a highly skewed distribution. However, visual examination of averages clearly indicated higher retention from June to December regardless of the transport scenario (Fig. 6). The DVM behavior marginally enhanced the overall retention on the nursery ground (0.21 ± 0.25 SD % on average; Wilcoxon test, $p < 0.001$). Paired monthly comparisons between the Lagrangian and DVM scenarios indicated that DVM yielded significantly higher retention in January and November (Wilcoxon test, $p < 0.001$)

3.2.2. SSI

Overall, the retention of virtual paralarvae around SSI according to both Lagrangian and DVM transport scenarios yielded higher retention for the blocks closest to the island (Blocks 1–3), and were higher at Block 2 than the remaining blocks (Fig. 7a, c). Regardless the scenario, non-zero retention data were mainly positively skewed, as most averages were greater than the medians. Very little or no virtual paralarvae were retained from the blocks to the north (Blocks 3–7). The DVM transport increased the proportion of virtual paralarvae retained from Block 1 in comparison to the Lagrangian transport (overall averages of 39.3 ± 9.12 and 32.6 ± 6.21 SD %, respectively; Fig. 7c). In contrast, average retention was higher in the Lagrangian scenario for virtual paralarvae released from Block 2 (overall average of 93.3 ± 3.52 vs. 89.9 ± 7.54 SD %) (Fig. 7a).

Regarding the overall seasonal patterns, only pooled data from Blocks 1–4 are shown because the other release blocks did not indicate virtual paralarvae retention (Fig. 7b, d). A seasonal signal was evident for the Lagrangian scenario, which had the highest average retention detected between April and September. This pattern was somewhat broken by the lowest average retention recorded in May (Fig. 7b). Although the DVM scenario did not present a seasonal signal, it also yielded the lowest average retention in May (Fig. 7d). However, DVM average retention was generally higher than in the Lagrangian scenario (15 % on average; Wilcoxon test, $p < 0.0001$) and two peaks of retention could be distinguished: a higher peak between March and July and a smaller peak between October and December (Fig. 7d).

Seasonal retention patterns per release block were similar for both transport scenarios on Blocks 1 and 2 (Fig. 8). Overall retention on Block 1 was higher in the DVM scenario (Fig. 8a, c), while the inverse was recorded on Block 2 (Fig. 8b, d). Retention was somewhat constant all year on Block 1 except in May, August, and September, when overall retention dropped as much as 50 % (Fig. 8). Block 2 showed a clear pattern for both scenarios; the retention steadily increased from

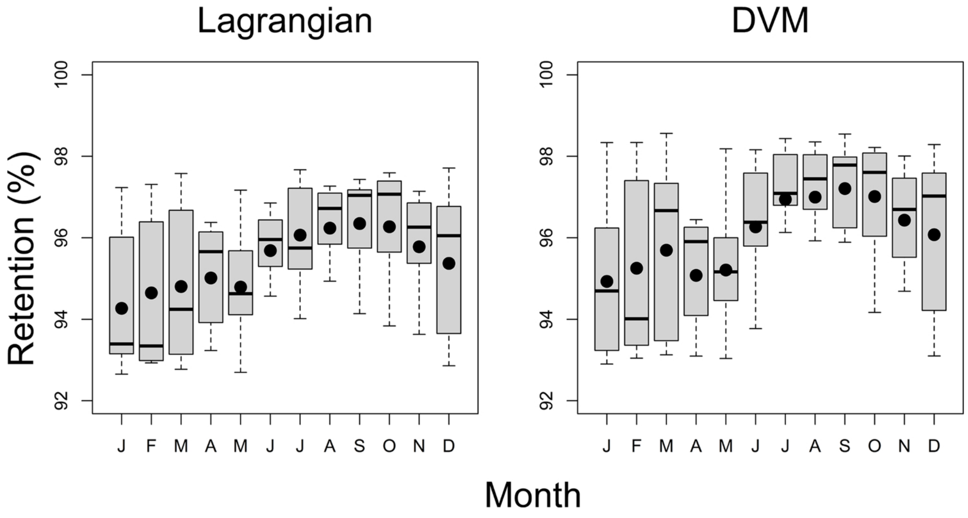

Fig. 6. Box–Whisker plots of seasonal retention patterns around Ilha Grande. Only retention on release Block 1 is shown because the remaining blocks had 100 % retention. Boxes span the 25th–75th percentiles, horizontal bars in the middle of the box indicate the median value, and the whiskers stretch to the most extreme data points (excluding outliers). Black circles represent the average retention.

