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Diel vertical migration and seamount stepping stones promote species connectivity from coastal to offshore insular systems in the Tropical Southwestern Atlantic

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Abstract

The recruitment of marine species in isolated oceanic island systems can be challenged by prevailing currents, as exemplified by the Tropical Southwestern Atlantic. In this region, the Fernando de Noronha ridge hosts several seamounts, the Rocas Atoll and the Fernando de Noronha Archipelago, which are home to great marine biodiversity. However, along the ridge, the central branch of the South Equatorial Current (cSEC), flowing westward, poses a challenge to the recruitment of organisms toward Fernando de Noronha. To unveil critical insights into the intricate processes shaping biodiversity in these insular ecosystems, we use a dispersal Lagrangian tool to explore the role of diel vertical migration (DVM) to depth strata influenced by the South Equatorial Undercurrent (SEUC), which flows eastward bellow the cSEC, in shaping species dispersal and metacommunity dynamics. Our results show that while not a direct journey, the DVM into SEUC-influenced strata increases the possibility that the seamounts and the Rocas Atoll act as stepping stones between the continental shelf and Fernando de Noronha. Propagules of organisms originating primarily from the continental shelf are transported to the western seamounts of the ridge. Upon reaching the western seamounts, organisms can find suitable habitats to recruit. The progeny of these communities that migrate to SEUC-influenced strata have the opportunity to reach suitable habitats at the Rocas Atoll and the Eastern seamounts, ultimately connecting to the Fernando de Noronha archipelago. These results provide scientific fundamentals for the development of a functional network of marine protected areas in the Tropical Southwestern Atlantic.

Oceanic islands within tropical regions stand out as marine biodiversity hotspots in the global ocean, sustaining high levels of endemism in their biota (Roberts et al. 2002; Jefferson and Costello 2020). This biodiversity holds critical relevance, especially for islands in tropical countries, where many small villages and cities depend on small-scale fisheries and ecotourism

for their economic and social development (Lam et al. 2020). Despite their socioecological significance, insular marine systems are increasingly threatened by anthropogenic pressures. Their isolation, which shields them from mainland pressures, is offset by specific vulnerabilities, such as high species endemism, limited shallow-water habitats, and a disproportionately large

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coastlines-to-land area ratio, making even minor coastal activities impactful (Nunn et al. 1999; Triantis et al. 2010). As a result, oceanic islands have experienced the majority of marine species extinctions reported in recent history (Triantis et al. 2010).

The establishment of marine protected areas (MPAs) has been recognized as a key strategy to protect the ecosystems surrounding oceanic islands (Roberts et al. 2003; Frascchetti et al. 2005; Zhao et al. 2020). However, oceanic islands are inherently open systems that exchange large amount of organisms, species, and resources with other islands, seamounts, and coastal areas. Such exchanges occur mostly through passive transport by ocean currents. Consequently, in addition to establishing MPAs around insular systems, identifying and protecting key areas connected to these islands is a highly recommended strategy that provides mutual benefits to both systems (Magris et al. 2016, 2017; Endo et al. 2019).

In the Tropical Southwestern Atlantic, the Fernando de Noronha Ridge hosts the Fernando de Noronha Archipelago, Rocas Atoll, and several seamounts emerging from the seabed to the east and west of Rocas Atoll (Stramma and England 1999; Silva et al. 2021). This Archipelago and Atoll are known to harbor great marine biodiversity and abundance of organisms, and MPAs were established around them (Krajewski and Floeter 2011; Magris et al. 2013; Pimentel et al. 2020; Salvat et al. 2022). However, questions remain regarding the recruitment of benthic and demersal marine organisms around these islands in the face of prevailing ocean currents.

Along the ridge, the central branch of the South Equatorial Current (cSEC), flowing westward, poses a challenge to the recruitment of organisms at the eastern end of the ridge, especially in the Fernando de Noronha Archipelago. Indeed, this unidirectional flow coming from the open ocean can transport drifting planktonic larvae spawned in the waters surrounding the islands to recruit along the Northeast Brazilian coast, but not the other way around (Endo et al. 2019; Tosetto et al. 2023). Thus, a question arises: how can benthic and demersal marine organisms (reef fish, crustaceans, corals, and many other animal groups of ecological and economical relevance), whose dispersal occurs predominantly among planktonic stages, recruit in Fernando de Noronha Archipelago at the eastern margin of the ridge? Given the similarities in biodiversity patterns there with systems further west, such as Atoll das Rocas (Floeter et al. 2001), it is unlikely that the Fernando de Noronha Archipelago could be a nearly isolated system that depends solely on the retention of organisms that have sporadically colonized the system over time for the maintenance of its local communities. Therefore, to investigate the question, we delve deeper: beneath the westward flow of the cSEC, at depths greater than ~ 150 m, the counter-directional South Equatorial Undercurrent (SEUC) flows from west to east (Silva et al. 2021), potentially carrying organisms from the coast to the islands. Since many epipelagic planktonic organisms migrate to deeper waters during the day to avoid predators in photic layers (Brierley 2014; Bianchi and Mislan 2016), diel vertical migration (DVM) emerges as a crucial

factor for epipelagic organisms to reach the SEUC strata. Therefore, we assume that DVM to the SEUC-influenced strata may contribute to the dispersal of organisms spawned along the coast to the seamounts and islands of the Fernando de Noronha Ridge, thereby interconnecting these systems.

Understanding such patterns of dispersal and exchange of planktonic organisms between systems is essential to design a science-based functional network of MPAs in the Tropical Southwestern Atlantic (Magris et al. 2013, 2017; Zabala 2018). However, planktonic animals are too small for traditional devices used to track the movement of adult fish and other large marine animals. Dispersal Lagrangian tools, which combine hydrodynamics and species traits to simulate the transport of organisms in marine systems (Siegel et al. 2003; Lett et al. 2008; Swearer et al. 2019), allow overcoming this drawback to better understand connectivity patterns in marine systems. Such tools can be used both to confirm patterns previously observed *in situ*, and to generate hypotheses for subsequent field validation. The latter is particularly important to properly guide future *in situ* work for regions or animal groups where information is limited or absent such as the Tropical Southwestern Atlantic. Here, we use a dispersal Lagrangian tool (Ichthyop; Lett et al. 2008) to investigate how DVM patterns observed through active acoustics data could affect the recruitment of organisms in the Fernando de Noronha Archipelago, Rocas Atoll and seamounts of the Fernando de Noronha Ridge and its connectivity with the Northeastern Brazilian Continental shelf. In contrast to previous work suggesting low connectivity in the area (Endo et al. 2019), our experiment explores a wider range of connectivity pathways by considering diel vertical migration to SEUC layers and the possibility of recruitment and spawning over seamounts. This provides valuable insights to improve our understanding of connectivity and recruitment patterns in the region, and contributes to the further development of a robust network of MPAs in the Tropical Southwest Atlantic.

