Species dispersal and community assembly facing the Atlantic meridional Overturning circulation

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ABSTRACT

The strong advective circulation governing western boundary current systems poses challenges to coastal organism to retain their planktonic larvae and assembly in local communities. However, instabilities around the predominant current, generating features such as eddies, may increase retention and thereby enhance local diversity. Here, we have investigated this hypothesis through high-resolution (1/36°) community-based Lagrangian dispersal modelling experiments conducted along the Pernambuco Plateau and adjacent open ocean off Brazil, which is part of the strong Atlantic Meridional Overturning Circulation. In the highly advective north portion of the plateau, we found that retention is reduced and advection from open ocean is intense. Under such circumstances, the assembly of local communities is likely driven by mass effect, which results in homogeneous communities with reduced biodiversity. In contrast, in the south portion of the plateau, eddies and meanders associated with the interaction of the currents with the plateau topography and the seasonal variability of the South Equatorial Current bifurcation increase local retention and reduce advection from open ocean. In such conditions, both, species sorting and mass effect assembling archetypes, likely drive the distinct and rich biodiversity inhabiting the region to the south of the plateau. The dispersal patterns obtained from the Lagrangian experiments align with the known spatial patterns of biodiversity distribution along the Tropical Southwestern Atlantic and provide important insights for regions and taxa for which knowledge is limited or absent. These results also provide elements for the proper definition of biodiversity conservation and management strategies and for a better understanding of the processes regulating community assembly in highly advective systems around the globe.

1. Introduction

In tropical marine systems, the western boundaries of ocean basins are heavily constrained by strong currents advecting open ocean waters over continental shelves and transporting local neritic water away along the shelf (Loder et al., 1998; Tosetto et al., 2021). These currents also interact with continental margins and flow fast along coastlines and/or continental slopes (Dossa et al., 2021; Lumpkin and Garzoli, 2005; Stramma and England, 1999). The dispersal of marine biota occurs primarily during their early planktonic life stages, which are transported through ocean currents (Bradbury et al., 2008). Therefore, coastal and neritic species may face a challenge to recruit in suitable habitats present in these western boundary systems, as the dominant current pattern transports their planktonic propagules away (Byers and Pringle, 2006).

The Tropical Southwestern Atlantic, which is part of the Atlantic Meridional Overturning Circulation (AMOC), is a typical western boundary system. Within this region, the southern portion of the South Equatorial Current (sSEC) reaches the Brazilian coast, seasonally ranging between 12 and 20°S, and bifurcates into two branches. The northern branch feeds the North Brazil Undercurrent (NBUC), which

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flows strongly northward along the continental slope (Dossa et al., 2021; Stramma and England, 1999). The NBUC system promotes highly advective dispersal dynamics that spread oceanic plankton over the continental shelf (Neumann-Leitão et al., 1999; Santana et al., 2020; Tosetto et al., 2023, 2022, 2021).

Despite this predominant dispersal pattern, a specific portion of the shelf, bounded by the Pernambuco Plateau (7.5–10°S, Fig. 1), has shown a rich and distinctive marine biodiversity, making it a hotspot for coastal conservation in Brazil (Eduardo et al., 2018; Ferreira et al., 2006; Pereira et al., 2021). In this zone, during their planktonic phase, coastal species may extend nearly to the shelf break, contrasting with the predominance of oceanic plankton species over the shelf further north (Tosetto et al., 2021). Thus, understanding the drivers of enhanced biodiversity along the Pernambuco Plateau can help deciphering the processes regulating community assembly in highly advective systems and establishing a proper definition of biodiversity conservation and management strategies in the Tropical Southwestern Atlantic.

The Pernambuco Plateau is located just beyond the northernmost limit of the sSEC bifurcation and is characterized by a large widening of the continental slope at around 1500 m depth (Buarque et al., 2016; GEBCO, 2019). A possible explanation for the enhanced biodiversity in this highly advective system is that fluctuations around the predominant western boundary current increase the retention of planktonic stages of organisms that are able to recruit (Byers and Pringle, 2006) in the region of the Pernambuco Plateau. These fluctuations are likely associated with uplifted water (Silva et al., 2022), barotropic instabilities leading to the generation of eddies and meanders arising from the interaction of the NBUC with topography or from the sSEC bifurcation and wind stress curl (Dossa et al., 2022; Soutelino et al., 2011).

However, to date, only a few studies, spatially and temporally limited, have evaluated the current dynamics and their fluctuations along the continental shelf within the Pernambuco Plateau. Results indicate that in winter, when wind fields are stronger and oriented

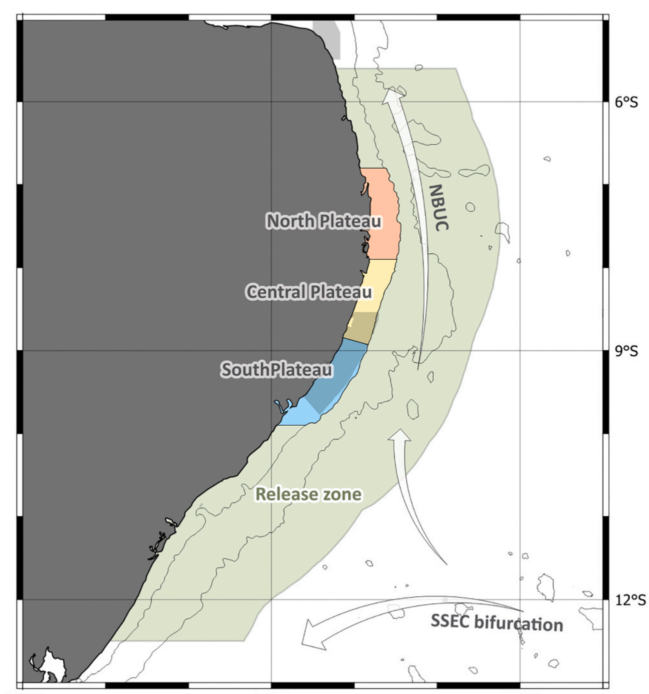

Fig. 1. Study area in the Tropical Southwestern Atlantic showing the polygon used for release (green) and the recruitment zones (Blue, yellow and red) along the Pernambuco Plateau. Shaded polygons indicate marine protected areas. Grey contours correspond to the 90 and 3000 m depth isobath. NBUC = North Brazilian Undercurrent. SSEC = Southern branch of the South Equatorial Current.

northwest, coastal currents in the region follow the NBUC pattern along the slope, predominantly flowing northwards (Lira et al., 2010; Schettini et al., 2017). However, in summer, when winds are weaker and predominantly oriented westwards, a southwestward flux along the coast has been observed (Lira et al., 2010; Parente et al., 2021; Schettini et al., 2017). Although this flux may potentially represent a seasonal coastal countercurrent, it has yet to be properly assessed. Fluctuations in the predominant current direction have also been observed in both winter and summer (Schettini et al., 2017).