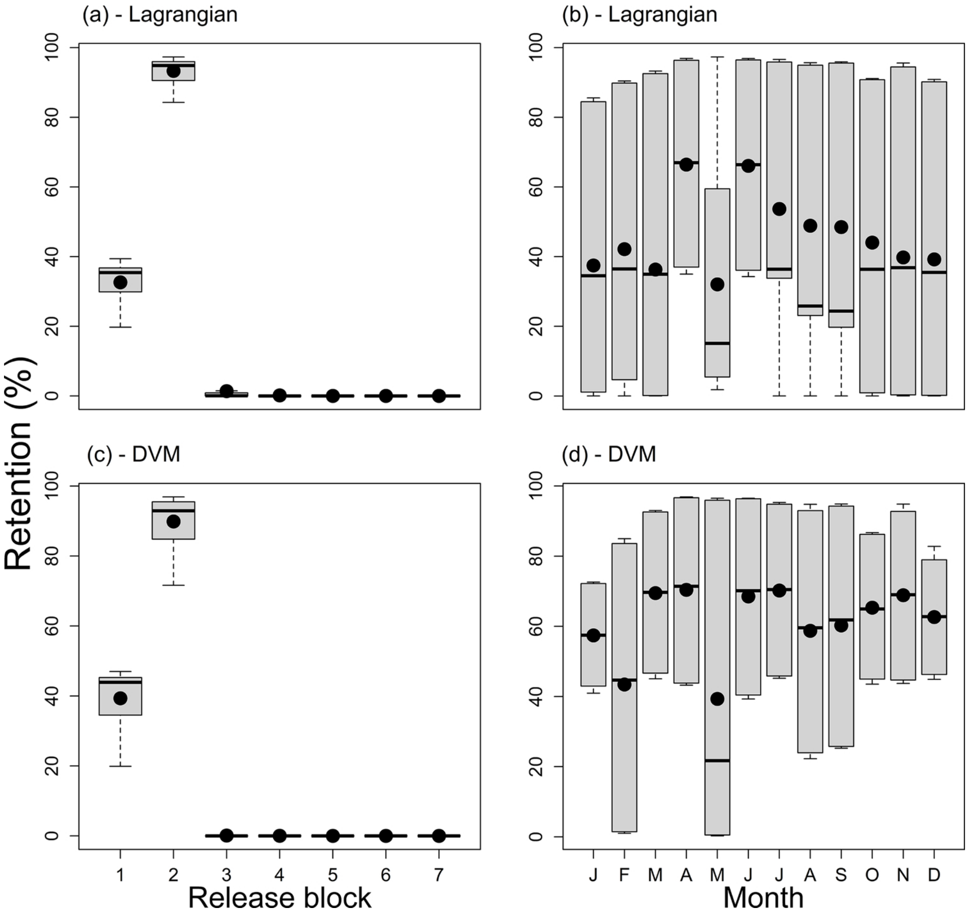

Fig. 7. Box–Whisker plots of spatial and seasonal retention patterns around SSI. Panels (a) and (b) show retention from each release block (Blocks 1–7). Panels (c) and (d) show pooled data of release blocks with non-zero retention (Blocks 1–4). Boxes span the 25th–75th percentiles, horizontal bars in the middle of the box indicate the median value, and the whiskers stretch to the most extreme data points (excluding outliers). Black circles represent the average retention.

January to April and then decreased from September to December, with a distinguishable single peak on November (Fig. 8).

All terms added to the binomial GLM fitted for Blocks 1–7 were statistically significant ($p < 0.001$). The overall model explained 99.9 % of the variance, and *area* and *transport* were the most important terms, explaining 97.4 % and 2.56 % of the total deviance. The remaining terms had much lower explanatory power (Table 1).

3.2.3. Satellite-inferred biological production (sea surface Chla concentration) in the retention areas during the study period

Averaged seasonal satellite-derived sea surface Chla varied between 0.16–1.53 and 0.14–2.46 mg m^{-3} for IG and SSI regions, respectively (Fig. 9). Sea surface Chla concentrations were significantly higher and more variable at SSI than in IG (1.00 ± 0.53 SD vs. 0.68 ± 0.30 SD mg m^{-3}; Student's *t* test, $p < 0.001$) and were higher during austral autumn-winter months (April to September) than the rest of the year. This pattern was more evident at SSI (Fig. 9).