Methods

Study domain

The study domain encompasses the Tropical Southwestern Atlantic Ocean between 1°S , 38°W and 12.5°S , 30°W (Fig. 1). Located 230 and 350 km off the coast, the Rocas Atoll and the Fernando de Noronha Archipelago rise from the seabed around 4°S , accompanied by a series of seamounts forming the Fernando de Noronha Ridge (Motoki and Freire Motoki 2012). The distance between the nearest seamount and the shelf break is about 80 km, and the maximum distance between offshore features is about 90 km. The Northeast Brazilian continental shelf is relatively narrow, ranging from 40 to 80 km, followed by a steep slope extending from 100 m to about 3500 m depth (Loder et al. 1998; Castro et al. 2006). MPAs have been established around the Fernando de Noronha Archipelago, Rocas Atoll and over the continental shelf off the Pernambuco and Rio Grande do

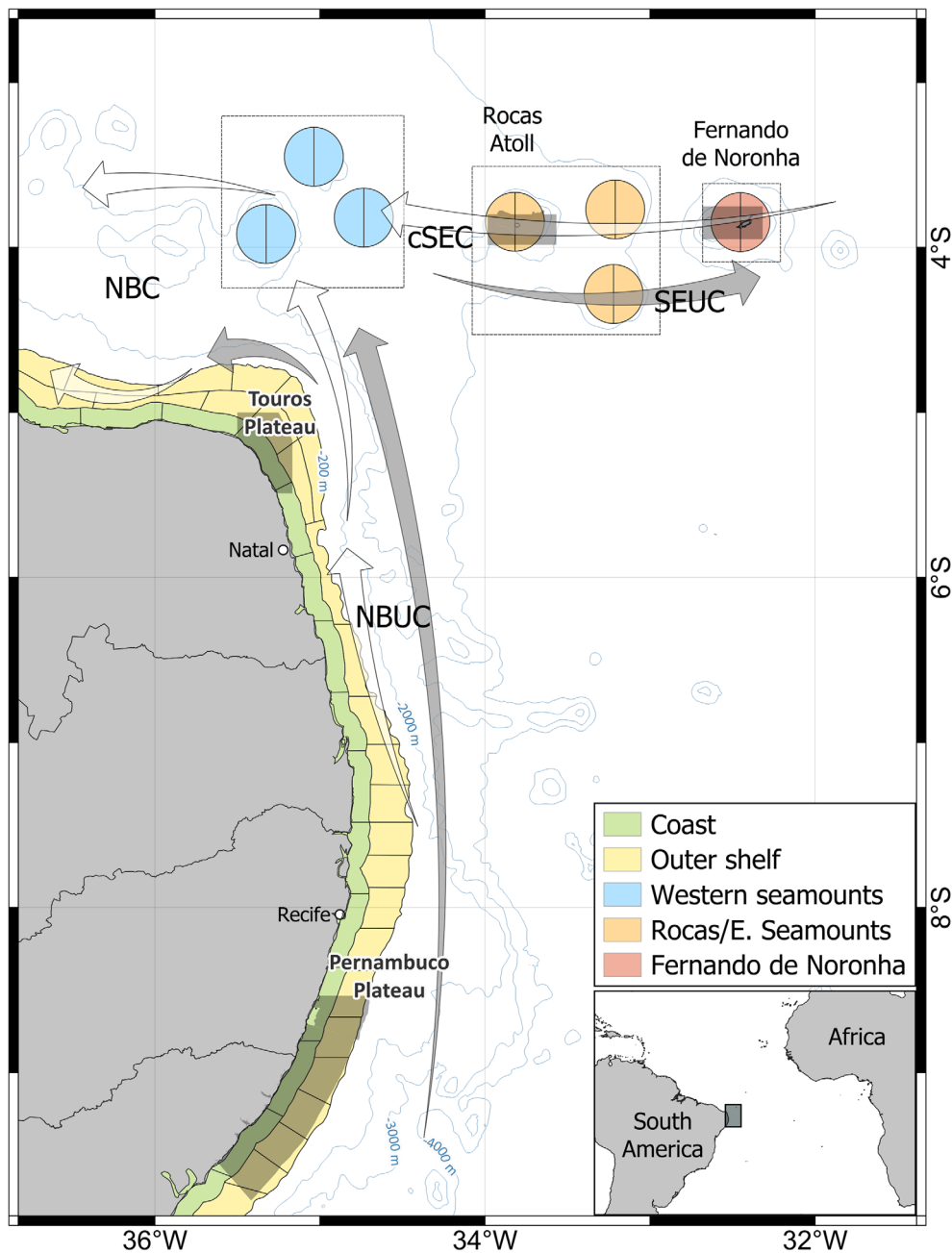


Fig. 1. Study area in the Tropical Southwestern Atlantic showing the areas used for release (coast, outer shelf, western seamounts, Rocas Atoll and eastern seamounts, and Fernando de Noronha Archipelago) and recruitment (western seamounts, Rocas Atoll and eastern seamounts, and Fernando de Noronha Archipelago) of particles. Shaded areas indicate marine protected areas. Arrows indicate predominant circulation surface (white) and subsurface (gray) waters. cSEC, Central branch of the South Equatorial Current; NBC, North Brazil Current; NBUc, North Brazil Undercurrent (core in subsurface but reaching surface waters); SEUC, South Equatorial Undercurrent.

Norte states in Northeast Brazil (shaded areas in Fig. 1). A strong western boundary current, the North Brazil Undercurrent (NBUc), flows northward along the continental slope. The core of the current flows below 150 m depth, but it can be traced up to surface waters, where it spreads warm salty and oligotrophic waters over the continental shelf and in

direction to the western seamounts of the Fernando de Noronha Ridge (Fig. 1; Stramma and England 1999; Dossa et al. 2021). Meanwhile, north of 5°S, the cSEC flows westward, crossing the Fernando de Noronha ridge. In the region of the western seamounts, both currents converge and raise the North Brazilian Current (NBC), which flows westward

along the North Brazilian Coast in direction to the Caribbean Sea. Below the cSEC and the strong cline present along the Fernando de Noronha ridge (~ 150 m), the SEUC flows in the opposite direction, from the coast to the islands, with its core around 200 m depth (Assunção et al. 2020; Silva et al. 2021).

Identifying diel vertical migration patterns

DVM patterns of organisms were identified using multi-frequency echosounder datasets obtained during the ABRACOS surveys performed in Austral spring 2015 and autumn 2017 off Northeast Brazil (Bertrand 2015, 2017). Multifrequency echograms using a RGB additive color model, where red, green, and blue indicate the contribution of backscatter (S_v) at 38, 70, and 120 kHz, respectively, and brightness indicates the average intensity of the three frequencies combined, were plotted for each day sampled (echograms position in Supporting Information Fig. S1). Details on acoustic data collection and processing can be found in Ariza et al. (2023) and Assunção et al. (2023).

