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# ECOGRAPHY

## Research article

### Identifying community assembling zones and connectivity pathways in the Tropical Southwestern Atlantic Ocean

Everton Giachini Tosetto<sup>1,2,3</sup>, Christophe Lett<sup>1,2</sup>, Ariane Koch-Larrouy<sup>2,3,4</sup>, Alex Costa da Silva<sup>3</sup>, Sigrid Neumann-Leitão<sup>3</sup>, Miodeli Nogueira Junior<sup>5</sup>, Nicolas Barrier<sup>1,2</sup>, Alina Nathanael Dossa<sup>3,6,7</sup>, Michel Tchilibou<sup>4</sup>, Perrine Bauchot<sup>4</sup>, Guillaume Morvan<sup>4</sup> and Arnaud Bertrand<sup>1,2,3,8</sup>

<sup>1</sup>MARBEC, University of Montpellier, CNRS, IFREMER, IRD, Sète, France

<sup>2</sup>Institut de Recherche pour le Développement, Sète, France

<sup>3</sup>Departamento de Oceanografia, Universidade Federal de Pernambuco, Recife, PE, Brazil

<sup>4</sup>Laboratoire d'Etudes en Géophysique et Océanographie Spatiales (LEGOS), Toulouse, France

<sup>5</sup>Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, João Pessoa, PB, Brazil

<sup>6</sup>International Chair in Mathematical Physics and Applications (ICMPA), Université d'Abomey-Calavi, Cotonou, Benin

<sup>7</sup>Institut de Recherches Halieutiques et Océanologiques du Bénin (IRHOB), Cotonou, Benin

<sup>8</sup>Departamento de Pesca e Aquicultura, Universidade Federal Rural de Pernambuco, Recife, PE, Brazil

Correspondence: Everton Giachini Tosetto ([everntosetto@hotmail.com](mailto:everntosetto@hotmail.com))

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Dispersal is more intense in the ocean than on land because most marine taxa present planktonic life stages that are transported by currents even without specific morphological traits. Thus, species dispersal shapes the distribution of biodiversity along seascapes and drives the composition of biodiversity assemblages. To identify marine assembling zones which characterise spatial areas particularly prone to receive and retain similar animal assemblages from the regional pool of species through passive dispersal, we propose a community-based approach grounded on Lagrangian simulations of plankton dispersal. This novel approach was applied to communities (coast, outer shelf, slope, seamounts and islands; 0–80 m depth) of the Tropical Southwestern Atlantic and used to assess connectivity pathways. For that, we classified the modelled particles in 15 categories according to biological traits (planktonic life duration and spawning habitat) of representative planktonic communities. From the hierarchical clustering of the multivariate matrix containing the amount of arriving particles from each category in each cell we defined 14 assembling zones. Results highlighted that the assembling zones were mostly shaped by the degree of exposure to currents and the presence of mesoscale features (eddies, recirculation) derived from the interaction between these currents and coastlines. The boundaries, dispersal and connectivity patterns of these zones consistently align with local and regional in situ spatial distribution and abundance patterns of organisms, and provide an appropriate basis for the formulation of ecological hypotheses in the metacommunity framework to be tested in situ, such as the balance between species sorting and mass effect assembling archetypes. This approach, when coupled with the knowledge of other processes shaping communities' structure and distribution, provides important insights for regions and animal groups for which knowledge is limited or absent, and more generally allows for a comprehensive overview of the distribution of distinct communities and connectivity pathways along marine environments.

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Keywords: community assembly, landscape ecology, mass effect, metacommunity, northeastern Brazil, species sorting

## Introduction

Species dispersal plays a critical role among the processes shaping biodiversity patterns along spatial and temporal scales. Understanding these processes is a central issue in ecology, particularly in the metacommunity framework. This framework extends traditional community ecology into spatially heterogeneous landscapes (Leibold et al. 2004, Logue et al. 2011, Jönsson et al. 2016). In this context, community assembly is the process determining which species successfully colonize and coexist at a local site. This process is constrained by the dispersal of species from a regional pool (metacommunity) to local sites, where they are filtered by environmental conditions, resource availability and inter-specific interactions (Fig. 1, HilleRisLambers et al. 2012, Stegen et al. 2013, Mittelbach and Schemske 2015, Suzuki and Economo 2021).

Intensity of dispersal is appointed to govern the balance between species sorting and mass effect assembling archetypes (Leibold et al. 2004, Suzuki and Economo 2021). In a given metacommunity with low dispersal rates, species have time to establish populations along the more favorable habitats according to their ecological niche and local competition takes place, excluding less efficient competitors. In such conditions, species sorting by environmental filtering and species interactions control the assembly of local communities (Leibold et al. 2004). Otherwise, when dispersal rates are intense, the constant arrival of new individuals (mass effect) may sustain viable populations of

species in habitats outside their optimal niche and reduce the effects of local competition, leading to more homogeneous metacommunities.

Progress in accounting dispersal processes in community assembly are notable in terrestrial ecosystems (Viljor and Teder 2018, Rapacciolo and Blois 2019, Schlägel et al. 2020, Salgueiro et al. 2021). In marine environments, however, animal dispersal primarily involves planktonic life stages that are too small to be tracked (Sardet 2015, Burgess et al. 2016), leading to less emphasis on the role of dispersal in assembling marine communities. These planktonic life stages are passively transported by currents without specific morphological traits, thus dispersal in the ocean is typically more intense than on land (Sardet 2015, Burgess et al. 2016). Nevertheless, species life cycles profoundly affect dispersal extent. Duration of the planktonic stage, which can last from a few days to more than a month, plays a major role in the process, controlling the extent of dispersal by currents (Lester et al. 2007, Bradbury et al. 2008, Crochelet et al. 2020). Holoplanktonic species, which remain in the plankton for their entire life cycle, have the potential for wide oceanic dispersal, since these organisms do not require specific environments for settlement (Goetze 2011, Mapstone 2014, Burgess et al. 2016, Ser-Giacomi et al. 2018). Consequently, many holoplanktonic species exhibit circumglobal distributions (Pierrot-Bults 1976, Goetze 2011). Conversely, meroplanktonic species rely on suitable substrates for recruitment (Pan et al. 2011), constraining their assembly into communities where these habitats are present.