The intraseasonal (autumn-winter) relationship between modeled retention and Chla concentration showed a discernible, strong, and significantly positive correlation ($R = 0.85$, $p = 0.01455$) at Ilha Grande following the removal of two outliers (Fig. 10). In contrast, apparent correlations were not clear for SSI.

3.3. Modeled autumn-winter retention and biological production in relation to spring-summer squid landings

3.3.1. Ilha Grande (IG)

Autumn-winter retention and spring-summer landings yielded straightforward negative linear trends for both artisanal and commercial data (Fig. 11). Although fitting linear regressions to the data yielded a good fit ($R^2 = 0.89$ for artisanal landings and $R^2 = 0.84$ for commercial landings), a statistically significant relationship was identified only for artisanal landings ($p = 0.004$). Three outliers (two from artisanal landings and one from commercial landings) altered the otherwise clear linear trends (dashed lines), resulting in an $R^2 \leq 0.28$, and no statistical significance (solid lines) (Fig. 11).

Autumn-winter surface Chla concentrations and spring-summer squid artisanal and commercial landings also showed negative linear relationships with good fit ($R^2 = 0.94$ and 0.97, respectively) (Fig. 12). A statistically significant trend was found only for artisanal landings ($p = 0.005$). Some outliers (three for artisanal landings and one for commercial landings) deteriorated the fit (solid lines) for artisanal ($R^2 = 0.62$) and commercial landings ($R^2 = 0.48$). The regression between Chla and artisanal landings was statistically significant even when all data points were used for the fit ($p = 0.019$) (Fig. 12).

3.3.2. São Sebastião Island (SSI)

Autumn-winter retention indexes showed a statistically significant positive linear relationship (dashed line; $R^2 = 0.95$; $p = 0.026$) with artisanal landings (Fig. 11), although a single outlier affected the otherwise straightforward fit (solid line). In contrast, no particular trend could be discerned from commercial landings data.

Autumn-winter Chla surface concentration showed a statistically significant negative linear relationship (solid line; $R^2 = 0.98$; $p = 0.001$) with the following spring-summer artisanal landings. The same plotting exercise did not yield any discernible trend in the results from commercial landings (Fig. 12).