Despite the potential relevance of such circulation features in influencing the dispersal of planktonic stages, community assembly, and consequently biodiversity patterns, a direct evaluation of dispersal patterns in marine systems requires tracking the movement of planktonic organisms, which are too small for traditional tagging methods. To overcome this drawback, Lagrangian dispersal models combining hydrodynamics and species traits have been developed to simulate planktonic dispersal in marine systems (Lett et al., 2008; Siegel et al., 2003; Swearer et al., 2019). This approach provides a mechanistic framework to link physical ocean circulation to biologically meaningful dispersal and recruitment processes. Here, we aim to use such an approach to explicitly investigate how physical circulation dynamics shape larval transport and community assembly, in order to test the hypothesis that mesoscale (∼20–100 km) variability in ocean circulation, such as eddies, meanders and counter flows, along and likely related to the Pernambuco Plateau, increases the retention of planktonic stages of organisms, (Suzuki and Economo, 2021; Tosetto et al., 2023). To this end, we used a community-based Lagrangian dispersal framework that integrates high-resolution ocean circulation with dispersal ecology (Lett et al., 2008; Tosetto et al., 2023) to investigate spatial and temporal patterns in community assembly and the recruitment of autochthonous and allochthonous organisms along three zones of the continental shelf in the vicinity of the Pernambuco Plateau.

2. Methods

2.1. Study area

The study focuses on the portion of the Northeast Brazilian continental shelf bounded by the Pernambuco Plateau and its vicinity in the Tropical Southwestern Atlantic (Fig. 1). The shelf along this region is relatively narrow, generally less than 40 km wide (Castro et al., 2006). The Pernambuco Plateau extends up to the 1500 m isobath with approximately 200 km over the shelf and 100 km offshore (Buarque et al., 2016). In this area, the shelf supports high biodiversity including extensive coral reefs (Eduardo et al., 2018; Pereira et al., 2021), sustaining some of the main tourism hotspots in northeast Brazil. To protect this biodiversity, the area has been designated a biodiversity hotspot and a marine protected area for sustainable development (Ferreira et al., 2006).

2.2. Hydrodynamic model

We used the hydrodynamic model NEMO – Nucleus for European Modelling of the Ocean (NEMO v4.0.2; Madec et al., 2017) to simulate ocean circulation in the study domain. The model has a horizontal resolution of 1/36° (∼3 km) and 75 fixed z-coordinate levels, ranging from 0 to 5000 m, with increased vertical resolution near the surface (23 levels in the first 100 m) and cell thickness reaching 160 m near the bottom. These resolutions allowed us to capture submesoscale features (∼1–20 km) such as meanders and eddies, which strongly influence passive dispersal. The boundary conditions are from the global ocean reanalysis GLORYS12V1 which includes assimilation of *in situ* and satellite data (Lellouche et al., 2018). At the open boundaries, velocity, temperature, salinity, sea level and derived baroclinic currents were prescribed. We used the General Bathymetric Chart of the Oceans (GEBCO, 2019) bathymetry interpolated onto our grid, with the minimum depth set at 12.8 m. The model was forced using ERA-5 reanalysis atmospheric fluxes (Hersbach et al., 2020). River discharges were based on daily runoff data from the ISBA-CTRIP model (Decharme et al., 2019), and were injected into the model as null-salinity surface mass sources at river mouths. Additionally, the model incorporated tidal forcing from the fifteen major tidal components (M2, S2, N2, K2, 2 N2, MU2, NU2, L2, T2, K1, O1, Q1, P1, S1, and M4), including elevation and barotropic currents derived from FES2014 (Carrère et al., 2016). Momentum advection was computed using a third-order upstream biased scheme (UP3) with built-in diffusion. The temporal integration was performed using an Asselin filter with a 150 s time step. The vertical diffusion coefficients were computed from a $k - \varepsilon$ turbulent closure scheme. Bottom friction was represented using a quadratic drag law with a coefficient of 2.5×10^{-3}, and free-slip lateral boundary conditions were assumed. The free surface was resolved using a time-splitting technique, integrating the barotropic component explicitly. The simulation was run from 1 January 2005 to 31 December 2017, with analyses focused on the 2009–2017 period. We verified that the model reached an equilibrium in seasonal cycles after four years of spin-up. For the Lagrangian simulations, we extracted daily velocity fields from the NEMO outputs to drive particle advection. A detailed model validation and realism assessment was conducted in Tosetto et al. (2023). To provide a study-specific evaluation of the circulation relevant to larval transport and cross-shelf exchange along the Pernambuco Plateau, we compared the monthly climatology of the NEMO simulation with the GLORYS12V1 reanalysis over the study region. The comparison focused on sea surface height and depth-averaged (0–80 m) current structure over the continental shelf and slope, as well as on the seasonal variability of along-shelf circulation. This assessment was used to verify that the model realistically reproduces the dominant circulation patterns controlling particle transport in the region (Supplementary fig. 1, 2).

2.3. Lagrangian simulations

We used the Lagrangian modelling tool Ichthyop (Lett et al., 2008) to track particles representing passive numerical larvae transported by the NEMO velocity fields. Rather than targeting specific species, our approach focused on community-level dispersal patterns (Tosetto et al., 2023). For that, we considered two planktonic larval durations (PLD): 15 days, representing most marine invertebrates, and 30 days, representing most marine fish (Bradbury et al., 2008). Particles were also classified based on their release habitat: continental shelf (0–90 m depth) and open ocean (>90 m depth), since the shelf break represents a major boundary in marine communities.

Simulations were run monthly, with a 30-day duration and a 300-second time step, from January 2009 to December 2017 (108 runs). On the first day of each month, 52,000 particles were randomly released between the surface and 30 m depth within a large polygon designed to encompass the entire Pernambuco Plateau and its immediate surroundings (green zone in Fig. 1), capturing both shelf and adjacent open-ocean waters. The southern portion of the polygon was extended to account for the predominant northward currents in the region, ensuring that advective pathways along and away from the shelf were adequately sampled. The release depth range (0–30 m) was chosen to represent the vertical distribution of planktonic stages in the upper water column, where most larvae are likely to occur. The number of particles (52,000) ensures sufficient statistical coverage to resolve dispersal patterns and the relative contributions of shelf versus oceanic sources. Monthly single releases were used to capture temporal variability across the year while maintaining computational feasibility, and the 30-day simulations allow for tracking dispersal over relevant PLDs. We note that the size and geometry of the release area influence the proportion of particles classified as shelf- or ocean-derived; the chosen polygon was intended to reflect realistic circulation patterns and to maximize the representativeness of both habitat types. Particles were tracked using forward Euler advection, with bouncing behaviour at the coastline and seabed. Particles leaving the study domain were considered lost. No swimming, horizontal dispersion, buoyancy, vertical migration or lethal environmental filters were included. Particle positions were recorded at 15 and 30 days to capture both PLDs.

We conducted limited sensitivity analyses to evaluate the robustness of our findings to key methodological choices, including particle number, release depth range, and release polygon size. Across all tested configurations, the relative patterns of particle retention and neritic and oceanic advection remained consistent among recruitment zones and circulation scenarios (Supplementary Fig. S3).