We observed three main patterns of DVM in spring 2015 and four in autumn 2017. In spring 2015, a first community (red line in Supporting Information Fig. S2) migrated to 100–150 m depth, around the shear between cSEC and SEUC. A second group (blue line in Supporting Information Fig. S2) migrated to 200–250 m depth, around the core of the SEUC. A last group (yellow line in Supporting Information Fig. S2) migrated to 300–400 m depth, also in the strata under influence of the SEUC. In autumn 2017, a first group (red line in Supporting Information Fig. S3) performed shallow migrations, with a maximum depth of ~ 100 m. A second group (green line in Supporting Information Fig. S3) performed migrations to ~ 100 –180 m depth, around the upper shear of the SEUC. A third group (blue line in Supporting Information Fig. S3) migrated to ~ 200 –250 m depth, around the core of the SEUC. A last group (yellow line in Supporting Information Fig. S3) migrated to ~ 300 –400 m depth, also in the strata under the influence of the SEUC. During the night, all acoustic communities were concentrated above 80 m depth in both surveys (Supporting Information Figs. S2, S3).

Hydrodynamic model

Ocean circulation over the study domain was simulated using the Nucleus for European Modeling of the Ocean (NEMO v4.0.2; Madec et al. 2008). The model has a horizontal resolution of $1/36^\circ$ (~ 3 km) and 75 fixed z -coordinate levels, ranging from 0 to 5000 m, with finer grid refinement near the surface counting 23 levels in the first 100 m of the ocean, and cell thickness reaching 160 m when approaching the bottom. These horizontal and vertical resolutions allow capturing sub-mesoscale features such as meanders, jets, and eddies and low-mode internal tides that can have strong influence on passive dispersal and connectivity. Lateral conditions were provided by assimilative global circulation model simulations (GLORYS12V1; Lellouche et al. 2018). We used the General Bathymetric Chart of the Oceans (GEBCO 2019) bathymetry,

interpolated to our grid, with a maximum depth set to 12.8 m. The model was forced by the ERA-5 reanalysis atmospheric fluxes, which is an improved version of the ERA-Interim reanalysis (Hersbach et al. 2020). River discharges were based on a 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 specific grid points around the mouth of each river. Note that there is no restoring of the model towards observed or climatological temperature. At the open boundaries, we prescribe MERCATOR-GLORYS12v1 (Lellouche et al. 2018) for velocity, temperature, salinity, sea level, and derived baroclinic current. The model is also forced at the open boundaries by the 15 major tidal components (M2, S2, N2, K2, 2N2, MU2, NU2, L2, T2, K1, O1, Q1, P1, S1, and M4), both with elevation and barotropic currents derived from FES2014 (Carrère et al. 2016). A third-order upstream biased scheme (UP3) with built-in diffusion was used for momentum advection. The temporal integration is performed using an Asselin filter with a time step of 150 s. The $k - \epsilon$ turbulent closure scheme was used for the vertical diffusion coefficients. Bottom friction is quadratic with a bottom drag coefficient of 2.5×10^{-3} , while lateral wall free-slip boundary conditions were assumed. A time-splitting technique was used to resolve the free surface with the barotropic part of the dynamical equations integrated explicitly. The simulation was initialized on January 1, 2005, until 2017, and we analyzed the data over the period 2009–2017. We verified that the model had reached an equilibrium in terms of seasonal cycles after 4 yr of run. Model evaluation details are in Tosetto et al. (2023).

Lagrangian simulations

Lagrangian simulations were performed using the Ichthyop modeling tool (Lett et al. 2008), tracking particles representing numerical larvae transported by NEMO velocity fields. Rather than focusing on a particular species or set of species, we adopted a community approach (Tosetto et al. 2023). For that, we considered two larval duration ranges: 13–18 d (hereafter medium PLD), encompassing the larval duration of most marine invertebrates; and 25–30 d (hereafter long PLD), encompassing the larval duration of most marine fish (Bradbury et al. 2008). Based on the observed DVM patterns described above, four patterns of vertical migration were considered in the model: no migration and migration to 120, 220, and 320 m depth. During night time, particles always returned to 50 m depth. Since these patterns were not associated with specific organisms, we considered the four observed patterns for the two larval durations, resulting in eight categories of particles. Simulations were run monthly from January 2009 to December 2017 (108 runs). The study domain was split into 56 cells of similar area (Fig. 1). In each run, for each category of particles, 500 particles per cell were released randomly between the surface and 80 m depth. Their trajectories were then tracked for maximum larval duration. In simulations including DVM, the

corresponding DVM scheme was applied from age 0. Recruitment occurred when a particle reached the minimum age (13 or 25 d) and crossed a recruitment (seamounts or islands) cell. Particles stopped moving after recruitment.

Data analysis

Cells where particles could recruit were classified into three community assembling zones as identified by Tosetto et al. (2023): Western Seamounts, Rocas Atoll and Eastern Seamounts, and Fernando de Noronha Archipelago (Fig. 1). For statistical analysis, data were log-transformed. Nonparametric Kruskal–Wallis tests were performed for each of the three assembling zones, two PLDs, and five release habitats, to test for significant differences ($p < 0.05$) in the number of recruiting particles among DVM patterns. Nonmetric multidimensional scaling (NMDS) analysis based on a Bray–Curtis similarity matrix was used to identify particle categories with similar seasonal and spatial recruitment patterns. One-way analysis of similarity (ANOSIM) was used to test for differences between groups identified by NMDS. Kruskal–Wallis tests were performed in Statsoft Statistica 10 (StatSoft Inc. 2011). (R Core Team 2020). NMDS and ANOSIM were performed in PRIMER 6 (Clarke and Gorley 2006). Maps were produced in QGIS 3.16 (QGIS Development Team 2022).

Results

Source systems

Most of the particles recruiting in the Fernando de Noronha zone were released and retained there, regardless of the PLD values and the DVM migration patterns (Figs. 2–4). Particles without DVM behavior that were released at other sites never reached the Fernando de Noronha Archipelago (Fig. 2). Particles migrating to depths of 220 and 320 m showed the highest retention (up to 38.7 ± 103 particles month⁻¹), with significant differences for long PLD particles (Fig. 2). Particles migrating to these depths and recruiting in Fernando de Noronha were not only of local origin, but also from the Rocas Atoll and the Eastern Seamounts (up to 10.8 ± 65.6 particles month⁻¹), and even some from the Western Seamounts in the case of medium PLD (0.3 ± 3.4 particles month⁻¹, Figs. 2–4). Migrants to 120 m depth were advected from the Rocas Atoll and the Eastern Seamounts to Fernando de Noronha exclusively for the medium PLD (Fig. 2).