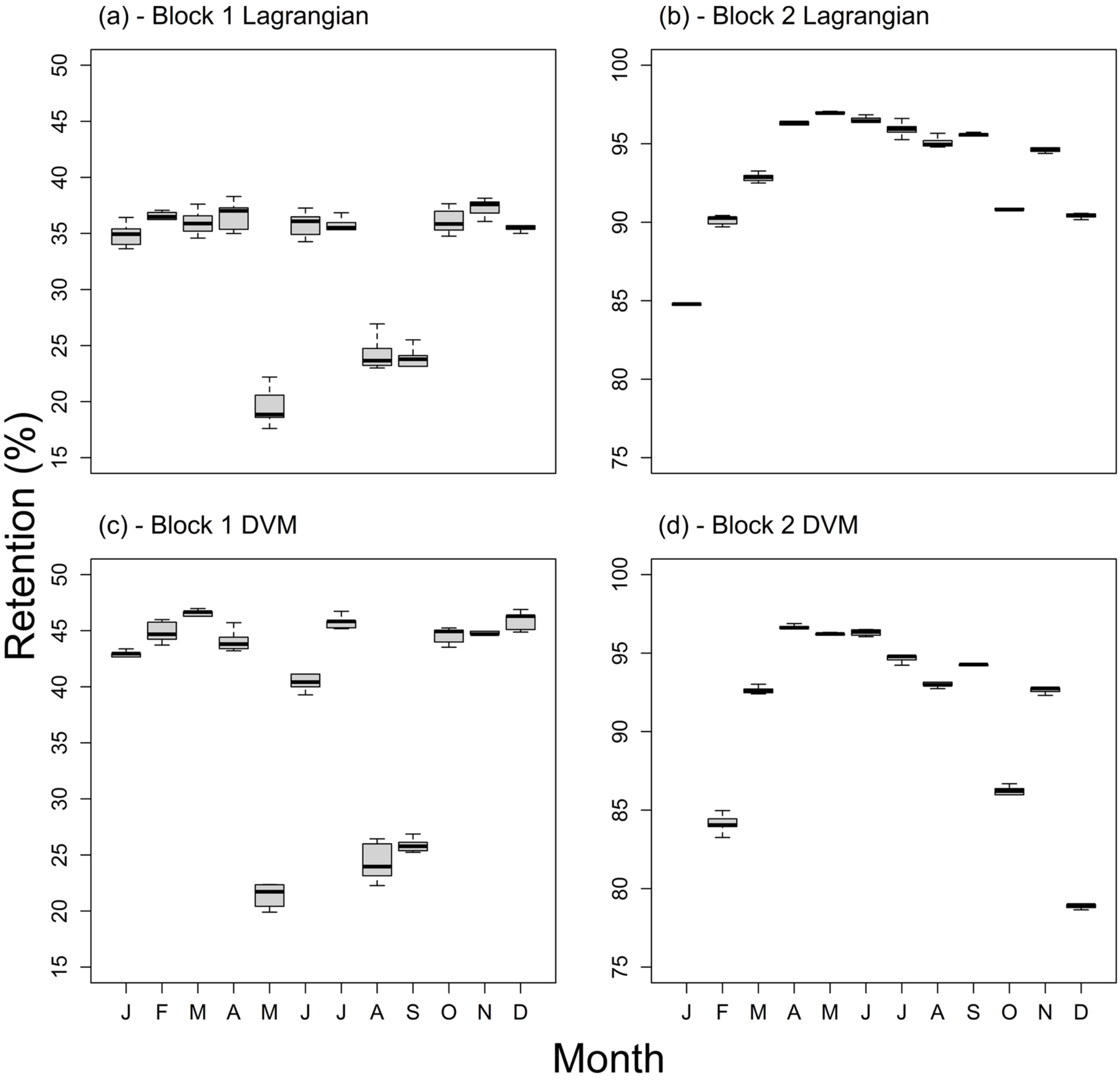

Fig. 8. Box–Whisker plots of seasonal retention patterns from release blocks around SSI. Only Blocks 1–2 areas are shown. Boxes span the 25th–75th percentiles, horizontal bars in the middle of the box indicate the median value, and the whiskers stretch to the most extreme data points (excluding outliers).

Table 1
Deviance analysis in the GLM models of successful retention of virtual paralarvae in the nursery ground around SSI.

Best model: GLM (retention ~ area + transport + area × transport + area × month + transport × month)

AIC: 8516

BIC: 9059

Deviance explained (%): 99.9

Predictor	Df	Deviance	Deviance d.f.	Resid. Dev.	$P(\|>Chi\|)$	Dev. expl. (%)	AIC
Null model				5370640			
area	6	5230831	1505	139809	0.001	97.40 %	143901
transport	1	2517	1504	137292	0.001	2.56 %	141386
area × transport	77	116158	1427	21134	0.001	0.39 %	25382
area × month	6	14656	1421	6478	0.001	0.12 %	10738
transport × month	11	2244	1410	4234	0.001	0.08 %	8516

Resid. Df, residual degrees of freedom; df, degrees of freedom; Resid. Dev., residual deviance; P(> |Chi|), Chi-test P-value; Dev. expl. (%), explained deviance by each model; AIC, Akaike information criterion, BIC: Bayesian information criterion.

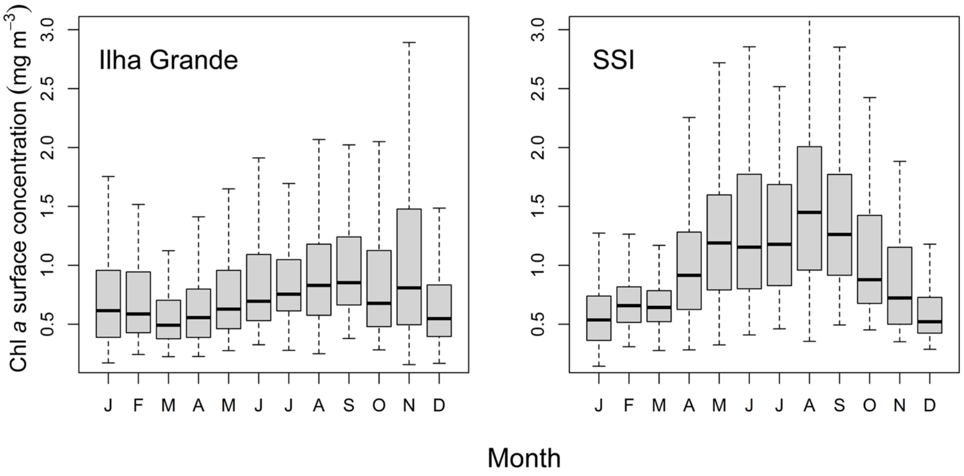

Fig. 9. Box–Whisker plots of satellite-measured (SeaWiFS) seasonal Chla sea surface concentrations in the study area between 2002 and 2010. Boxes span the 25th–75th percentiles, horizontal bars in the middle of the box indicate the median value, and the whiskers stretch to the most extreme data points (excluding outliers).