2.4. Data analysis

We defined three recruitment zones along the Pernambuco Plateau's continental shelf (north, central and south plateau; Fig. 1). For each recruitment zone, monthly run, and PLD, we recorded the amount of particles (i) retained in the zone (i.e., released and recruited in the same zone); (ii) advected from other parts of the continental shelf; and (iii) advected from the open ocean. These monthly counts of retained and advected particles were then used as input for statistical analyses to compare spatial and seasonal patterns of dispersal and recruitment across zones and circulation scenarios. Monthly statistics were calculated solely from particles released in that month. Although the maximum planktonic larval duration can slightly exceed the end of the release month (e.g., in February), each month was treated independently, and particles were not carried over to subsequent months.

Factorial analyses of variance (ANOVA) were performed to compare differences in retention and advection patterns after $\log_{10}(x + 1)$ transformation of the data, across recruitment zones and seasonal circulation scenarios (see circulation dynamics section below). Non-metric multidimensional scaling, based on a Bray-Curtis similarity matrix, after $\log(x + 1)$ transformation of the data, was used to identify and order spatial and seasonal recruitment patterns (retention, advection from the continental shelf and advection from the open ocean, for both PLDs).

To investigate the hydrodynamic drivers of local particle retention, we used Generalized Additive Models (GAMs; Hastie and Tibshirani, 1990). For each recruitment zone and monthly run, we considered mean current speed and the proportion of positive values in the zonal and meridional current components as indirect measures of circulation variability during the first 10 days after particles were released. Alternative predictors (e.g., mean zonal and meridional speeds, and Eddy Kinetic Energy were tested, but showed weaker or no explanatory power (Supplementary fig. 4). Factorial ANOVA and GAMs were performed in Statsoft Statistica 10 (StatSoft Inc, 2011). Non-metric multidimensional scaling was performed in PRIMER 6.1.16 (Clarke and Gorley, 2006). Maps were produced in QGIS 3.36.2 (QGIS Development Team, 2024).

3. Results

3.1. Circulation dynamics

When analyzing the climatology of monthly current outputs (averaged over 0–80 m depth) from the hydrodynamic model (Fig. 2), we observed the NBUC flowing strongly northward along the continental slope. Along its entire length, the current is stronger in Austral winter, peaking in July, and weaker in summer. In all months, the NBUC is more intense north of the Pernambuco Plateau, where the coastline and continental slope shift orientation, aligning more closely with the trade winds. Over the continental shelf, the climatology of coastal currents revealed distinct seasonal patterns. North of the Pernambuco Plateau, coastal currents followed the northward NBUC flow year-round, strengthening in winter and weakening in summer. In the central and southern regions of the Pernambuco Plateau coastal currents also flowed northwards, parallel to the NBUC, in winter (April-August). We refer to this period as the regular flow scenario. In contrast, from September to March, a southward coastal counterflow was observed in this region

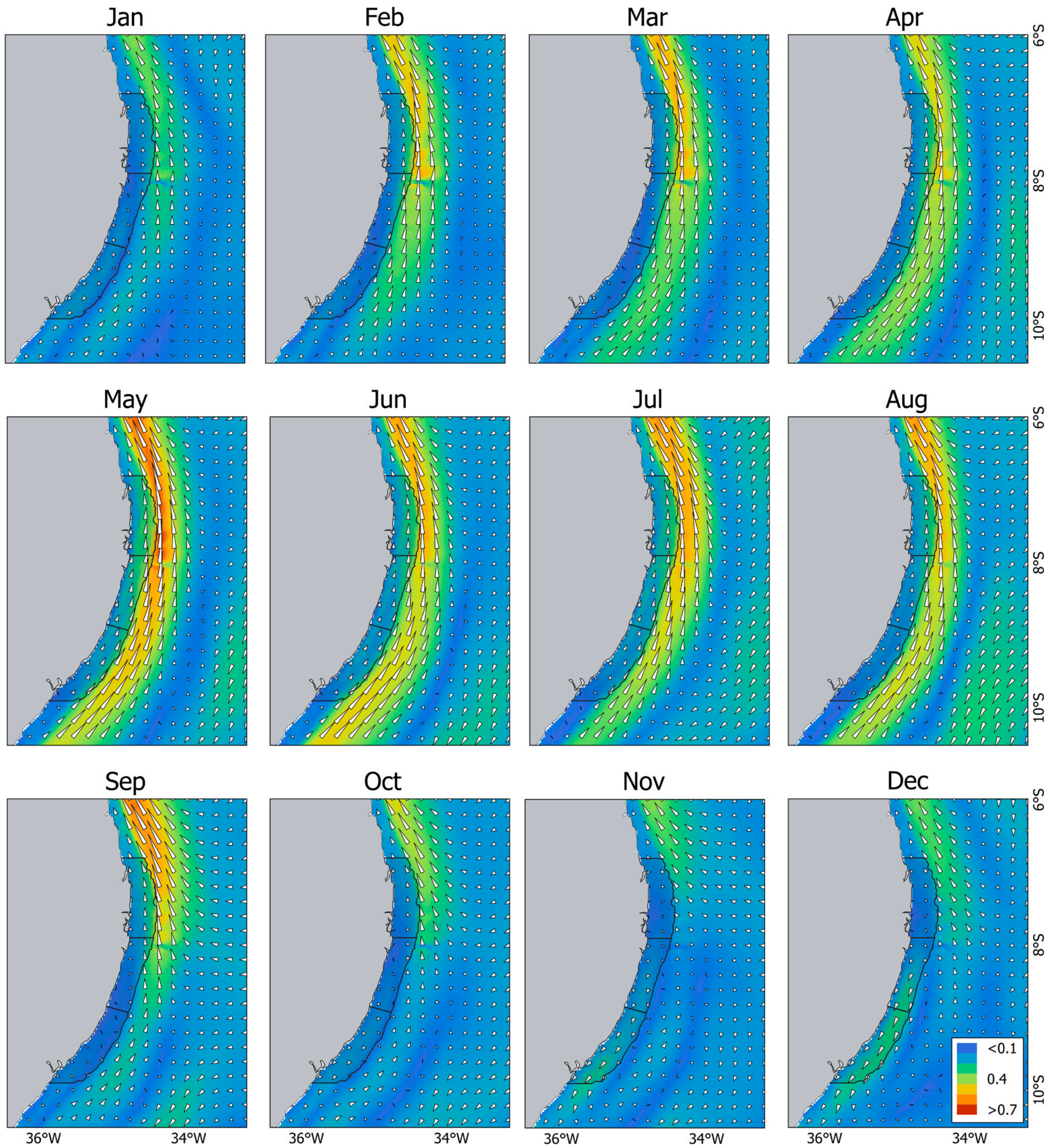

Fig. 2. Monthly climatology (2009–2017) of 0–80 m depth integrated current speed (colour scale) and directions (arrows) from the hydrodynamic model outputs.