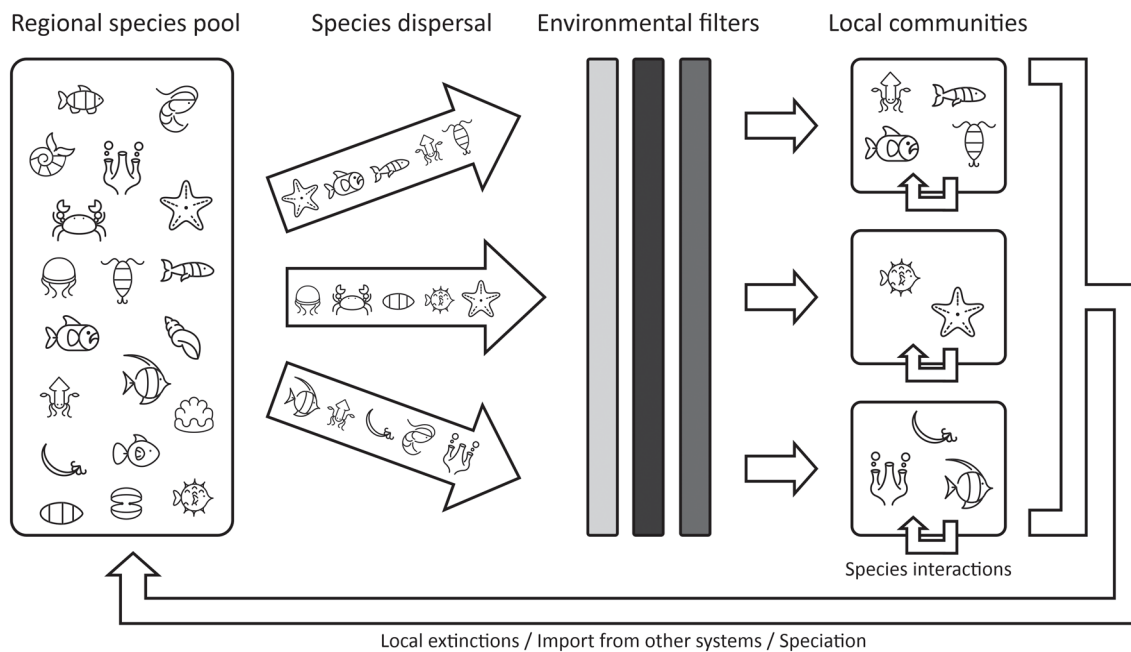


Figure 1. Conceptual model of community assembly where local communities comprise a subset of species from the regional species pool constrained by dispersal, environmental filters and species interactions (adapted from HilleRisLambers et al. 2012, Mittelbach and Schemske 2015).

Apart from these species traits, the seascape features play a major role in shaping dispersal. Ocean circulation is a primary determinant, facilitating the transport across ecosystems and regions, possibly reaching new adequate habitats for recruitment. Concurrently, ocean circulation can preclude or restrict movement of species with weak swimming capacity against the flow (Rocha et al. 2005, Burgess et al. 2016). Thus, distinctly than on land, marine dispersal is often unidirectional. Geomorphological features impose additional constraints. Large landmasses and seafloor topography influence current paths and intensities (Gille et al. 2004), impacting dispersal range. Interactions between circulation and geomorphology yield diverse consequences, including aggregations of planktonic organisms in sloping topography induced by currents (Cotté and Simard 2005, Sourisseau et al. 2006, Hazen et al. 2009). Specific geomorphological features and shorelines create sheltered areas, in scales ranging from the lee of small headlands to large bays and gulfs, restricting circulation and retaining planktonic organisms (Graham and Largier 1997, Wing et al. 1998, Archambault and Bourget 1999, Mace and Morgan 2006).

The development of biophysical models combining hydrodynamics and species traits to simulate the transport of organisms along marine systems (Siegel et al. 2003, Lett et al. 2008) permitted conspicuous progress to be made in seascape ecology. However, hitherto, these models were mostly used in single species metapopulation connectivity approaches (Endo et al. 2019, Schilling et al. 2020). The few applications of these models to the community level focused on habitat connectivity, and for few target species or larval durations, without considering results in a broader community assembly perspective (Melià et al. 2016, Magris et al. 2016, Crochelet et al. 2020). Therefore, the comprehensive role of dispersal patterns in shaping local communities across seascapes remains largely unexplored.

Hence, the assessment and quantification of dispersal patterns emerge as central elements in understanding biodiversity patterns across heterogeneous seascapes and in formulating hypotheses within the metacommunity framework for subsequent in situ validation. This study introduces a novel community-based Lagrangian approach to delineate community assembling zones, which characterise spatial areas particularly prone to receive and retain similar animal assemblage patterns from the regional pool of species through passive dispersal. Although local environmental filters within the seascape, resource availability and species interactions must be taken into consideration, these zones are likely to harbor local communities that are more similar within their respective boundaries. We applied this approach to the Tropical Southwestern Atlantic Ocean (Fig. 2) and compared local and regional in situ spatial distribution and abundance patterns of organisms to the distribution of assembling zones. Additionally, we innovatively considered the assembling zones as spatially explicit metacommunity units, to undertake an experiment assessing connectivity pathways at the community level within the Tropical Southwestern Atlantic.

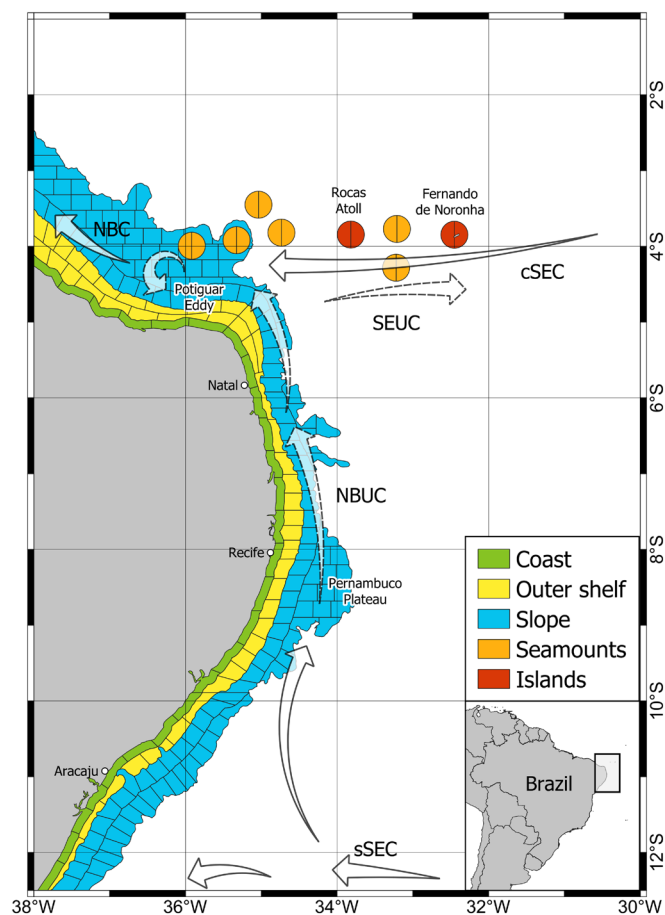


Figure 2. Study area in the Tropical Southwestern Atlantic showing the grid of 225 cells classified by broad geomorphological provinces. Arrows indicate predominant circulation surface (solid line) and subsurface (dashed line) waters. NBC=North Brazil Current, NBUC=North Brazil Undercurrent, cSEC=Central branch of the South Equatorial Current, sSEC=Southern branch of the South Equatorial Current, SEUC=South Equatorial Undercurrent.