Moving westward into the zone encompassing the Rocas Atoll and the Eastern Seamounts, most of the recruited particles were released locally or were transported from the Fernando de Noronha archipelago (Fig. 2). The recruitment of particles exhibiting DVM was significantly higher (up to 166.4 ± 235.6 particles month⁻¹) than those without DVM behavior (maximum of 79.5 ± 176.3 particles month⁻¹) for both PLD values (Fig. 2). Few particles (up to 3.9 ± 31.8 particles month⁻¹) released in the western seamounts reached this zone, the majority being particles with long PLD and migrating to 220 and 320 m. Exclusively in the case of long PLD, a limited number of particles (up to 0.1 ± 9.9 particles month⁻¹),

including all DVM patterns, released over the continental outer shelf in the southern edge of the study domain reached this zone (Figs. 2, 4). Most of these recruiting particles were advected from the Pernambuco Plateau region (Fig. 4).

In the far west, the Western Seamounts recruited the highest number of particles of the three zones, considering both PLD values and the four DVM patterns (Fig. 2). Most of the recruited particles were released further east, mostly from Rocas Atoll and the eastern seamounts. Among them, particles migrating to 220 and 320 m were the most efficiently recruiting (up to 458.9 ± 491.4 particles month⁻¹). However, particles migrating to 120 m depth and without DVM behavior were also numerous (Figs. 2–4). In the case of particles released in Fernando de Noronha, the second most representative source system for this zone, no significant differences between DVM patterns were observed. The Western Seamounts also received a substantial number of particles from the coast and outer shelf. Although this eastward transport was observed for both PLD values and the four DVM patterns, it was significantly higher for particles without DVM behavior (Figs. 2–4). Although the zone received particles from almost the entire length of the continental shelf, the Pernambuco and Tourois Plateaus regions were particularly relevant for this zone (Figs. 3, 4).

Seasonal patterns in recruitment

Particles without DVM behavior and with medium PLD showed a clear seasonal pattern with increased recruitment rates from July/August to January/February (Austral late winter to summer) in the three recruitment zones. Although this pattern was observed in all three recruitment zones, it was more pronounced in the Western Seamounts (Fig. 5). When considering the long PLD particles without DVM behavior, the same pattern was also observed in particles recruiting in the western seamounts. In the Fernando de Noronha Archipelago, Rocas Atoll and eastern seamounts zones, the peak of recruitment of this category of particles was limited to October and November, respectively.

Particles migrating to 120 m depth in both PLD values also showed recruitment peaks from July/August to January/February, but these were more variable and with a less clear pattern than for non-migrating particles, with some high values also observed during autumn and winter (Fig. 5). The seasonal patterns observed for particles migrating to the 220 and 320 m depth were contrasting. While particles with medium PLD showed increased recruitment in spring and summer in Fernando de Noronha, in other areas high rates were observed throughout the year with no clear seasonal pattern (Fig. 5).

Recruitment patterns according to particles categories

In the NMDS analysis, the eight particle categories were ordered primarily by their PLD (Fig. 6). For each PLD, particles migrating to 220 and 320 m depth were closely grouped in the analysis (Fig. 6), reflecting their similar recruitment patterns in each zone as shown in the previous sections.

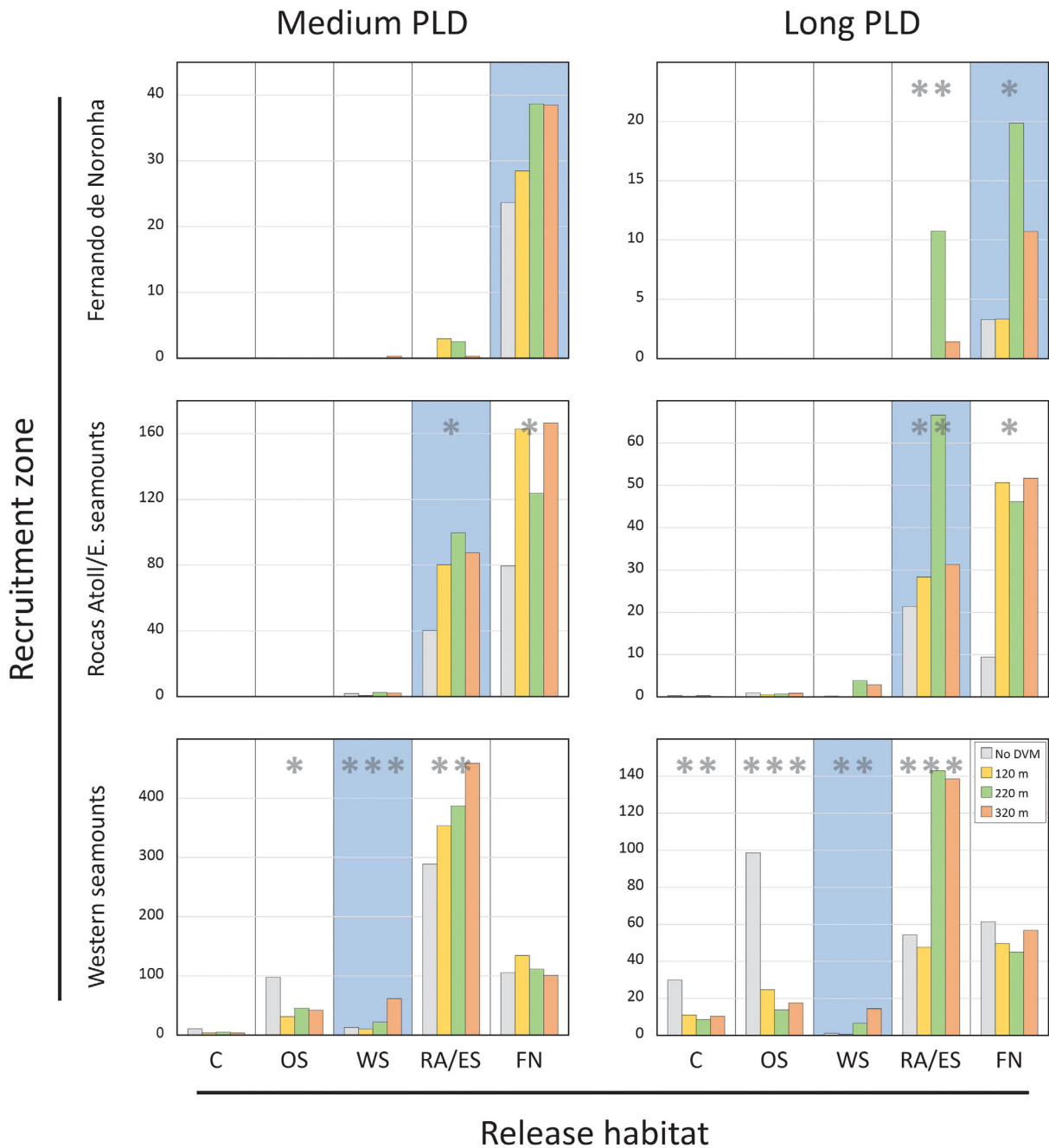


Fig. 2. Number of particles (particles month⁻¹) that recruited in each recruitment zone classified according to their planktonic larval duration (PLD), release habitat and their diel vertical migration (DVM) depth. Blue background indicates the retention of particles in the same habitat as their release site. **p* < 0.05; ***p* < 0.01; ****p* ≤ 0.001 in Kruskal–Wallis test. Standard deviations are available in Supporting Information Table S1. C, coast; FN: Fernando de Noronha Archipelago; OS, outer shelf; RA/ES, Rocas Atoll/Eastern seamounts; WS, western seamounts.