4. Discussion

4.1. Overview

The particle-tracking Lagrangian modeling experiments allowed us to critically evaluate the conditions of *D. pleii* paralarvae retention and subsequent recruitment along the South Brazil Bight coast in Brazil. Our results show that the studied actual and putative nursery areas were very retentive during autumn-winter season, at the time when the squid fished in spring-summer would have hatched according to a nine-month post-hatching lifespan (Perez et al., 2006). The retention conditions resolved by our modeling approach had direct effects on recruitment strength of adult squid exploited by commercial and artisanal fisheries in the spring-summer period. They also indicated a clear correlation with sea surface Chla concentration. Data also showed that there was a subtle but statistically significance difference in the modeled autumn-winter retention around Ilha Grande between the different transport scenarios adopted. This can be explained by the high level of modeled retention at this nursery ground recorded annually. In contrast, DVM clearly enhanced the modeled arrival and retention of virtual paralarvae from some release blocks around the SSI nursery ground, particularly in the months of lower passive (Lagrangian) retention.

4.2. Retention and biological production during autumn-winter and the implications for *D. pleii* recruitment

Primary production at the study sites, expressed as remotely-measured sea surface Chla concentration recorded by SeaWiFS, was higher during autumn-winter than in spring-summer, which agrees with previous studies in the region (Mazzuco et al., 2015). Thus, tropical squid paralarvae that hatched in autumn-winter may find a food-rich environment to fuel their high metabolism, which would encourage their growth and further development, and ultimately lead to recruitment. In addition, these paralarvae may benefit from an environment with relaxed competition and predation, as most fishes and invertebrates in the South Brazil Bight spawn during spring-summer (Matsuura et al., 1992).

Our data strongly suggest that there is significant paralarval retention in nursery grounds off the coasts of southeastern Brazil. Modeled retention was found to be high regardless of the geographic area, season, or paralarval transport scenario. Retention was much higher in the vicinity of IG than in the surrounding areas of SSI and represented more virtual paralarvae retained from blocks inside the bays located between the island and the continent than from the block at the seaward face of the island. These results agreed with field observations that showed a quasi-permanent clockwise flow around the island (Signorini, 1980a).

In contrast, retention around SSI was lower than around IG, retaining over 44 % virtual paralarvae in our simulations. Despite the less

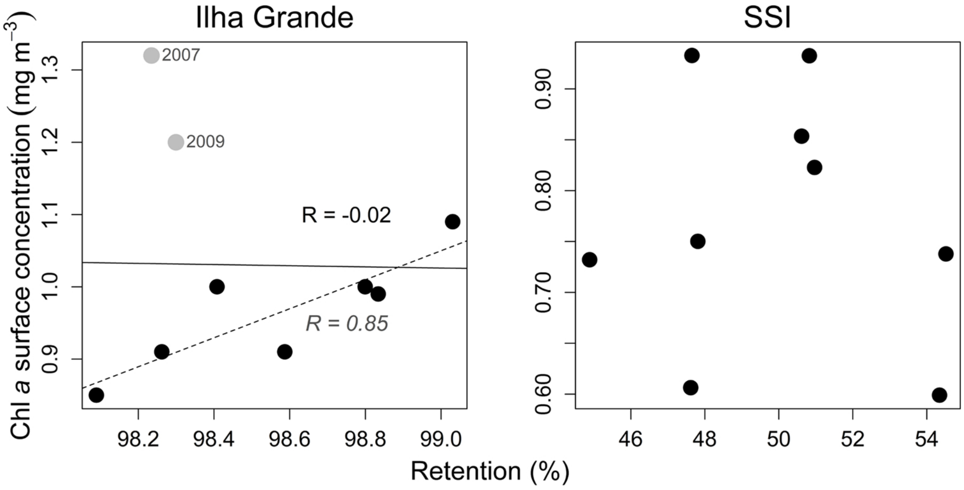

Fig. 10. Correlations between intraseasonal (autumn-winter) average Chla sea surface concentrations (SeaWiFS) and average modeled retention in the study area between 2002 and 2010. Grey data points refer to the noted years from which the data were excluded for best fitting.