## Material and methods

### Study area

The study area is the Tropical Southwestern Atlantic Ocean off northwestern Brazil between 01°S, 38°W and 12°S, 30°W (Fig. 2). In this area, the continental shelf is relatively narrow, ranging from 40 to 80 km, and is followed by a steep slope extending from 100 m to approximately 3500 m depth (Loder et al. 1998, Castro et al. 2006). Most of the coastal region is oligotrophic with high salinity, and coral reefs are present along the entire continental shelf (Brandini et al. 1997, Castro et al. 2006, Farias et al. 2022). Offshore at ~ 04°S, a series of seamounts and islands, including the Fernando de Noronha Archipelago and the Rocas Atoll, form the Fernando de Noronha Ridge (FNR). Strong western boundary currents, carrying warm and salty waters, flow towards the coast. At approximately 10–20°S, the southern South Equatorial Current (sSEC) reaches the Brazilian coast,

bifurcating and generating several cyclonic and anticyclonic eddies (Stramma and England 1999, Soutelino et al. 2011). The northern branch feeds the North Brazil Undercurrent (NBUC), which flows northward along the Brazilian coast (Fig. 2, Stramma and England 1999, Dossa et al. 2021). Meanwhile, the central South Equatorial Current (cSEC) crosses the FNR north of 05°S. Upon reaching the Brazilian coast, the cSEC merges with the NBUC to form the North Brazil Current (NBC; Fig. 2, Stramma and England 1999, Lumpkin and Garzoli 2005, Dossa et al. 2021). In this particular area, the change in direction of the coastline and the presence of seamounts lead to a less exposed area where the large Potiguar anticyclonic eddy forms in the subsurface (Fig. 2, Krelling et al. 2020).

## Hydrodynamic model

We used the hydrodynamic model Nucleus for European Modelling of the Ocean (NEMO ver. 4.0.2; Madec et al. 2017) to simulate the ocean circulation over the study domain. 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 allowed us to capture submesoscale features such as meanders, jets and eddies and low-mode internal tides, which can have a strong influence on passive dispersal and connectivity. To obtain a realistic representation of the circulation at each frontier of the model configuration, lateral conditions are provided by assimilative global circulation model simulations (GLORYS12V1; Lellouche et al. 2018b). We used the General Bathymetric Chart of the Oceans (GEBCO 2019) bathymetry interpolated onto our grid, with the 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 through 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 toward observed or climatological temperature. At the open boundaries, we used MERCATOR-GLORYS12v1 (Lellouche et al. 2018b) for velocity, temperature, salinity, sea level and derived baroclinic current. The model was also forced at the open boundaries by the fifteen 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 was 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  $2.5 \times 10^{-3}$ , 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 1 January 2005 and continued until 2017, and we analysed the data over the period 2009–2017. We verified that the model had reached an equilibrium in terms of seasonal cycles after four years of run. We used the daily output of the simulated oceanic variables in the Lagrangian model.

To assess the realism of the model, we compared its outputs with ADCP data acquired during two cruises (ABRAÇOS 1 spring 2015 and ABRAÇOS 2 fall 2017; Bertrand 2015, 2017) and with outputs of the Global Ocean Physics Reanalysis model (GLORYS12v1; Lellouche et al. 2018a). Results of validation are described in the Supporting information.

## Lagrangian model and simulations

We used the Lagrangian modelling tool Ichthyop (Lett et al. 2008) to track particles representing numerical larvae passively transported by the NEMO velocity fields. Rather than focusing on a particular species or set of species, our aim was to take a community approach. In order to model the regional species pool, we first classified representative animal assemblages present in the marine plankton of the study area according to the broad provinces where they are more commonly found (i.e. coast, outer shelf, slope, seamounts and islands) and their planktonic life stage duration, hereafter referred as PLD (short=5 days, medium=15 days or long=30 days). These traits were then associated with the particles to be released in the dispersal model (i.e. particles were classified according to the broad province where they were released and PLD), resulting in 15 categories (Supporting information). Simulations were run monthly from January 2009 to December 2017 (108 runs). The broad provinces were split into 225 cells of similar area (Fig. 2). In each run, 150 particles per cell were released randomly between the surface and 80 m depth, for a total of 33 750 particles. Their trajectories were then followed for 30 days and their locations recorded at 5, 15 and 30 days to represent the three categories of PLD.

## Data analysis

To analyse the data, we computed the number of particles of each category (15 variables) ending in each cell of the grid in each simulation ( $225 \times 108$  samples) and the number exported out of the domain. To reduce the distance between variables, the data were transformed by  $\log(x+1)$  in statistical analyses. We first tested for interannual differences (cells were pooled by province to improve computing power) with a permutational analysis of variance (PERMANOVA; Anderson et al. 2008). Since no difference were observed between years (Pseudo-F=1.238,  $p=0.185$ ) the pooled dataset was used for further analyses.

We used a hierarchical cluster analysis based on the Ward method and Euclidian distance (Langfelder and Horvath 2012) to classify the cells into coherent assembling zones

according to the number of particles of each category they received. The assembling zones were then used to estimate retention (proportion of particles released in a zone that remained there) and connectivity (proportion of particles exchanged between zones).

Data analysis was performed in R ver. 4.1.0 ([www.r-project.org](http://www.r-project.org)). Spatial classification of individual particles according to their final position in the cell grid was performed using the *st\_join* function from the 'sf' package. PERMANOVA was performed with the *adonis2* function from the 'vegan' package. Hierarchical clustering analysis was performed using the *hclust* function from the 'stats' package. Maps of the particle distribution were generated using the heat map function (radius=0.15°) in QGIS 3.16 (QGIS Development Team 2022).

## Results

### Dispersal patterns

Particles representing planktonic organisms with short PLD released along the coast tended to remain there (56.5%), although some of these were transported to the outer continental shelf (28.5%) and to the slope (8.8%), particularly in the southern part of the domain (Fig. 3). For medium and long PLDs, the highest particle concentrations also occurred along the coast (28.8 and 14.7%) and the outer shelf (28 and 18.3%), particularly in the north (marks a and b in Fig. 3) and center (marks c, d) of the domain, and also in the south for the medium PLD (mark e in Fig. 3). Compared to short PLD, medium and long PLD particles were more scattered over the slope (~ 18% for both) and open ocean (8.2 and 10.8%), even reaching the closest seamounts (< 0.5%, mark f). A large fraction (15.8 and 37.6%) of the particles was also exported to outside the domain from the south and north-west, respectively.