Particles without DVM behavior were the most isolated when considering both PLD values. Particles migrating to 120 m depth exhibited distinct patterns for each PLD value. While long PLD showed a pattern more similar to particles without DVM behavior, medium PLD was at an intermediate position between particles without DVM behavior and particles migrating to deeper levels (Fig. 6). ANOSIM depicted

significant differences (*R* = 0.938, *p* = 0.01) between the four groups defined in the NMDS.

Discussion

This study provides insight into the understanding of processes shaping the rich biodiversity of the insular systems of

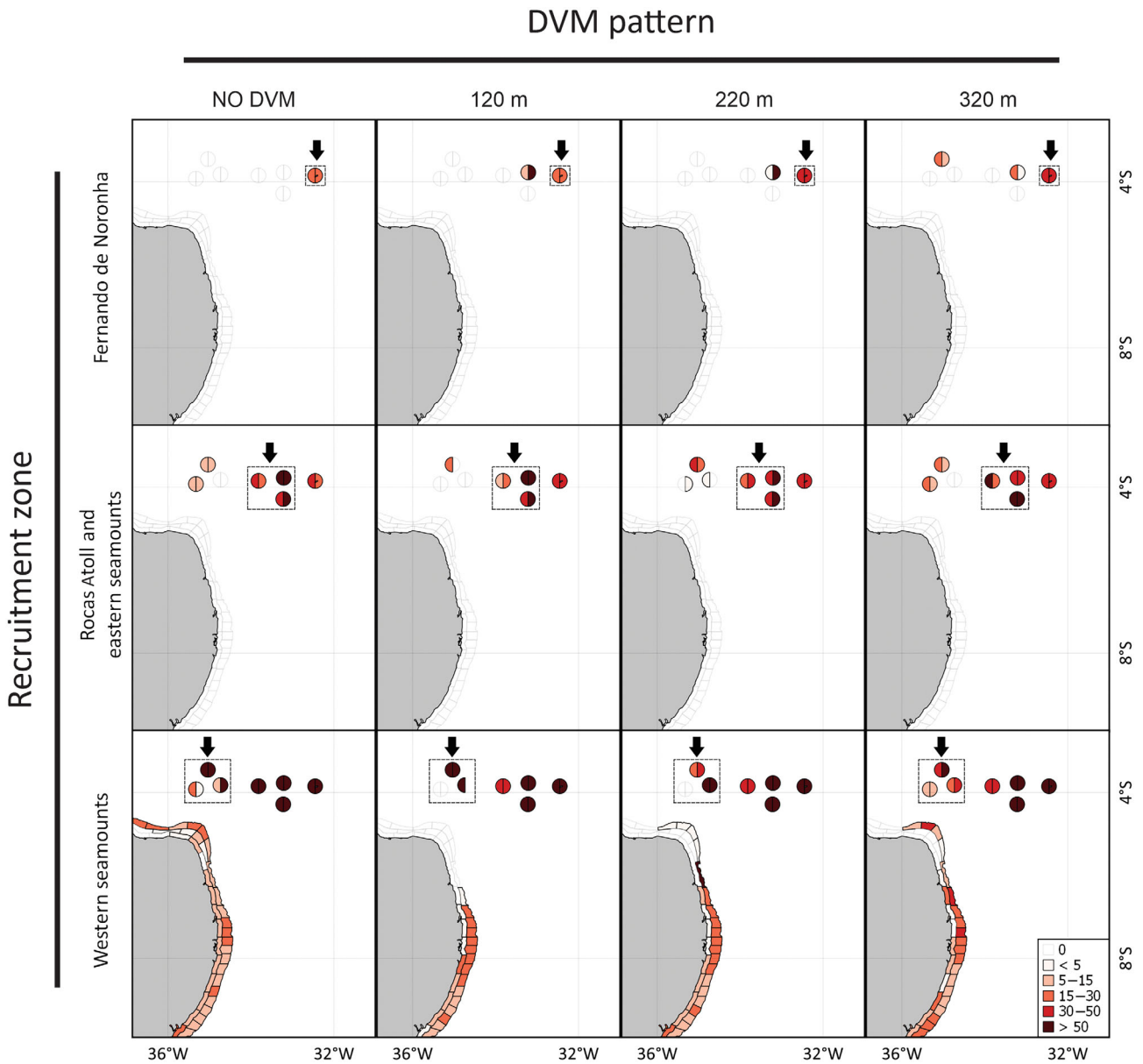


Fig. 3. Distribution of the release cells of particles with medium planktonic larval duration recruiting (particles month⁻¹) in each recruitment zone according to their diel vertical migration (DVM) depth. Arrows indicate the referred recruitment zone.

Fernando de Noronha Archipelago and Rocas Atoll in the Tropical Southwestern Atlantic Ocean. Beyond self-recruitment, the recruitment of organisms in these areas and the assembly of local biodiversity have long been enigmatic, with previous modeling studies suggesting low connectivity in the Tropical Southwestern Atlantic, including these islands and coastal ecosystems (Endo et al. 2019).

In our study, we show that while most recruitment is due to self-recruitment by local communities, accounting for the DVM of organisms to depth strata influenced by counter currents can significantly enhance biodiversity connectivity between the marine systems present in the area (Fig. 7). Focusing on the

Fernando de Noronha Archipelago and Rocas Atoll, two biodiverse oceanic insular systems, we provide clues to the enigmatic source locations of recruiting organisms. Interestingly, our simulations did not show particles released along the continental shelf reaching the Fernando de Noronha Archipelago directly, even when organisms performed DVM to SEUC-influenced strata, opposing the coastward flow of surface currents. While not a direct journey, migration to SEUC-influenced strata notably increases the possibility that the seamounts of the Fernando de Noronha Ridge and the Rocas Atoll act as stepping stones between the continental shelf and Fernando de Noronha.