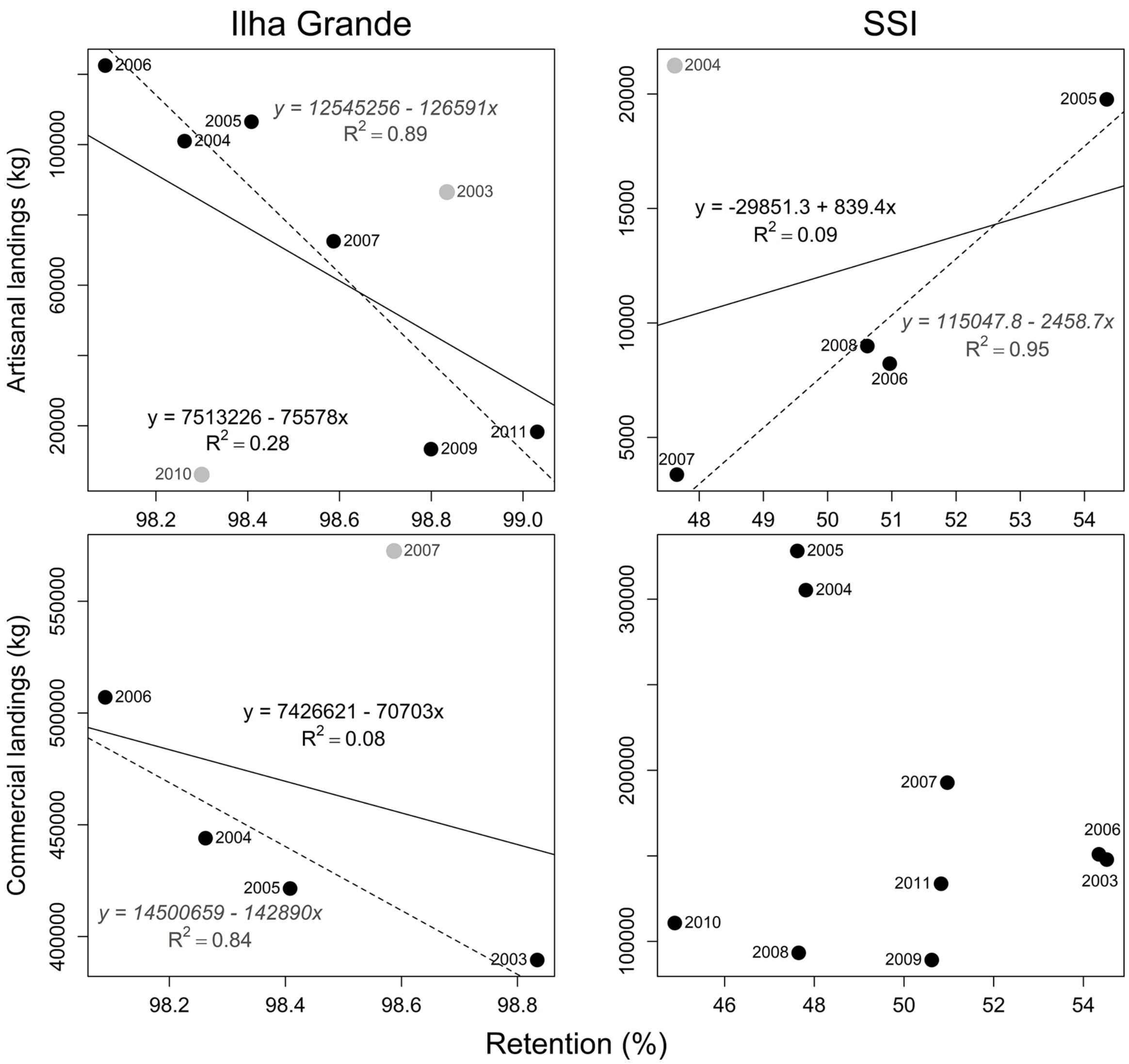

Fig. 11. Correlations between autumn-winter modeled retention vs. *Doryteuthis pleii* landings during the following spring-summer. Years alongside data points refer to the year of the recorded landing. The linear fit is improved if the anomalous years are excluded (dashed line). Grey data points refer to the noted years from which the data were excluded for best fitting.

retentive environment, the SSI surroundings, particularly the northeast portion, have been recognized as both a plankton retention area and a nursery ground for ichthyoplankton (Katsuragawa et al., 2008). Therefore, it can be assumed that this area also comprises a suitable environment for paralarvae.