For particles released over the outer shelf, large hotspots of particle final locations were observed for all PLD values in the north of the domain, mainly over the outer continental shelf (Fig. 3 marks g, i, k), but also extending to the slope (marks h and j). Particles with short PLD released on the outer shelf presented high concentrations over the whole continental shelf (44.8%) and the adjacent coastal (5.9%) and slope areas (34.2%, especially at the locations indicated marked l and m in Fig. 3). Conversely, those with medium and long PLDs were more concentrated in a wide area over the slope, in the north of the domain west of the seamounts (Fig. 3 marks n and o). A smaller proportion of these particles were also present in the remaining parts of the outer shelf, along the coast, slope and in the open ocean, reaching the nearest offshore seamounts and even the Rocas Atoll but in very small quantities (< 0.01%, Fig. 3 mark p).

Similar patterns were observed for particles released over the slope for all PLDs, which were largely retained in the same broad part of the slope domain mentioned above (Fig. 3 marks q, r and s) and more broadly along the slope domain

(51.2, 25.4 and 9.8% for short, medium and long PLDs, respectively), but also reached the outer shelf (1–6%), the coast (< 0.5%), the seamounts (< 1%) and the Rocas Atoll (< 0.01%). A large proportion of the particles released over the outer continental shelf and slope areas were exported westward out of the domain, up to 61.3 and 71.6% in the cases of long PLD (Fig. 3).

Particles released around seamounts and islands showed similar dispersal patterns for the three PLD values (Fig. 4). For short PLD, dispersal was mainly westward. Although a significant number of particles ended up in the open ocean (77.3 and 58.78% for islands and seamounts, respectively), many were retained around the release area (particularly on the western side of the islands; Fig. 4 marks a, b) or transported to the adjacent seamounts or islands. Short PLD particles released around seamounts also reached the slope (18.55%) in the northern part of the domain (Fig. 4 mark c) or were exported westward to outside the domain. Particles with medium and long PLDs released around seamounts and islands ended up scattered throughout the northern and central parts of the domain (down to ~ 8°S), reaching other islands and seamounts (0.1–2.3%), regions of the slope (1.5–11%), the outer shelf (< 1%) and even coastal areas (< 0.1%, Fig. 4). Particularly, the shelf break in the north of the domain was a hotspot of particle concentration in the case of long PLD (Fig. 4 marks d and e). The westward export of particles released on islands and seamounts with medium and long PLDs to the outside of the domain was very large, reaching up to 88.4% (Fig. 4).

### Identification of assembling zones

Using cluster analysis, we classified the 225 cells of our study area into 14 assembling zones, each with a specific structure in the types of particles they received and/or retained (Fig. 5). Assembling zone 1 included most of the coastline and a few cells from the outer shelf (Fig. 5). This zone received and/or retained more coastal particles with short and medium PLDs ( $79.8 \pm 34.4$  and  $37.4 \pm 28.7$  particles  $\times$  cell<sup>-1</sup> on average, Fig. 5). Coastal particles with long PLD ( $15.6 \pm 16.2$  particles  $\times$  cell<sup>-1</sup>) and outer shelf particles with short PLD ( $17 \pm 14.7$  particles  $\times$  cell<sup>-1</sup>) were also abundant. To a lesser extent, particles from the outer shelf with medium and long PLDs, from the slope for all PLDs and even from seamounts and islands for long PLD reached this zone (Fig. 5). Assembling zone 2 gathered the remaining coastal cells, all located in the northwestern part of the domain (Fig. 5). This zone is a hotspot for coastal particles with short, medium and long PLDs ( $110.8 \pm 21.5$ ,  $98.7 \pm 22.8$  and  $71.6 \pm 26$  particles  $\times$  cell<sup>-1</sup>) and also received significant amounts of particles from the outer shelf (Fig. 5).

Outside the coast, in the southern part of the domain, two similar assembling zones were obtained in the same branch of the cluster dendrogram: zone 4, containing mainly cells over the outer shelf, and zone 11, gathering mainly cells from the slope and the inner part of the Pernambuco plateau (Fig. 5). These two assembling zones received/retained similar