(from ~ 8.2 to ~ 12.2°S), which we define as the counterflow scenario. Although the climatological data suggest that this counter flow acts as a seasonal coastal countercurrent, daily model outputs (Supplementary movie S3) reveal highly variable current vectors, with sub-mesoscale eddies, meanders and bifurcating open ocean intrusions occurring without clear patterns in either scenario.

3.2. Spatial and seasonal patterns in the assembly of particles

The majority of particles recruited in the three zones of the Pernambuco Plateau came from the open ocean (Fig. 3). In the South Plateau, the advection of oceanic particles with medium PLD varied significantly between the regular flow and counter flow scenarios, with lower advection occurring in the latter (691 ± 359 vs. 1024 ± 415; Fig. 3). In the remaining recruitment zones, the advection of oceanic particles fluctuated across both circulation scenarios, and no significant differences were observed (Fig. 3).

Advection from the continental shelf, i.e., particles coming from other regions of the continental shelf, was markedly seasonal, with significant differences between circulation scenarios across all recruitment zones and both PLDs (Fig. 3). The three recruitment zones presented similar assembly patterns, with higher advection from the continental shelf in the regular flow scenario (426 ± 173, 377 ± 221 and 337 ± 173 medium PLD particles month^{-1} and 218 ± 123, 239 ± 128 and 250 ± 120 long PLD particles month^{-1} for the North, Central and South Plateaus respectively; Fig. 3). During this period, advection from the continental shelf occurred predominantly along the coastline, following the flux of the regular northward current, leading to the recruitment of particles in the zones to the north. Conversely, under the counter flow scenario, particles released over the shelf were mostly transported away from the recruitment zones, either southward (when released south of ~ 8.2°S) or northward (when released north of ~ 8.2°S).

The North and South Plateaus displayed distinct patterns in autochthonous particle retention (Fig. 3). The North Plateau retained very few particles during the regular flow scenario, as strong coastal

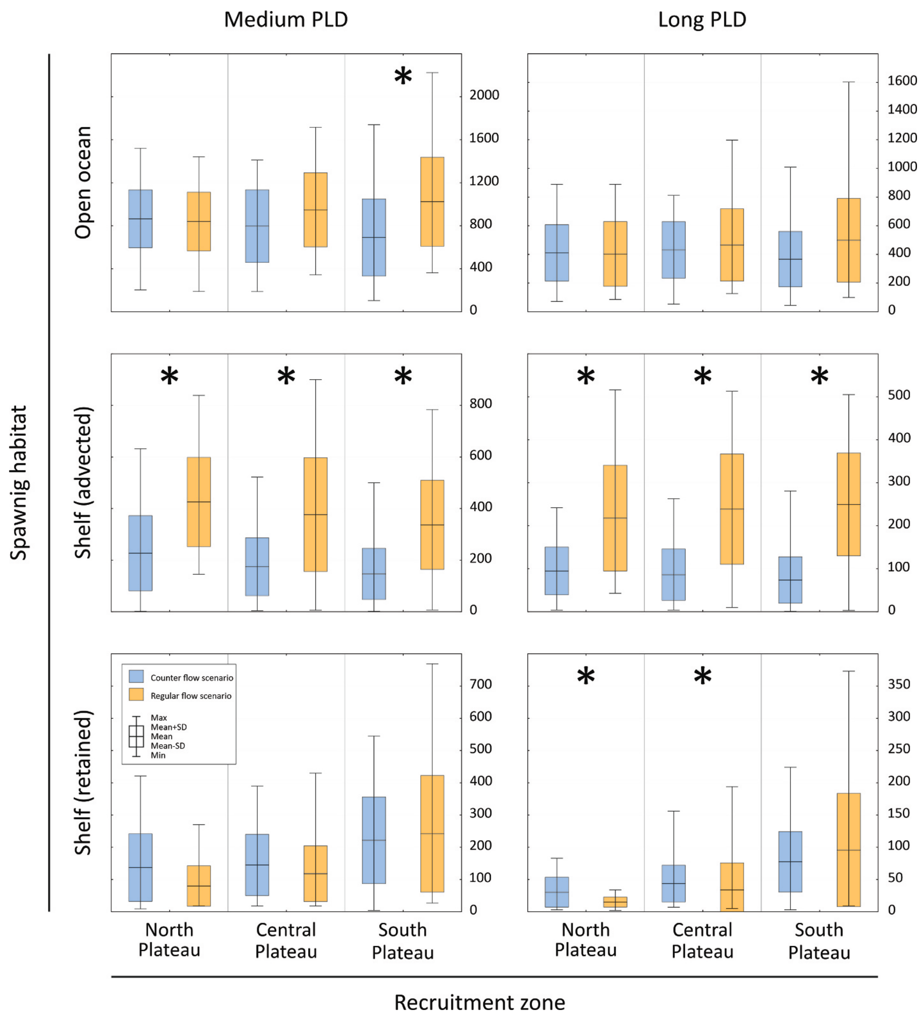

Fig. 3. Number of advected (open ocean and shelf) and retained particles (particles month^{-1}; Mean ± SD) that recruited in each recruitment zone in each circulation scenario, classified according to their planktonic larval duration (PLD). * = Significant differences between scenarios in pair-wise Tukey test.

currents transported most particles northward. In the counter flow scenario, when northward current speed decreased, retention slightly increased (137 ± 105 and 30 ± 23 particles month^{-1} for the medium and long PLDs respectively), with significant differences between scenarios for the long PLD (Fig. 3). In contrast, the South Plateau retained a consistently high number of particles across both scenarios, assembling retained particles year-round (222 ± 134 medium PLD particles month^{-1} and 77 ± 47 long PLD particles month^{-1} in the counter flow scenario and 242 ± 181 medium PLD particles month^{-1} and 95.7 ± 87.8 long PLD particles month^{-1} in the regular flow scenario; Fig. 3). The Central Plateau, serving as a transitional zone between the North and South Plateaus, showed an intermediate retention pattern, with slightly higher values in the counter flow scenario (145 ± 95 and 44 ± 29 particles month^{-1} for the medium and long PLDs, respectively) (Fig. 3), and significant differences between scenarios for the long PLD (Fig. 3).

In the non-metric multidimensional scaling analysis, the assembly patterns of the six categories of particles were structured both seasonally and spatially (Fig. 4). Seasonally, regular flow scenario months clustered in the top-left half of the diagram, while counter flow scenario months clustered in the bottom-right half (Fig. 4). Spatially, during the regular flow scenario, the North and South Plateaus were clearly separated (Fig. 4), reflecting strong differences, particularly in retention. The central plateau was spread between the other two recruitment zones (Fig. 4). In the counter flow scenario, North and South Plateaus remained distinct (Fig. 4) but some North Plateau months and all Central Plateau months plotted closer to the South Plateau, reflecting increased retention in these zones (Fig. 4).

3.3. Hydrodynamic drivers of local retention

The number of particles retained was highly correlated between medium and long PLDs within each recruitment zone (North Plateau: $r = 0.631 p < 0.001$; Central Plateau: $r = 0.491$, $p < 0.001$; South Plateau: $r = 0.794$, $p < 0.001$) as well as across all recruitment zones combined ($r = 0.749$, $p < 0.001$). Thus, to investigate the drivers of local retention we pooled results across both PLDs.