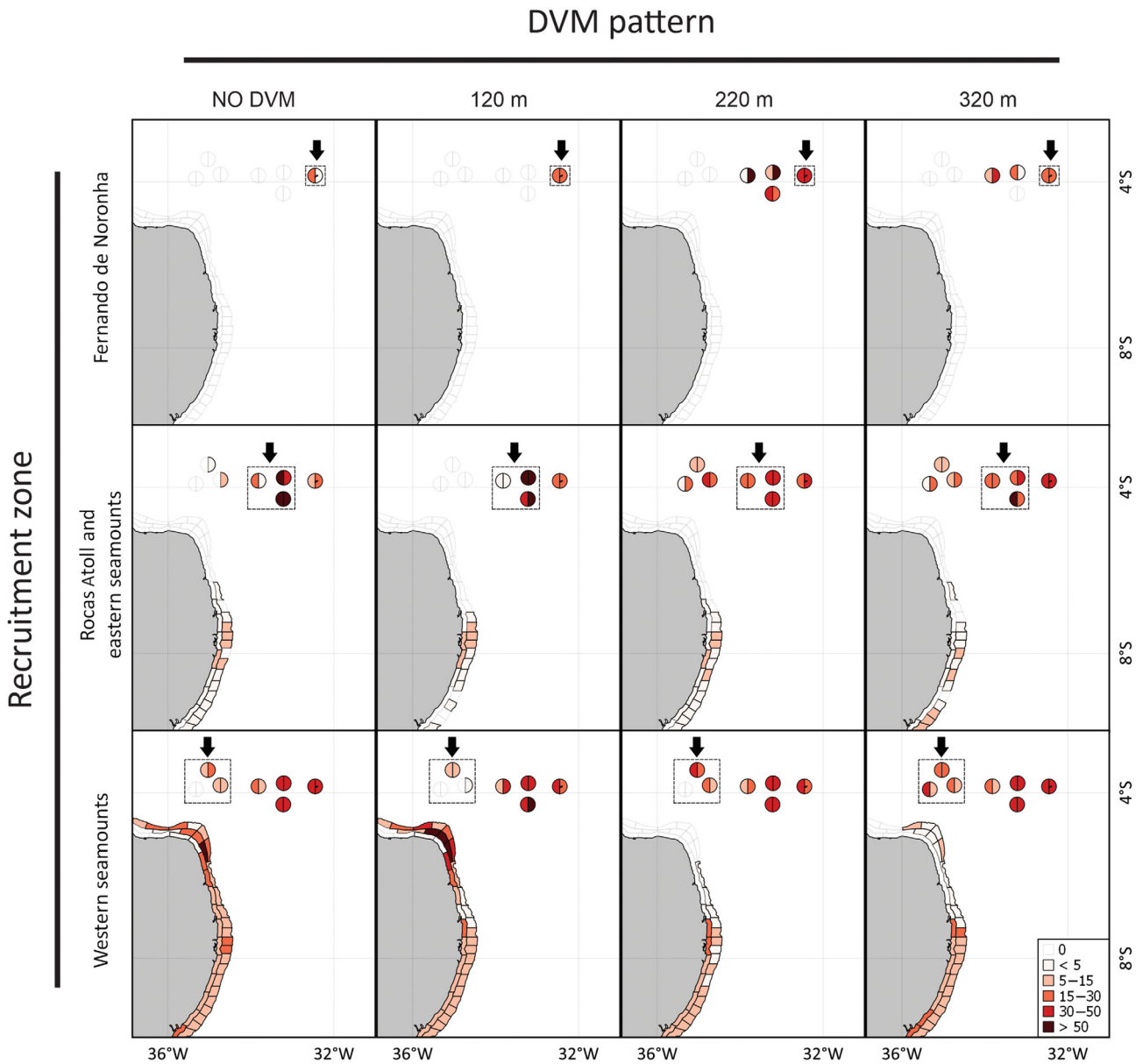


Fig. 4. Distribution of the release cells of particles with long planktonic larval duration recruiting (particles month⁻¹) in each recruitment zone according to their diel vertical migration (DVM) depth. Arrows indicate the referred recruitment zone.

Hence, the continental shelf off Northeast Brazil emerges as a potential indirect source of organisms in the Tropical Southwestern Atlantic Ocean. Along this extensive shelf, a variety of ecosystems including shallow water and mesophotic reefs, seagrass meadows, sandy banks, plateaus and mangroves, exist, offering a variety of habitats for the assembly of animal communities (Castro et al. 2006; Soares et al. 2018; Tosetto et al. 2023) that can reproduce and spawn their propagules in pelagic waters. In our conceptual scenario (Fig. 7), propagules of organisms originating from the continental shelf would first be transported towards the seamounts in the western part of the Ridge. This dispersal pathway was intense in our simulations

for both migrating and nonmigrating particles, and both considered PLDs. Two large regions of the shelf were found particularly noteworthy as source systems to the Western Seamounts, the Pernambuco Plateau, and the Touros Plateau (Fig. 7). Both plateaus are located in areas showcasing major changes in coastline and current direction (Dossa et al. 2021) and a widening of the shelf. The Pernambuco Plateau is also known to harbor high biodiversity (Eduardo et al. 2018).

Upon arrival at the Western Seamounts, organisms can find suitable habitats to recruit and assembly local communities. The offspring of these communities, migrating into SEUC-influenced layer would then have the opportunity to reach