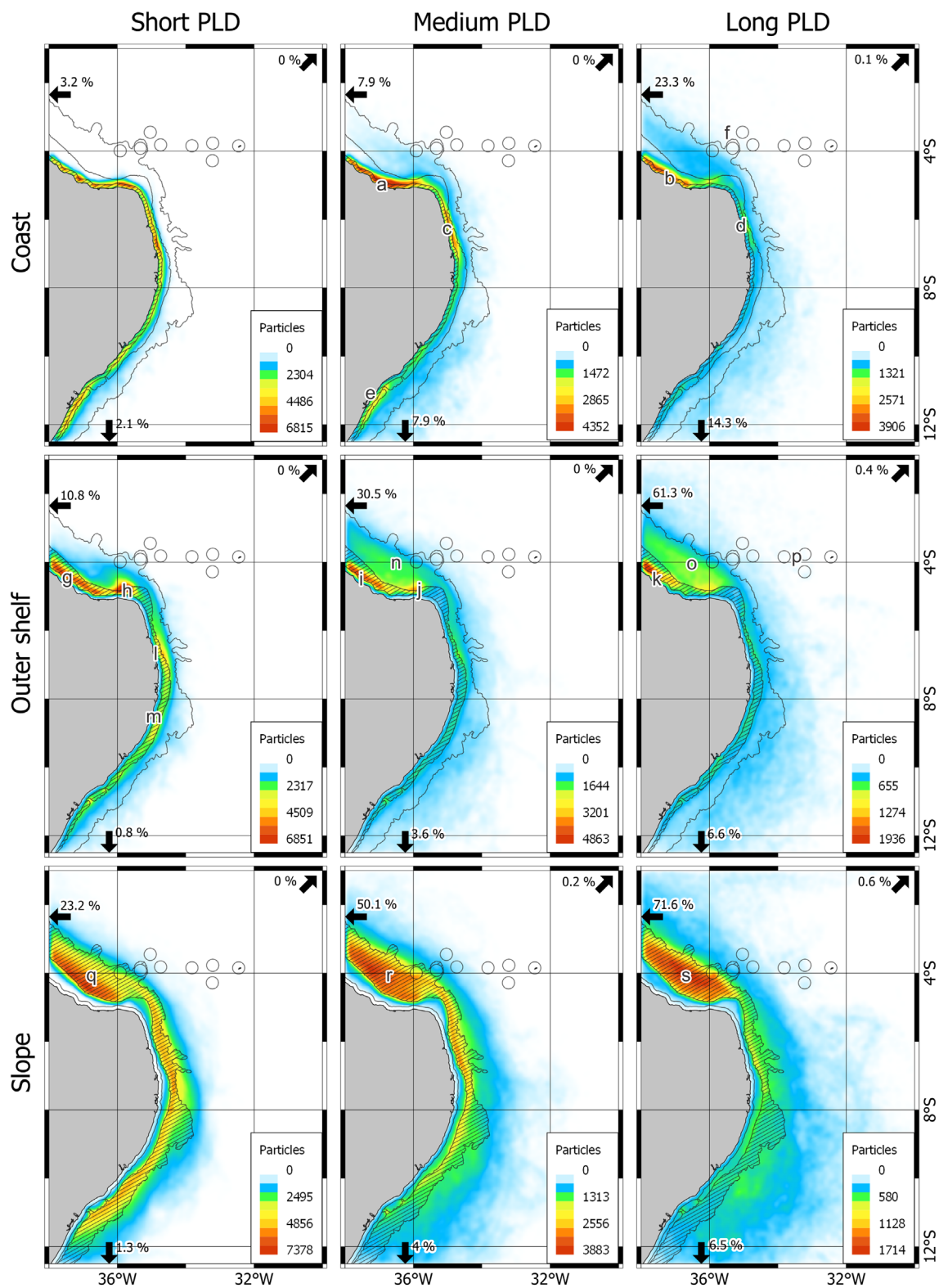


Figure 3. Kernel maps of the pooled data (108 runs) of final distribution of particles with short (5 days), medium (15 days) and long (30 days) pelagic life durations (PLD) released over the coast, outer shelf and slope. Dashed zones indicate release area. Arrows indicate export of particles to outside the domain. Marks refer to in-text citations.

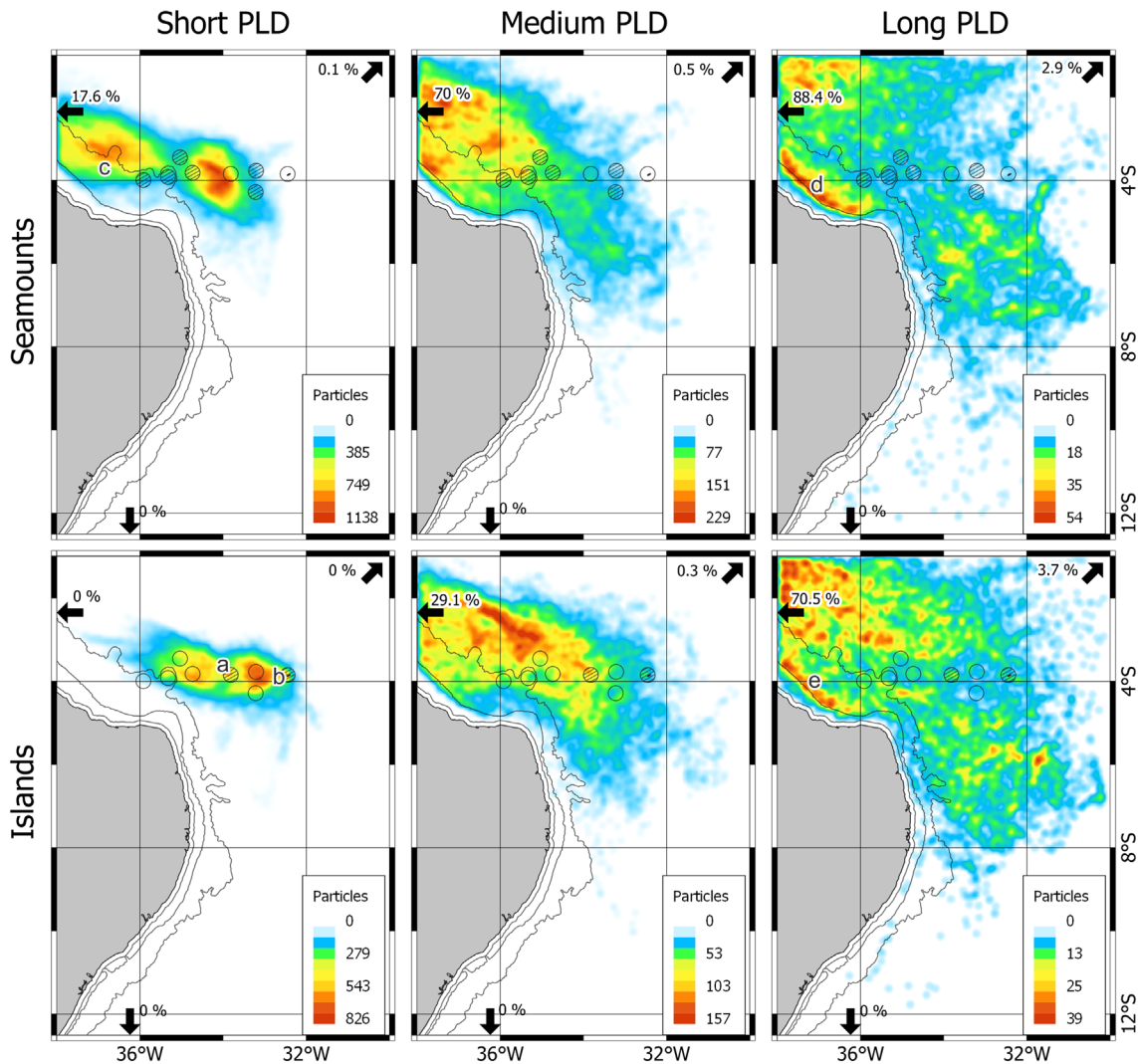


Figure 4. Kernel maps of the pooled data (108 runs) of final distribution of particles with short (5 days), medium (15 days) and long (30 days) pelagic life durations (PLD) released around the seamounts and islands. Dashed zones indicate release area. Arrows indicate export of particles to outside the domain. Marks refer to in-text citations.

categories of particles originating from the coast, outer shelf and slope, always in the highest amount for short PLD and the lowest for long PLD, and received a few particles from seamounts and islands. The main difference between the two zones was that assembling zone 4 retained more particles with short PLD from the outer shelf ( $56.5 \pm 26.5$  particles  $\text{cell}^{-1}$ ), whereas zone 11 retained more particles with short PLD from the slope ( $77.1 \pm 48.4$  particles  $\text{cell}^{-1}$ , Fig. 5).