Mean current speed and predominant flow direction during the first 10 days after release were strong predictors of retention. In all recruitment zones, highest retention was observed at lower current speeds, peaking below 0.15 m s^{-1} (Fig. 5). The South Plateau presented more release events with such conditions, partially explaining its higher retention. However, even at current speeds below 0.15 m s^{-1}, retention varied depending on current direction. Lower retention was observed when currents predominantly flowed northward and/or eastward (Fig. 5). This flow, which was more predominant in the North and Central plateaus, carries particles in the direction of the NBUC or towards the continental shelf to the north, where stronger currents transporting particles away are observed. Distinctly higher retention occurred in periods dominated by southward (all zones) and/or westward (Central and South Plateaus) flows, even at currents speed up to 0.3 m s^{-1} (Fig. 5). Such flows shelter particles from the NBUC influence, enhancing local retention. These conditions occurred more frequently in

Fig. 4. Non-metric multidimensional scaling plot showing seasonal (months) and spatial (recruitment zones) patterns in the recruitment of particles along the Pernambuco Plateau. Point labels indicate months. The x- and y-axes are dimensionless and do not have direct ecological interpretation; the plot should be interpreted based on the ranked distances between points rather than absolute axis values.

the South Plateau, further explaining its higher retention.

Since northward and eastward currents proportions were correlated ($p < 0.001$; $r2 = 0.212$), we fitted two GAMs to predict particle retention, each incorporating current speed and predominant flow direction as explanatory variables. Both models indicated significant ($P < 0.01$) relationships with current speed and predominant direction. The model including northward current proportion showed higher explanatory power, accounting for 53% of the retention variance across the three recruitment zones. After removing the effect of the northward current proportion (i.e., based on the partial effect estimated by the GAM), current speed displayed an almost linear negative relationship with retention, declining from zero to 0.3 m s^{-1} (where most data were concentrated; Fig. 6). After removing the effect of current speed (partial GAM effect), retention peaked when northward flow was minimal (0–20%) but declined as northward flow increased (Fig. 6).

4. Discussion

Here, we used a community-based approach on Lagrangian dispersal simulations (Lett et al., 2008; Tosetto et al., 2023), with a high resolution model of ocean circulation, explicitly coupling physical circulation dynamics with dispersal ecology, to investigate spatial and temporal patterns in community assembly and the recruitment of organisms along the Pernambuco Plateau off Brazil, which is part of the strong Atlantic Meridional Overturning Circulation. Based on the recruitment patterns of retained and advected (from the shelf and the open ocean) particles in the simulations (Fig. 7), we provide valuable new insights into how circulation-driven dispersal pathways translate into observed biodiversity patterns along the Western tropical Atlantic that likely apply to highly advective coastal systems in general. This community-based approach focuses on identifying general dispersal processes that drive community assembly. It is important to recognize, however, that passive dispersal operates alongside environmental filters and species interactions, and these factors likely interact to produce species- or assemblage-specific biodiversity patterns (HilleRisLambers et al., 2012; Mittelbach and Schemske, 2015).

Here, we root our findings in two key ecological concepts. The first, which we call the retention concept, refers to the persistence of local populations in highly advective systems through circulation-driven retention of planktonic larvae near their source areas. In such systems, the maintenance of viable populations of benthic fauna with planktonic larvae depends on seasonal or stochastic fluctuations around the main current. These fluctuations retain planktonic larvae for recruitment into the region where they were spawned. Otherwise, larvae would be transported away, leading to local population extinction (Byers and Pringle, 2006). Our Lagrangian dispersal modelling of the Pernambuco Plateau and NBUC system provided useful insights into the physical mechanisms controlling larval retention and their ecological consequences for biodiversity.

Fluctuations in coastal circulation aside from the main western boundary current were observed at multiple scales within the Pernambuco Plateau. At the local scale, the submesoscale eddies, meanders and bifurcating open ocean intrusions were intense in the southern portion of the plateau, contrasting with the predominantly unidirectional northward flow observed along the continental shelf to the north. These features may be associated with barotropic instabilities, wind stress curl (Dossa et al., 2022), the intense eddy activity and meandering at the sSEC bifurcation (Soutelino et al., 2011) and the uplifted water and eddies generated by the interaction of the NBUC with the plateau topography (Silva et al., 2022). Most of the time, these features resulted in periods with reduced average flow speed (typically below $\sim$ 0.15.m s^{-1}), which proved to be the main driver of local particle retention. The exception was when, under the influence of these features, the predominant current flow was oriented northeast. In such cases, even at reduced current speed, particles entered the NBUC system over the slope and were transported away to the north (examples of the particle pathways in months when retention was higher and lower than the expected by current speed are shown in Fig. 8).

At a regional scale, seasonal variability in the intertropical convergence zone, wind fields and the SSEC bifurcation latitude (Dossa et al., 2021; Stramma and England, 1999) led to a general reduction in northward current speed along the entire NBUC system in summer. This