Interestingly, whereas high retention seemed to translate in higher recruitment for squid caught and landed by artisanal fisheries off the São Paulo coast, the inverse pattern was observed off Rio de Janeiro (i.e. high retention in the nursery grounds yielded lower recruitment for both artisanal and commercial fisheries). This suggests a threshold in retention improving recruitment. After this threshold, other physical and ecological factors might become more important than retention itself. In fact, there is a consensus that recruitment variability may not be caused by a single mechanism acting over early life stages (Leggett and Frank, 2008)

From an ecological perspective, it is possible that high retention increases paralarval mortality through (1) intracohort cannibalism, (2) interspecific predation, (3) food competition with more abundant zooplankters, (4) poor feeding opportunities if the planktonic assemblage is dominated by a single organism type and, (5) reduced oxygen availability in zooplankton-rich waters (Steer et al., 2003; Villanueva and Norman, 2008; Van Noord and Dorval, 2017). Alternatively, increased predation and/or competition pressure may be more prominent in some nursery grounds than others regardless of the degree of larval retention.

Interestingly, there was a negative correlation between Chla and squid landings, but a positive correlation between Chla and the retention index. This may be partially explained by the retention phenomenon itself. During years of moderate autumn-winter retention, higher biomass of planktonic grazers would be concentrated in the nursery grounds, which would result in low Chla accumulation owing to overgrazing and, in theory, abundance of food for *D. pleii* paralarvae which would positively affect the recruitment strength. In contrast, in years of high autumn-winter retention, competition and predation would negatively affect zooplanktonic grazer biomass, resulting in high levels of Chla and lower prey availability for carnivorous zooplankton (Huggett and Richardson, 2000; Fernandes et al., 2012). Van Noord and Dorval (2017) reported an *in situ* negative relationship between Chla concentration and paralarval market squid *D. opalescens* abundance off California coast. These authors propose that moderate zooplankton abundance may provide a suitable feeding opportunity for paralarvae, increasing their survivability likelihood.