Two other assembling zones (3 and 6) corresponded to cells located predominantly over the outer shelf. Compared to zone 4 reported above, zone 3 was composed mainly of cells located in the center of the domain (Fig. 5), which received/retained larger amounts of outer shelf particles with short PLD ( $78.9 \pm 53.8$  particles  $\text{cell}^{-1}$ ) and coastal particles with medium and short PLDs ( $41.9 \pm 30.7$  and  $32.1 \pm 24.8$  particles  $\text{cell}^{-1}$ ). Outer shelf particles with medium and long PLDs and particles from the slope for all PLDs were also abundant in zone 3 (Fig. 5). Zone 6 included cells

located in the northwestern part of the domain (Fig. 5). It is a hotspot for outer shelf particles with short, medium and long PLDs ( $117.8 \pm 23.3$ ,  $70.7 \pm 30.7$  and  $24.6 \pm 19.6$  particles  $\text{cell}^{-1}$ ) and also the non-coastal zone, receiving more coastal medium and long PLD particles ( $41.6 \pm 39.3$  and  $40.1 \pm 23.9$  particles  $\text{cell}^{-1}$ , Fig. 5).

The remaining cells of the slope and outer shelf were divided into five assembling zones (5, 7, 8, 9 and 12; Fig. 5). All five received/retained large amounts of slope particles with short and medium PLDs ( $27 \pm 26$  to  $110.5 \pm 38.7$  particles  $\text{cell}^{-1}$ ) and to a lesser extent long PLD ( $9.9 \pm 10.1$  to  $30.3 \pm 14.3$  particles  $\text{cell}^{-1}$ ). Outer shelf particles were also abundant in the five zones. Differences between these zones were mainly due to the total amount of particles received and to the fact that in zones 5, 7 and 12, outer shelf particles with short and medium PLDs were relatively more abundant than in zones 8 and 9. The five zones also received small amounts of particles from the coast, seamounts and islands (Fig. 5).



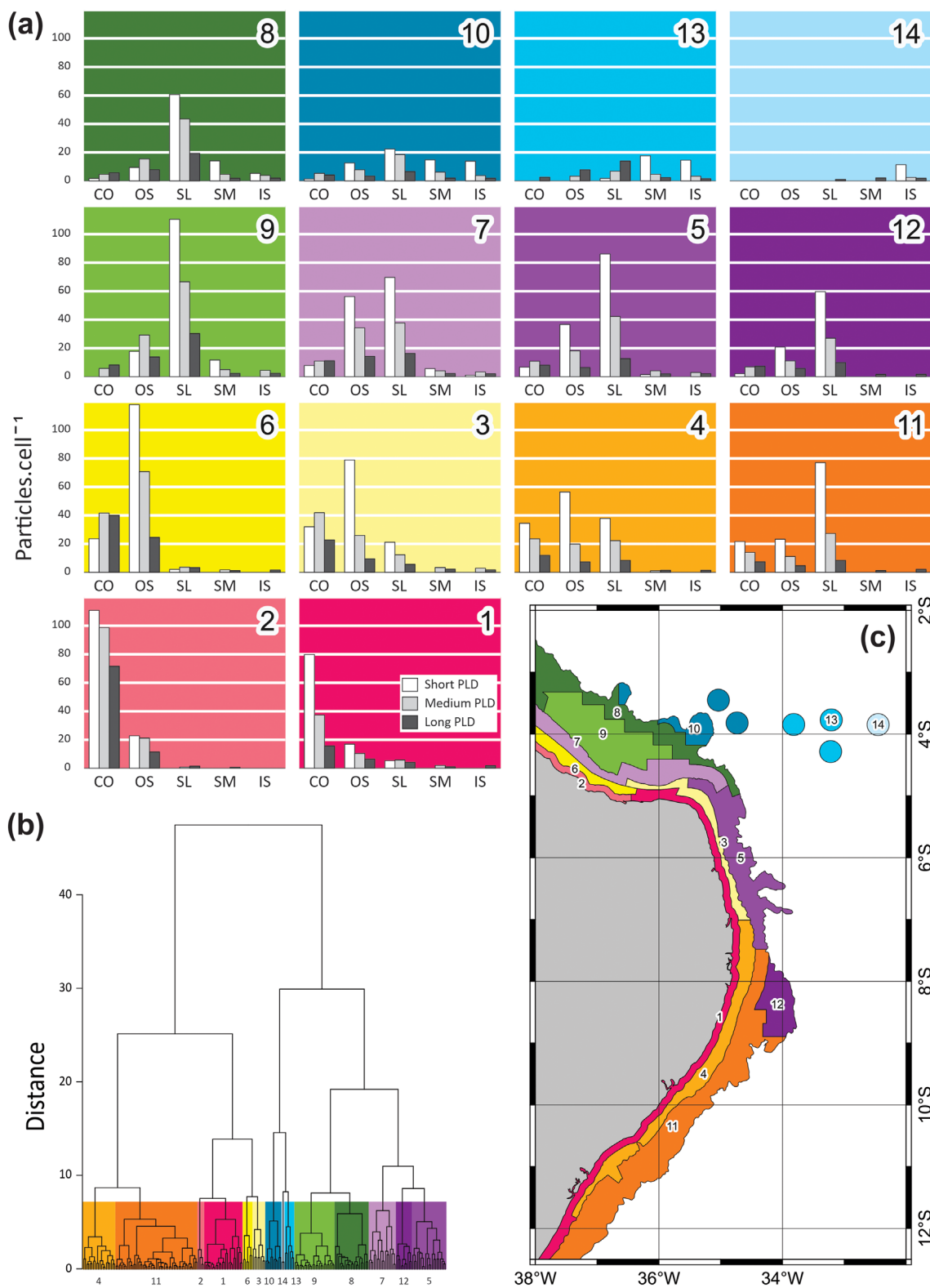


Figure 5. (a) Structure in the types of particles received and/or retained by each assembling zone. CO=coast, OS=outer shelf, SL=slope, SM=seamounts, IS=islands. (b) Hierarchical cluster dendrogram classifying the 225 cells into 14 assembling zones, each with a specific structure in the types of particles they received and/or retained and geographical distribution of the assembling zones. (c) Distribution map of assembling zones.

The cells covering the islands and seamounts were divided into three assembling zones (10, 13 and 14; Fig. 5). Zone 14 included the Fernando de Noronha archipelago, the furthest from the coast (Fig. 5). Compared to the other zones, this zone received/retained very few particles and of specific types: island particles with short, medium and long PLDs ( $11.4 \pm 11.6$ ,  $2.5 \pm 2.3$  and  $1.9 \pm 1.6$  particles cell<sup>-1</sup>), seamount particles with long PLD ( $2.1 \pm 1$  particles cell<sup>-1</sup>) and slope particles with long PLD (1 particles cell<sup>-1</sup>, Fig. 5). Assembling zone 13 included Rocas Atoll and the two seamounts further offshore (Fig. 5). This area received/retained particles from seamounts and islands for all PLDs, but in highest amounts for short PLD ( $14.6 \pm 13.6$  and  $17.6 \pm 17.9$  particles cell<sup>-1</sup> for islands and seamounts, respectively) and lowest for long PLD (particles cell<sup>-1</sup>). Particles for all PLDs originating from the slope also reached this area, especially those with long PLD ( $1.6 \pm 0.9$  and  $2.3 \pm 2.4$  particles cell<sup>-1</sup> for islands and seamounts, respectively). A few particles with long and medium PLDs from the outer shelf and long PLD from the coast also reached zone 13 (Fig. 5). Seamounts closest to the coast and a few cells above the slope made up assembling zone 10 (Fig. 5). This area received/retained all particle categories. Except for particles released along the coast, values were always highest for short PLD and lowest for long PLD (Fig. 5).