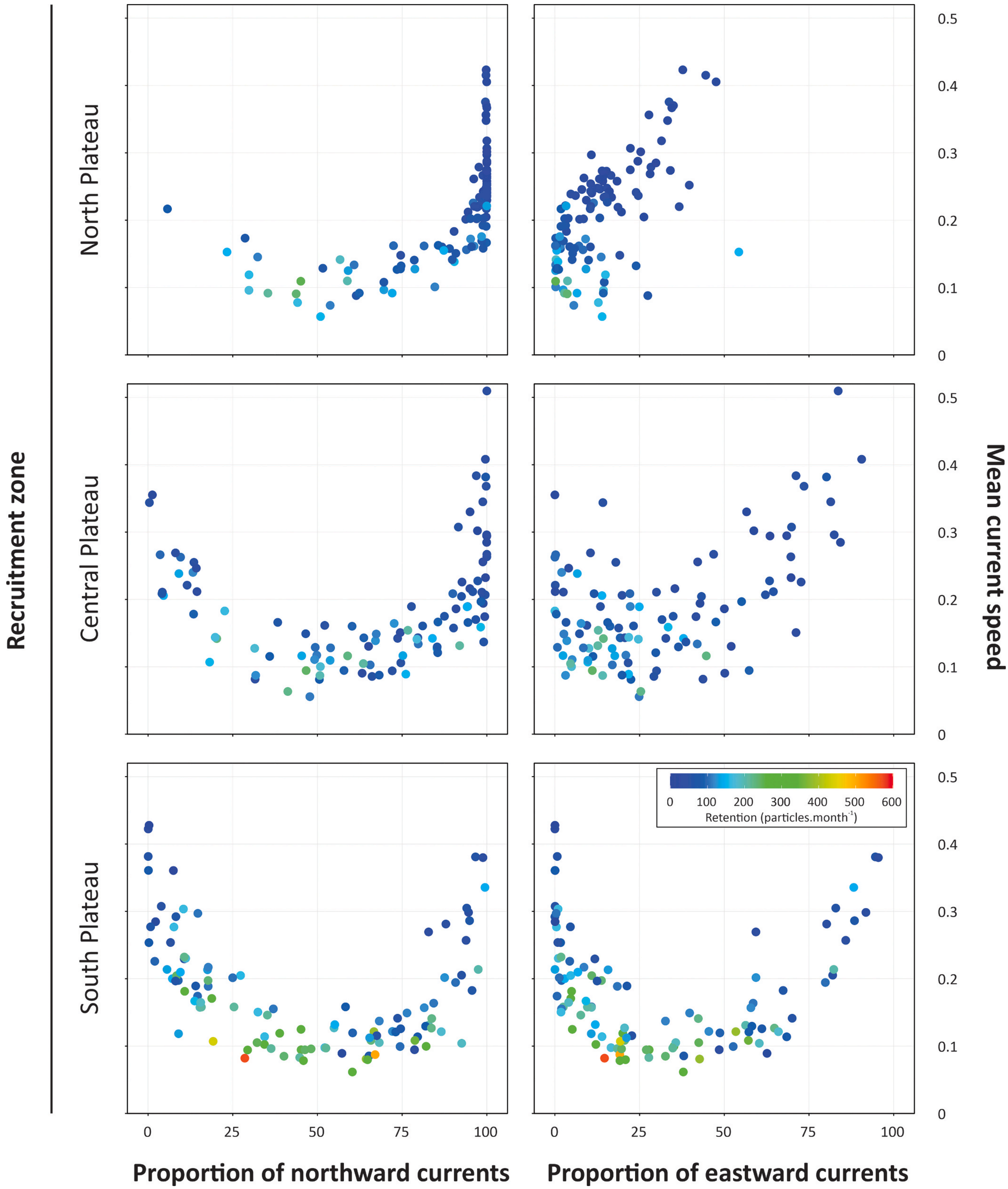

Fig. 5. Mean current speed averaged over 10 days after particle release vs. the predominant meridional (left) and zonal (right) directions of the mean currents in each recruitment zone. Colors indicate particle retention (mean of medium and long planktonic larval durations). A total of 108 points are represented, corresponding to the total number of times particles were released.

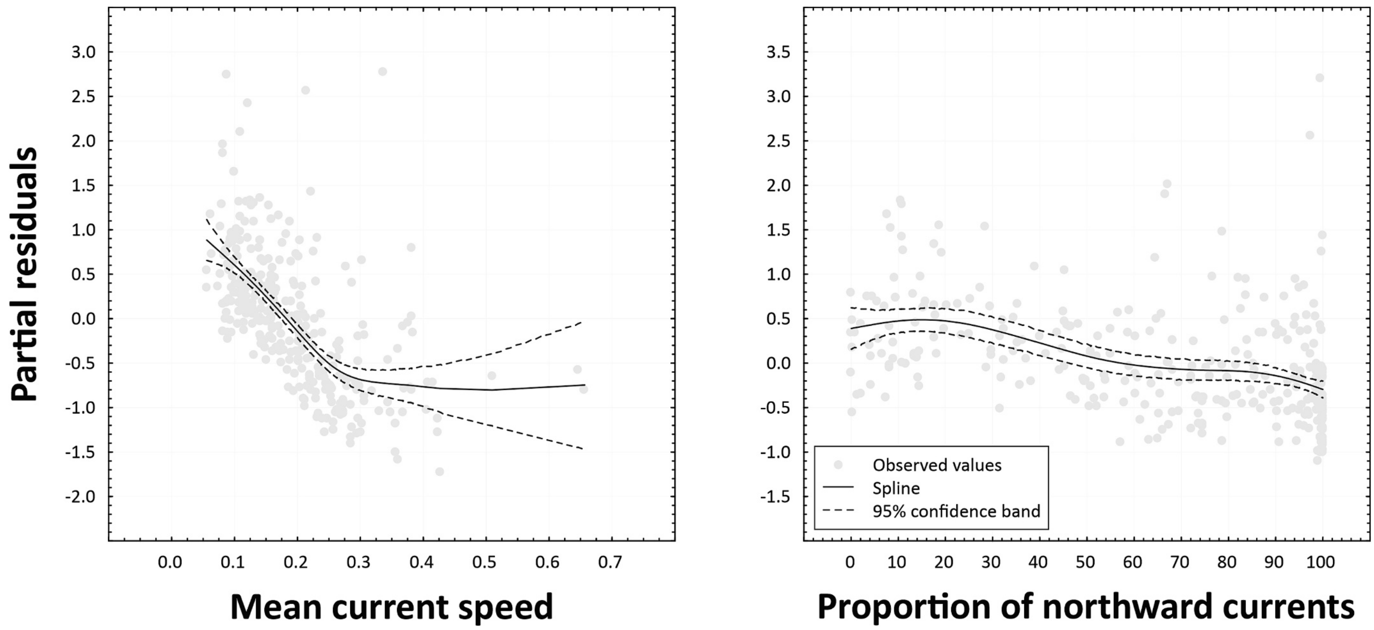

Fig. 6. Results of the Generalized Additive Model showing the retention trends along the Pernambuco Plateau and the modelled effects of current speed and the proportion of northward currents. Solid lines show the smoothing function and dotted lines the 95% confidence interval.

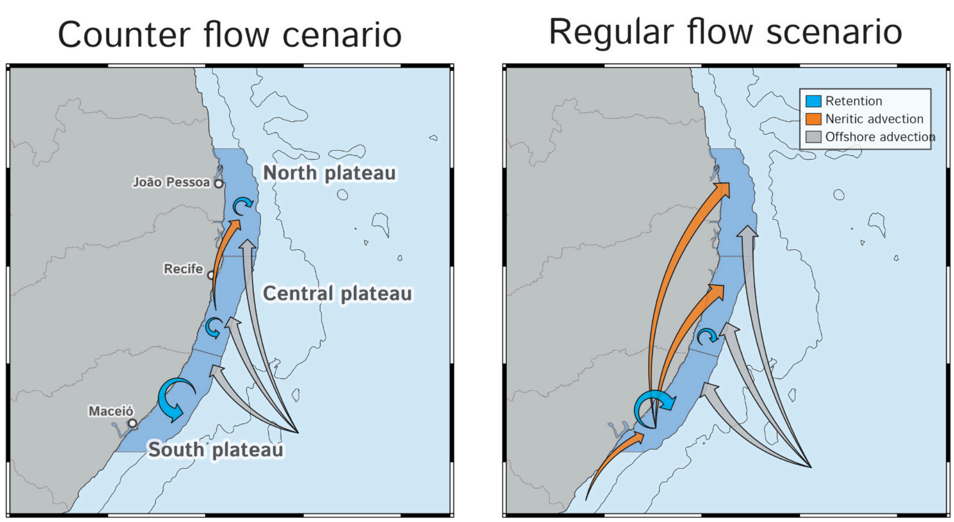

Fig. 7. Summary of particles retention and advection patterns along the Pernambuco Plateau in two distinct circulation scenarios.

led to the emergence of a coastal counter flow along the South Plateau. Under this scenario, particle retention slightly increased along the Central and North Plateaus, contrasting with the regular flow scenario, in which most particles were transported northward by the strong NBUC current.