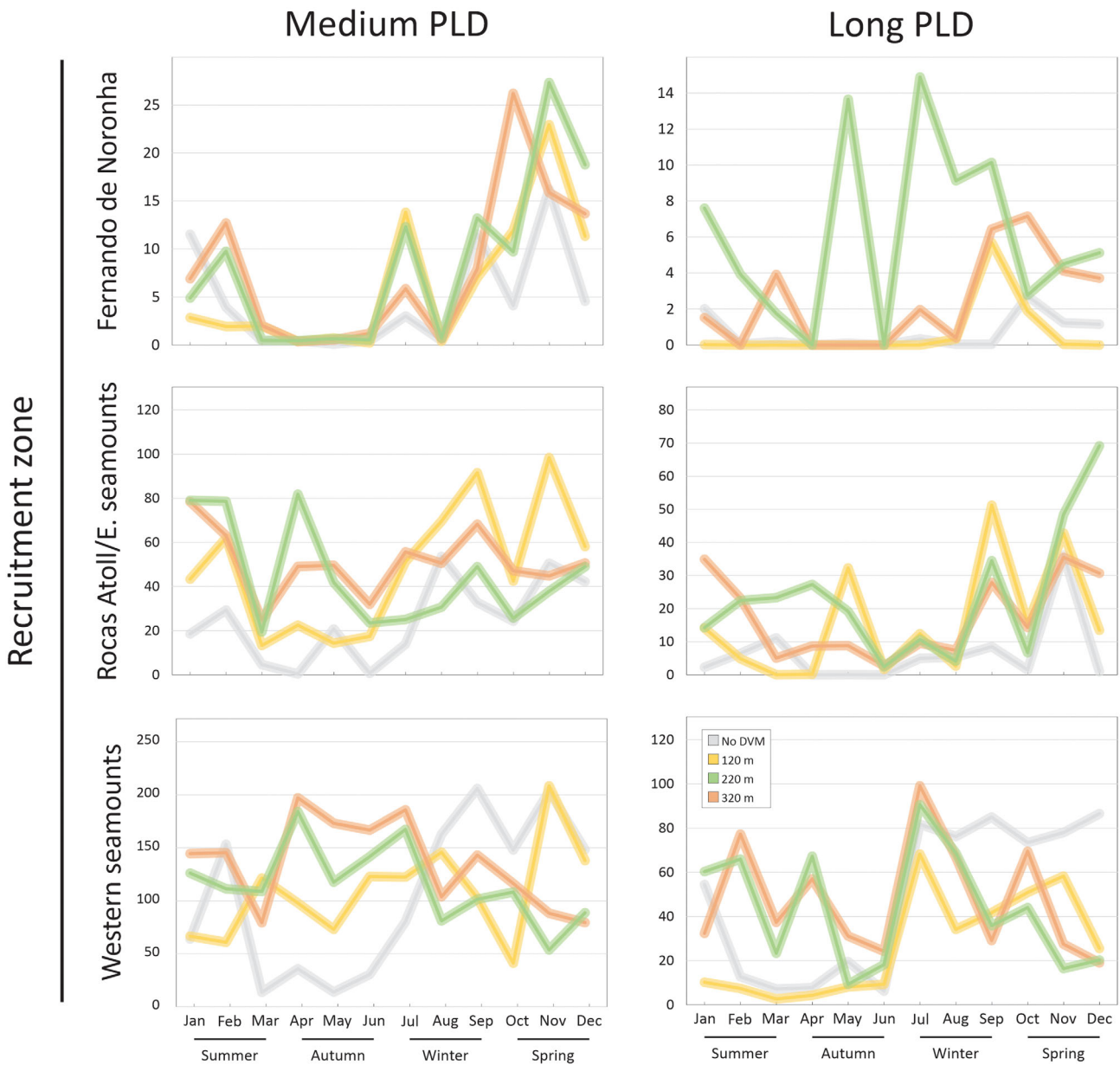


Fig. 5. Austral seasonal patterns in the recruitment of particles (particles month⁻¹) in each recruitment zone classified according to their planktonic larval duration (PLD) and their diel vertical migration (DVM) depth. Standard deviations are available in Supporting Information Table S2.

suitable habitats in Rocas Atoll and Eastern seamounts (Fig. 7). Contrastingly, organisms that do not perform DVM would be transported westward by the surface currents and never reach the eastern zones. Reaching and assembling at Rocas Atoll and the Eastern Seamounts opens the way for the offspring of migrating organisms to reach the Fernando de Noronha Archipelago, interconnecting the entire Fernando de Noronha Ridge with the Northeast Brazil Continental Shelf into a large metacommunity. Seamounts, which are among the least known marine ecosystems (Clark et al. 2012), especially those of the Fernando de Noronha Ridge, hold unknown biodiversity. In this context, our

conceptual model of connectivity, while challenging to validate due to limited current knowledge, is consistent with the known capacity of seamounts, similar to continental and insular shelves, to support a high diversity of epibenthic organisms (Rowden et al. 2010) and their role as stepping stones for reef fish connecting coastal and offshore insular ecosystems (Pinheiro et al. 2017; Mazzei et al. 2021; Simon et al. 2022).

Beyond coastal dispersal, in our model, DVM to SEUC-influenced strata increased larval retention of organisms spawning in the seamounts and islands of the Fernando de Noronha Ridge (Fig. 7). This migratory behavior also increased

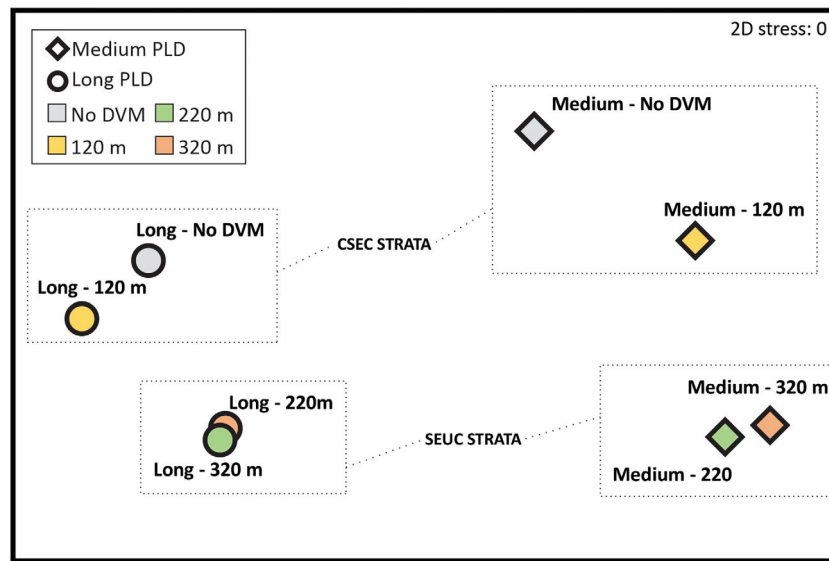


Fig. 6. NMDS plot showing particles categories (classified by planktonic larval duration and diel vertical migration depth) grouped according to their seasonal and spatial recruitment patterns. CSEC, Central branch of the South Equatorial Current; DVM, diel vertical migration; PLD, planktonic larval duration; NMDS, nonmetric multidimensional scaling; SEUC, South Equatorial Undercurrent.

their transport to the closest western assembling zone, that is, from Fernando de Noronha Archipelago to Rocas Atoll and Eastern Seamounts, and from Rocas Atoll and Eastern Seamounts to the Western Seamounts. The reduced exposure to the strong westward surface current (cSEC; Silva et al. 2021) played a crucial role in reducing the dispersal distances of particles performing DVM. This reduction is consistent with patterns observed in other Lagrangian modeling studies, where currents are generally stronger in surface waters than deeper (Domingues et al. 2012; Ospina-Alvarez et al. 2018). Therefore, DVM has been proposed as a retention strategy for zooplankton communities in highly advective systems, especially when surface and subsurface currents flow in opposite directions (Carr et al. 2008; Bandara et al. 2021).

The evolutionary strategy of reduced dispersal capacity is well-documented in terrestrial species that have colonized island systems, as the retention of organisms contributes to the maintenance of viable local populations in these isolated systems (Cody and Overton 1996; Waters et al. 2020). In marine ecosystems, the loss of planktonic life stages is a drastic strategy to reduce dispersal that has evolved in some benthic invertebrate taxa inhabiting shelves surrounding oceanic islands (Waters et al. 2020). However, even in species with long PLDs, genetic isolation between populations has been observed in such systems (Strathmann et al. 2002; Taylor and Hellberg 2003), suggesting that there may be other strategies to reduce dispersal. Particularly in highly advective systems, the maintenance of viable populations and the consequent effects on patterns of biodiversity are highly dependent on processes that enhance the retention of organisms (Byers and Pringle 2006). The results of our model suggest that DVM, in

addition to the benefits of avoiding predators during daytime, efficiently reduces exposure to strong surface currents and the consequent long-distance passive dispersal, thereby contributing to the maintenance of viable local populations in isolated insular marine systems. Additionally, our model shows that particles without DVM behavior exhibit marked seasonal recruitment, with higher rates corresponding to periods of weaker surface currents (Silva et al. 2021; supplementary material in Tosetto et al. 2023), suggesting that seasonal spawning during periods of weaker currents could be an efficient strategy to reduce dispersal among organisms without DVM behavior. In contrast, migrating particles can recruit throughout the year.