### Connectivity patterns

Connectivity among the assembling zones was almost unidirectional, northward from zones located in the south (4, 11, 12) and center (1, 3, 5) of the domain to zones located far to the northwest (2, 6, 7, 8, 9; Fig. 6, Supporting information). Bidirectional particle exchange was mostly significant between specific adjacent assembling zones (e.g. 4 with 1 and 11; 3 with 1 and 5; 11 with 12; and 6 with 2 and 7). Among islands and seamounts, connectivity was also unidirectional westward. Assembling zones 13 and 14 (islands and offshore seamounts) provided a significant influx of particles to the other zones north of 7°S (5, 7, 8, 9, 10) but received less than 1.5% of the particles released in these areas (except from zone 10 to zone 13; Fig. 6, Supporting information).

Coastal assembling zones had the highest particle retention (> 25% and up to 38.4% in zone 2; Fig. 6, Supporting information). Overall, retention decreased for assembling zones further from the coast and the lowest values (< 5%) were obtained for the islands and seamounts assembling zones (10, 13 and 14). An exception to this pattern was observed for slope zone 11, which retained more particles (20.7%) than its neighboring zone 4 in the shelf (18.9%; Fig. 6, Supporting information). No clear pattern was observed between assembling zone size and relative particle retention.

### Discussion

By applying a novel community-based approach to analyse Lagrangian simulations of plankton dispersal, we have identified 14 assembling zones within the Tropical Southwestern

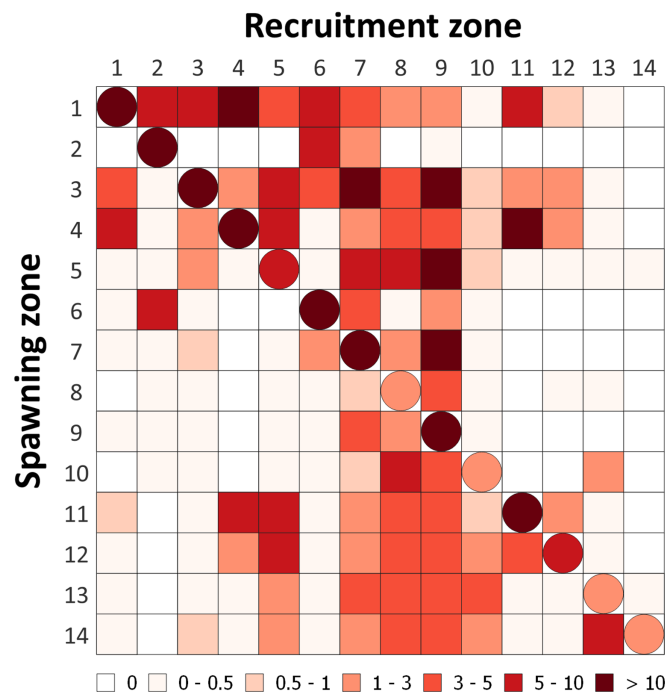


Figure 6. Retention (circles) and exchange (squares) of particles, relative to the amount released in the spawning zone, among the 14 assembling zones depicted in the cluster analysis.

Atlantic Ocean. These areas are particularly prone to receive and retain similar animal assemblage patterns from the regional pool of species through passive dispersal. They potentially harbor local communities that exhibit greater similarity within their respective boundaries. Thus, defining assembling zones with the methodology we propose here constitutes a key contribution to understanding diversity patterns across heterogeneous seascapes.

The dispersal patterns and boundaries of the assembling zones we obtained consistently align with local and regional in situ spatial distribution and abundance patterns of organisms observed in previous studies conducted in the region (Neumann-Leitão et al. 1999, Krajewski and Floeter 2011, Santana et al. 2018, Tosetto et al. 2022a). These observed patterns encompass a diverse array of marine animal taxa with distinct life histories, ranging from holoplanktonic copepods to reef fish, as detailed in Box 1. As such, these empirical findings substantiate the usefulness of the proposed method. Additionally, the method can yield important insights for subsequent field validation, particularly for regions or animal groups where information is limited or absent.

Another ecological outcome from our approach is considering the assembling zones as metacommunity spatially explicit units for connectivity experiments. Here, we considered the relative amount of particles that were retained and exchanged among assembling zones. Based on these results, we could identify the zones with higher potential to act as source (zones 1, 2, 3, 4, 11, 12, 13 and 14) or sink (zones 5, 6, 7, 8, 9, 10) of species along the seascape (Chen et al. 2008). Such an approach also provides an appropriate basis for the

### Box 1. Empirical confirmation of the patterns of dispersal and community assembly in the Tropical Southwestern Atlantic Ocean

Along the coast (assembling zone 1), typical coastal pelagic and benthic communities extending to ~ 30 km offshore have already been described for different groups of organisms, in particular coral reefs and their associated fauna (Floeter et al. 2001, Leão et al. 2003, Correia and Sovierzski 2012, Martinez et al. 2012, Giraldez et al. 2012), zooplanktonic communities (Neumann-Leitão et al. 1999, 2008, Tosetto et al. 2021) and estuarine fish, decapods, bivalves and gastropod larvae (Ekau et al. 1999, Neumann-Leitão et al. 1999, Schwaborn et al. 1999). The high coastal particle retention we observed for all considered PLD values probably provides an advantage to these coastal communities, reducing the possibility of organisms being transported offshore, where they would find poor conditions for subsequent recruitment. Previous studies have suggested high endemism of coral and sponge species in Brazilian waters (Correia and Sovierzski 2012, Leão et al. 2016), which is also consistent with the high retention and consequently reduced dispersal we obtained for short PLD coastal particles in the simulations.

In the northwestern region of our domain, we identified large hotspots receiving particles from both the coastal and outer shelf, mainly within assembling zones 2 and 6. Cells in these two zones had the highest retention rates and also received large amounts of particles from coastal zone 1. The few studies carried out in this area have shown that the biomass of zooplankton and the density of fish larvae are higher than in other coastal areas of northeastern Brazil (Mota et al. 2017, Souza and Mafalda Junior 2019). In the absence of large rivers that could enhance primary production and food availability, the observed high biomass of zooplankton and ichthyoplankton is likely due to high advection and retention of organisms (mass effect; Suzuki and Economu 2021), as suggested by our simulations.