From a metapopulation perspective, coupling our findings with the retention concept (Byers and Pringle, 2006) provides an interesting interpretation of the biodiversity patterns along the Pernambuco Plateau. In this framework, coastal species can spawn and recruit year-round in the South Plateau. As a result, more species can maintain viable populations there, increasing local biodiversity, as observed *in situ*. Otherwise, species inhabiting the Central and North Plateaus face greater challenges in maintaining local populations, relying on restricting their reproductive period to higher retention scenarios (Byers and Pringle, 2006) or functioning as sink systems (Aiken and Navarrete, 2011), sustained by larval advection from the continental shelf to the south.

However, beyond species-specific population dynamics, western boundary systems are characterized by strong coastward currents that spread open ocean plankton over the continental shelf. Depending on the intensity of dispersal, these organisms may outcompete local neritic species and dominate pelagic habitats (Tosetto et al., 2021). To extend our analysis beyond the metapopulation dynamics and retention concept (Byers and Pringle, 2006), and to better understand community assembly in highly advective systems, we frame our findings in a second concept, within metacommunity ecology (Leibold et al., 2004). Among the theories in this field, a key concept, here termed the balance concept, describes how community assembly reflects a balance between species sorting by local environmental conditions and mass effects driven by dispersal from surrounding regions (Leibold, 2018; Suzuki and Economo, 2021). Under strong mass effects, high dispersal allows non-resident species to persist locally despite unfavorable conditions, whereas lower dispersal promotes species sorting and locally adapted communities.

To quantify this balance in marine systems using Lagrangian dispersal modelling, the ratio of advected to retained particles has been

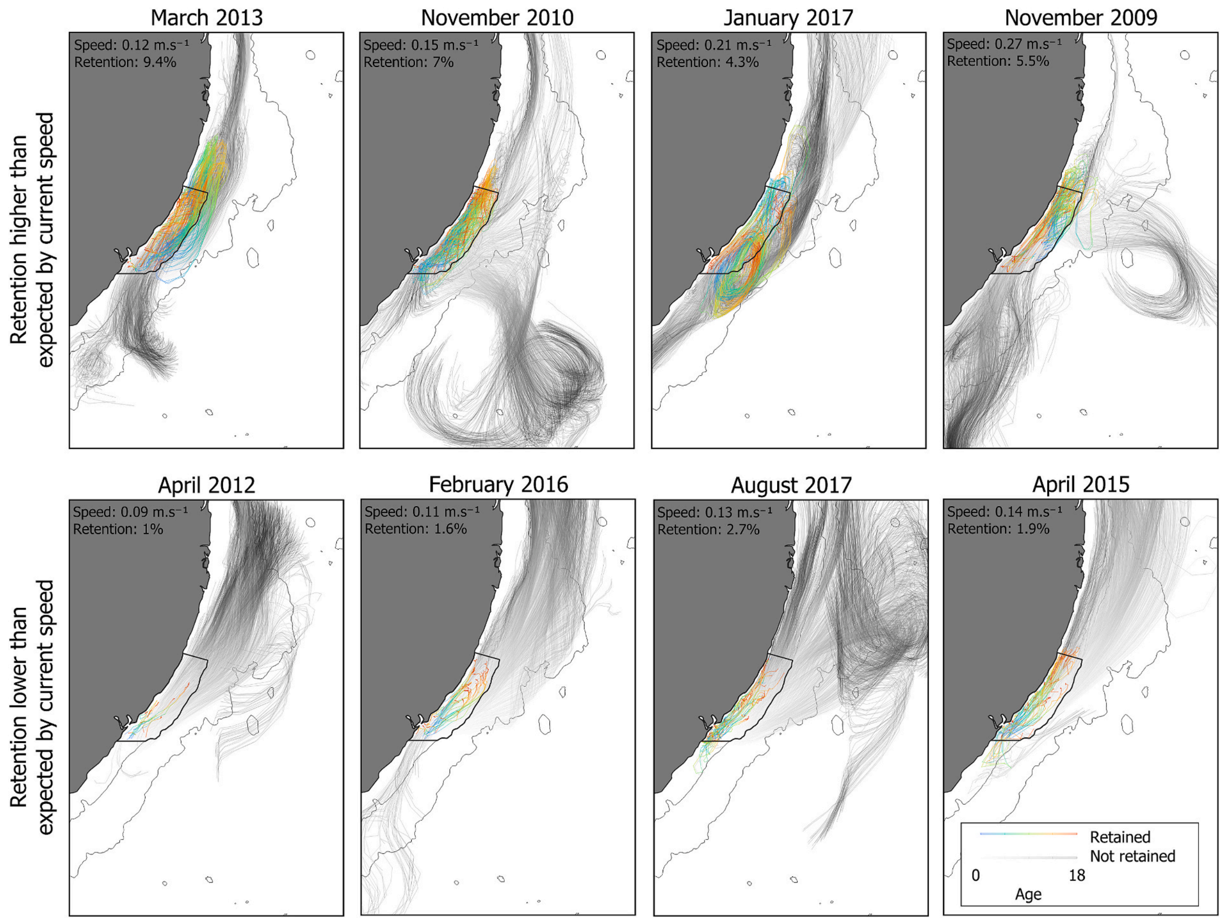

Fig. 8. Examples of pathways of particles released along the South Plateau where retention was higher (upper panels) and lower (lower panels) than expected by current speed. Panels ordered by current speed.

suggested (Tosetto et al., 2023). Here we quantified the retention to advection from open ocean proportion for each monthly model run (note that advection from the continental shelf was not considered), revealing distinct patterns for each recruitment zone (Fig. 9a). While in the North Plateau, mostly less than 20% of the recruiting particles originated there, in the South Plateau, the proportion of retained particles varied widely from 5% to 60%.

Under the balance concept, we hypothesize that community assembly in the north Plateau is primarily driven by mass effects (Fig. 9b), where continuous inflows of allochthonous organisms (dispersal surplus) overshadow local retention (Leibold et al., 2004; Suzuki and Economo, 2021; Tosetto et al., 2023). Such an assembly archetype is expected to produce homogenous local communities (low turnover) dominated by the best dispersers, even if environmental filters are suboptimal for their ecological niche. These species exclude autochthonous organisms, ultimately reducing both local and regional biodiversity (Fig. 9b; Suzuki and Economo, 2021).

In contrast, the South Plateau is likely influenced by both species sorting and mass effect assembling. In a metacommunity ruled solely by species sorting, in each local habitat, species are sorted according to their ecological niches and interactions with other autochthonous species, resulting in heterogeneous (high turnover) communities (Suzuki and Economo, 2021). When the advection of allochthonous species increases, though not enough to override local retention, both species sorting and mass effect interact, allowing local species to coexist with allochthonous species. This increases local biodiversity while reducing species turnover (Suzuki and Economo, 2021).