In understudied regions such as the Tropical Southwestern Atlantic, Lagrangian dispersal modeling provides a valuable foundation for formulating ecological hypotheses awaiting empirical validation (Tosetto et al. 2023). To move forward, identifying organisms migrating to SEUC-influenced strata observed in the acoustic data will be crucial. An interesting perspective may come from future studies considering the recent invasion of the lionfish *Pterois* spp. in the Northeast Brazilian coast and Fernando de Noronha Archipelago (Soares et al. 2018). This species has a relatively small home range and limited movement as a mature fish, but a pelagic larva which is known to perform diel vertical migration (Kitchens et al. 2017). This invasion may therefore have benefited from the dispersal pathways we describe. Furthermore, an in-depth assessment of the biodiversity inhabiting the islands and seamounts of the Fernando de Noronha Ridge will allow empirical validation of the connectivity patterns described here. We expect a lower turnover and greater nestedness (Baselga 2010)

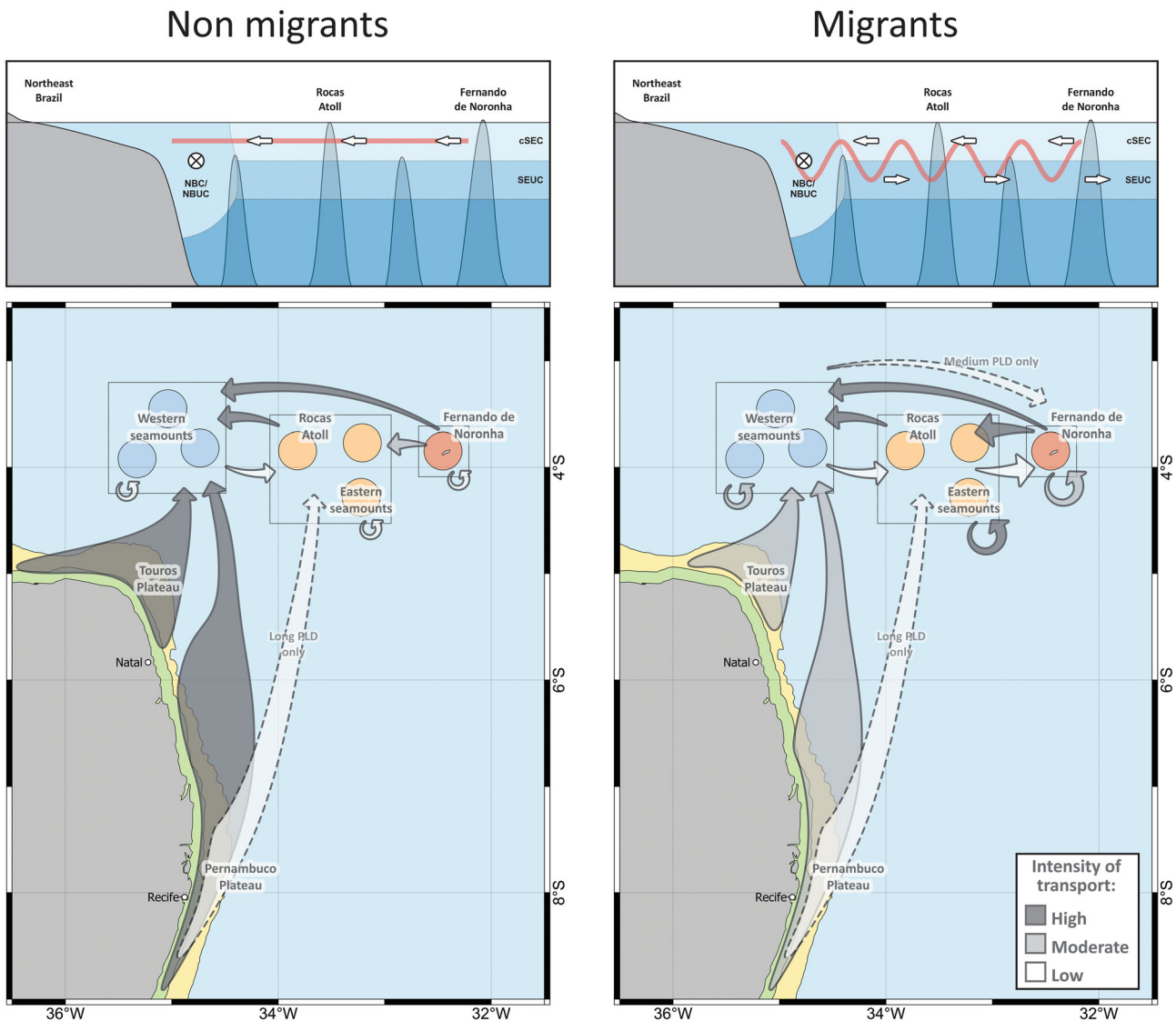


Fig. 7. Conceptual model of connectivity pathways for organism without DVM behavior and organism migrating to SEUC-influenced strata in the Fernando de Noronha Ridge. Dashed arrows indicate the flux occurs exclusively in one of the planktonic larval durations (PLD). Curved arrow indicates larval local retention. Upper panels are simplified representations of the vertical seascape integrated between 3°S and 6°S where the red lines indicate the position of organisms. cSEC, Central branch of the South Equatorial Current; DVM, diel vertical migration; NBC, North Brazil Current; NBUC, North Brazil Undercurrent; SEUC, South Equatorial Undercurrent.

among vertical migratory assemblages. Greater similarity in biodiversity between the Pernambuco and Touros plateaus and the Western Seamounts is also expected, as these are the two main sources of both migrating and not-migrating particles for this system (see also Tosetto et al. 2023). Beyond biodiversity similarities, molecular comparisons among populations in each system may provide further empirical validation of the connectivity patterns described here.

Our results provide new elements for the development of a functional network of MPAs in the Tropical Southwestern Atlantic. While the Fernando de Noronha Archipelago and Rocas Atoll are already protected by no-take MPAs (Magris et al. 2013), the Western Seamounts face high fishing pressure

(GFW 2023) and lack protection. Given the importance of these features in connecting the continental shelf to the Fernando de Noronha Ridge, implementing an MPA at this zone would bring dual benefits for the entire Ridge. Along the continental shelf, the two main sources of organisms for the Western Seamounts observed in our simulations (Touros and Pernambuco plateaus) include small zones protected by sustainable use MPAs (APA Costa dos Corais and APA Recifes dos Corais; MMA 2023). Expanding and increasing the level of protection of these MPAs emerges as a strategic management approach for the entire region. Such initiatives align with the importance of these features in potentially connecting the continental shelf to the Fernando de Noronha Ridge, thus

promoting a comprehensive and sustainable conservation strategy for the Tropical Southwestern Atlantic.

Data availability statement

The data underlying the results presented in the study are available in SEANOAE: <https://doi.org/10.17882/98785> (Tosetto et al. 2024).

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Conflict of Interest

None declared.

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