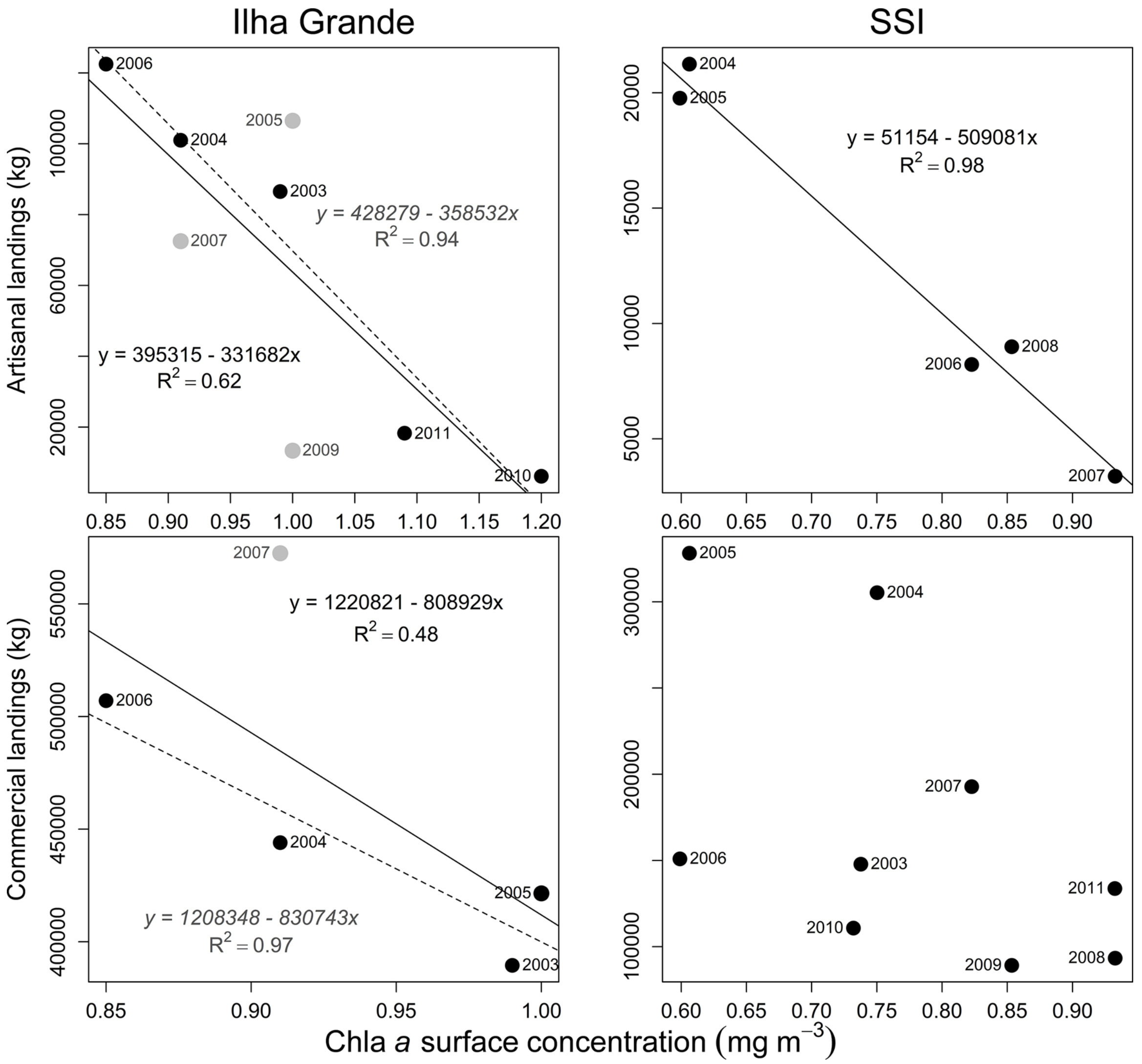

Fig. 12. Correlations between autumn-winter average Chla sea surface concentration (SeaWiFS) vs. *Doryteuthis pleii* landings in the following spring-summer. Years depicted alongside data points refer to the year of the recorded landing. The linear fit is improved if the anomalous years are excluded (dashed line). Grey data points refer to the noted years from which the data were excluded for best fitting.

4.3. Limitations

The major limitation of this study was our poor knowledge on actual locations of *D. pleii* spawning grounds off southeastern Brazil. It is quite likely that proper bottom availability for egg laying is not a constraint for *D. pleii* spawning, as the species lays eggs on soft sea bottoms (Vecchione, 1988), which cover most of the SBB seabed (Mahiques et al., 2004). A refined knowledge on spawning beds would improve particle-tracking squid paralarvae IBM outputs (Downey-Breedt et al., 2016).

Due to the lack of reliable effort data, we were unable to calculate the catch-per-unit-effort as the abundance index for our statistical models. Nevertheless, it seems valid to assume that landing data reflected the patterns of abundance/availability of tropical arrow squid because both artisanal and commercial fleets act upon squid concentrations that are densely aggregated in both time and space (Perez, 2002). Therefore, we assumed that landings were a reliable proxy for squid biomass available in a given year (Roberts, 2005). In other words, we assumed that the amount of squid landed reflected recruitment strength.

It is important to acknowledge that some data points had to be excluded in the autumn-winter retention vs. spring-summer squid landings linear regressions to ensure the best fit. These outliers introduced considerable noise to the otherwise direct relationships, suggesting that in some years environmental factors affected the tropical arrow squid early life history more than retention influenced its recruitment strength (Roberts, 2005; Leggett and Frank, 2008). The causal mechanisms underpinning such environmental noises deserve further investigation and should be pursued in future studies.

Finally, it should be considered that the time series of landing data used in the linear regression modeling (i.e. artisanal fishery data around SSI and commercial fishery data around Ilha Grande) only covered five years, which limited its use.

5. Conclusions

In summary, we demonstrated that our modeled retention conditions during austral autumn-winter were either positively or negatively linked to the spring-summer biomass of tropical arrow squid, depending on the region. In addition, modeled retention positively affected Chla concentration within the same season, at least around the Ilha Grande nursery ground. It was also found that Chla concentration in the spawning season negatively correlates with the recruitment strength. Although these modeled results remain to be confirmed by empirical measurements of retention by currents combined with *in situ* simultaneous estimations of Chla concentration on the studied areas, it is encouraging to find such strong and statistically significant links between modeled results and actual data. If our results endure the common "paradigm jinx" of environmentally based recruitment models that often fail when updated with new data (Leggett and Frank, 2008; Subbey et al., 2014), this modeling approach could be a useful tool for tropical arrow squid fisheries management off the coasts of southeastern Brazil. Future adult biomass could be predicted using updated versions of this coupled IBM–POM model and appropriate management strategies could be devised and enforced before the beginning of the fishing season.

CRediT authorship contribution statement

Rodrigo Silvestre Martins: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing - original draft, Writing - review & editing. **Ricardo de Camargo:** Data curation, Methodology, Software, Validation, Visualization, Writing - review & editing. **Maria A. Gasalla:** Funding acquisition, Project administration, Resources, Writing - review & editing.

Declaration of Competing Interest

None.

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