These expected biodiversity patterns align with *in situ* observations along the Pernambuco Plateau. In its northern portion, similar to patterns observed along the adjacent continental shelf to the north, mass effect dominates and planktonic assemblages are homogeneous and dominated by typically open-ocean species (Neumann-Leitao et al., 2008; Neumann-Leitão et al., 1999; Santana et al., 2020; Tosetto et al., 2021). Conversely, in the southern portion of the plateau, where species sorting and mass effect likely interact, coastal species may spread almost to the shelf break (Tosetto et al., 2021). The region is known for its rich and distinctive marine biodiversity, with well-developed coral reefs, and its status as a coastal conservation hotspot in Brazil (Eduardo et al., 2018; Ferreira et al., 2006; Pereira et al., 2021).

Nevertheless, a still missing piece in the balance concept is the role of habitat heterogeneity. Due to ocean currents, planktonic community distributions are especially prone to mass effect, particularly in western boundary systems where epipelagic water masses are relatively homogeneous, and coastal water influence is restricted to nearshore areas (Schettini et al., 2017; Tosetto et al., 2022). Many species, however, spend only part of their life-stages as plankton (meroplankton), still requiring suitable benthic habitats for recruitment. Since benthic environments are more heterogeneous, species sorting processes are likely stronger there, even with significant inflows of allochthonous larvae (i.e. larvae arrive but fail to recruit). Future studies comparing biodiversity patterns across taxa with distinct life histories (e.g. holoplankton, meroplankton with benthic/nektonic adults, and holobenthos) could help clarify the role of habitat heterogeneity in the balance concept within marine systems.

In conclusion, by applying a community-based approach to Lagrangian dispersal simulations, explicitly integrating high-resolution ocean circulation dynamics with dispersal ecology, we gained new insight into biodiversity patterns along the Pernambuco Plateau,

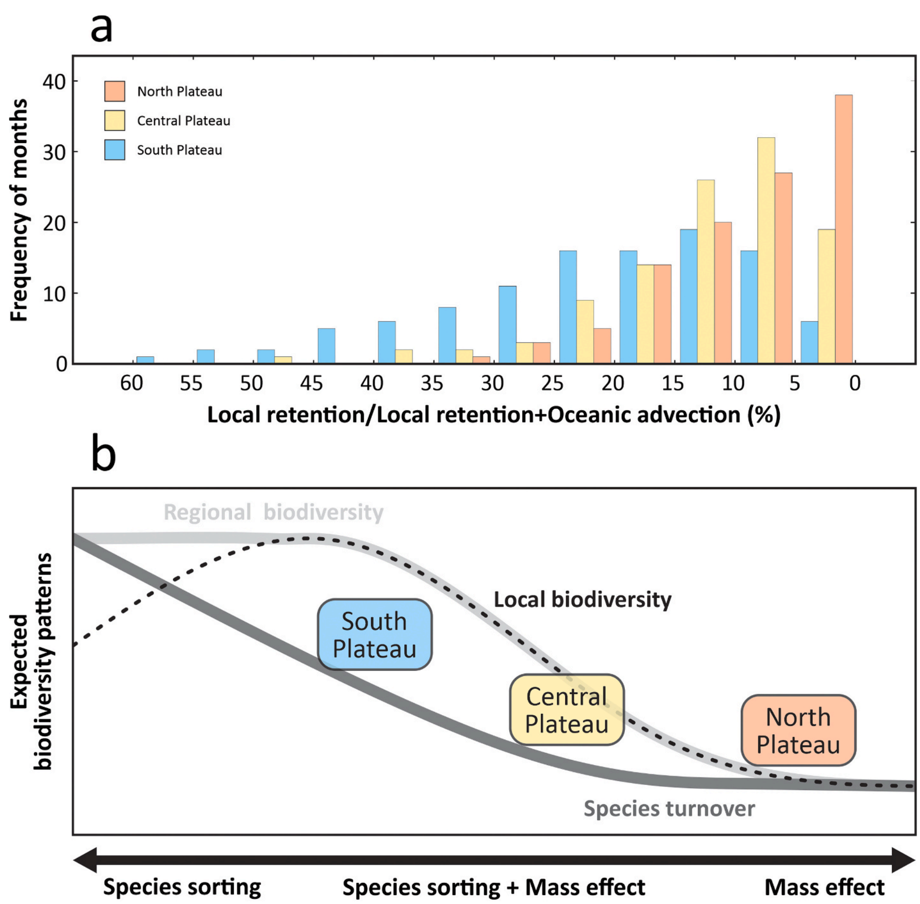

Fig. 9. (a) Frequency histograms of the proportion between retained and offshore-advected particles in each recruitment zone along the Pernambuco Plateau. (b) Suggested place of each recruitment zone in the relation between dispersal rate, assembling archetypes and biodiversity patterns as hypothesized by Suzuki & Economo (2021). Under species sorting, species are sorted according to their ecological niches and interactions with other autochthonous species, resulting in heterogeneous (high turnover) communities with an overall high regional biodiversity. When species sorting and mass effect interact, local species coexist with allochthonous species, increasing local biodiversity and reducing species turnover. Under mass effect the best dispersers dominate and exclude autochthonous organisms reducing both local and regional biodiversity and resulting in homogenous local communities (low turnover).

embedded in the highly advective western boundary system of the tropical southwest Atlantic. Grounded on the retention and balance concepts (Byers and Pringle, 2006; Suzuki and Economo, 2021), our findings suggest that circulation-driven dispersal and retention processes are key mechanisms shaping community assembly and the biodiversity structure of the region. Lagrangian dispersal models are also useful for generating new hypotheses for future field validation particularly by linking physical oceanographic variability to ecologically testable predictions, which is especially important for data-poor regions such as the Tropical Southwestern Atlantic. Finally, given its ecological significance, expanding and strengthening marine protected areas within the South Pernambuco Plateau, such as the APA Costa dos Corais (MMA, 2025), emerges as a strategic management measure for the entire Tropical Southwestern Atlantic.

CRediT authorship contribution statement

Everton Giachini Tosetto: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Christophe Lett:** Writing – review & editing, Visualization, Methodology, Investigation. **Sigrid Neumann-Leitão:** Writing – review & editing, Visualization, Supervision, Project administration, Methodology, Investigation. **Ariane Koch-Larrouy:** Writing – review & editing, Methodology, Data curation. **Nicolas Barrier:** Writing – review & editing, Software, Methodology. **Alex Costa da Silva:** Writing – review & editing, Visualization, Validation, Investigation. **Ramilla Assunção:** Writing – review & editing, Visualization, Methodology, Investigation. **Camila Artana:** Writing – review & editing, Visualization, Methodology, Investigation. **Alina Nathanael Dossa:** Writing – review & editing, Visualization, Methodology, Investigation, Formal analysis. **Guillaume Morvan:** Writing – review & editing, Methodology, Data curation, Conceptualization. **Arnaud Bertrand:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2026.103705.

Data availability

All data supporting the findings of this study are available within the article and its supplementary materials

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