Assembling zones 3 and 4, both located over the remaining outer continental shelf in the center and south of the domain, received significant amounts of particles from the coast and slope in our simulations. This is consistent with studies of zooplankton in these areas, which report either a typical oceanic community or a mixture of coastal and oceanic species (Neumann-Leitão et al. 1999, 2008, Santana et al. 2020, Tosetto et al. 2021). The intrusion of oceanic waters across the continental shelf is a process known to structure neritic communities in the Tropical Southwestern Atlantic Ocean, particularly in the region of assembling zone 3 where the continental shelf is narrow and intruding oceanic fauna can reach coastal areas, at least in spring when western boundary currents are stronger (Tosetto et al. 2021). Conversely, the transport of coastal species to the outer shelf in assembling zones 3 and 4, although intense in our simulations, may be limited by the ecological niches of species that may be strongly associated with coastal waters and/or estuarine plumes. For example, among planktonic cnidarians, while the siphonophore *Muggiaea kochii* is restricted to the coastal environment, the hydromedusa *Liriope tetraphylla*, which is also a dominant species along the coast, distributes at lower abundances throughout the shelf and even reaches the open ocean (Tosetto et al. 2021, 2022b), a pattern similar to what we obtained for medium PLD coastal particles.

Despite similarities, assembling zone 4, located in the southern part of the domain, showed interesting peculiarities compared to zone 3 located in the center. Zone 4 received and exported (i.e. mutual sharing) a relatively high amount of particles with both the coast (zone 1) and the slope (zone 11). It is noteworthy that zone 11 had a higher particle retention than the rest of the slope. Thus, the combination of high larval retention and high bi-directional exchanges of organisms between the coast, outer shelf and slope may have important implications for the biodiversity of these zones. In accordance with this, the inner region of the Pernambuco Plateau (located to the north of zones 4 and 11) presents distinct communities and high biodiversity and abundance of organisms, and was appointed as a conservation hotspot in Brazilian waters (Eduardo et al. 2018, Souza and Mafalda Junior 2019, Pereira et al. 2021, Tosetto et al. 2021).

Over the slope, assembling zones 5, 8, 10 and 12 are under the influence of the strong western boundary currents and therefore had low retention and high unidirectional northwestward transport of particles. These zones received a very limited number of particles from coastal areas. In situ studies showed that the communities of the region are dominated by holoplanktonic species associated with open waters, such as pyrosomes, copepods, siphonophores and chaetognaths, and mesopelagic lanternfish (Neumann-Leitão et al. 1999, 2008, Santana et al. 2020, Tosetto et al. 2021, 2022c). Unfortunately, the slope of the Potiguar eddy region (assembling zones 7 and 9), where we observed large concentration of particles, is understudied, preventing a comparison of simulation results with empirical evidence of species distribution and abundance. This particular area should be given more attention in future in situ studies.

For both islands included in the offshore assembling zones 13 and 14 (Rocas Atoll and Fernando de Noronha), we found greater retention of particles with short and medium PLD on their western side, which is protected from the strong westward cSEC (Silva et al. 2021). Consistent with this, in Fernando de Noronha, where there is no other island or seamount to the east to act as a source of larvae, distinct benthic and meroplanktonic communities have been observed in the less exposed southwestern coast of the island (Eston et al. 1986, Krajewski and Floeter 2011, Santana et al. 2018). In the Rocas Atoll, although differences in benthic communities between exposed and unexposed areas were also observed, the differences were less pronounced (Gherardi and Bosence 2001), possibly due to the larval transport from

the seamounts and island located to the east. Looking at particles with long PLD, retention was low in both zones 13 and 14, and most particles released there ended up in the open ocean or were exported outside the domain. Additionally, only a few long PLD particles reached these zones from the inshore zones, especially at Fernando de Noronha (zone 14) for which transport from the coast, shelf and slope was virtually zero. Based on these results, the maintenance of viable populations associated with shallow waters, such as reef fish, around the islands, is questionable. Indeed, reef fish diversity at the islands is low and dominated by a few species compared to coastal reefs (Krajewski and Floeter 2011, Longo et al. 2015). However, these dominant species typically occur at high abundances (Krajewski and Floeter 2011). In our simulations we only considered passive dispersal by currents, so active larval behavior may further increase retention or transport contributing to the maintenance of these specific large populations observed around both islands.

A previous study also based on dispersal modelling suggested low connectivity in the Tropical Southwestern Atlantic Ocean due to the absence or low simulated recruitment rate between marine protected areas, including the two islands we considered here (Endo et al. 2019). However, this study focused on a single fish species with a very long PLD (58 days) and disregarded spawning outside protected areas, which may not reflect the diversity of animal communities and habitats present in the region. With our community approach based on multiple PLD values released in diverse habitats, we observed particles from the coast, outer shelf and slope reaching Rocas Atoll and seamounts (assembling zone 13), and particles from this zone reaching Fernando de Noronha (assembling zone 14). Thus, although we indeed obtained relatively low number of particles recruiting around the islands and seamounts, direct or indirect (with Rocas Atoll and seamounts acting as stepping stones to Fernando de Noronha) exchanges of particles among the different coastal and offshore habitats occurred. Considering that most organisms can release thousands to hundreds of thousands of eggs in a single spawning event (Meekan et al. 1993, Britto et al. 2018), even a small fraction of released larvae reaching distant areas may be sufficient to maintain and interconnect populations and communities.

Finally, we found that a large amount of particles from all habitats was exported outside the domain westward to the Amazonian coast and the Caribbean Sea, mainly for medium and long PLDs. This larval flux is an important species input for both biogeographic provinces and likely contributes to the high biodiversity observed in the Caribbean Sea. In accordance with this, a recent study comparing the beta diversity from the coasts off northeastern Brazil, Amazon and south Caribbean found that sharing of species is always higher westward than in the opposite direction, and is greater in phyla with longer PLDs such as Chordata, Echinodermata and Arthropoda, whereas phyla with short PLD such as Porifera show greater turnover of species between northeastern Brazil and the Caribbean Sea (Tosetto et al. 2022a).

formulation of ecological hypotheses in the metacommunity framework to be tested in situ. For example, to evaluate the balance between species sorting and mass effect assembling archetypes (Leibold et al. 2004, Suzuki and Economo 2021), we considered the relative amount of particles recruiting in each assembling zone that were released there (autochthonous) or that arrived from other zones (allochthonous). Zones receiving a higher proportion of allochthonous particles are likely being controlled by mass effect, while species sorting potentially controls the zones retaining more particles than receiving them from other zones (Fig. 7). The precise location of the shift between the two archetypes is a hypothesis still to be tested. However, within the area of assembling zone 3, which received a higher proportion of allochthonous particles in simulations (Fig. 7), in situ studies indicate the significance of mass effect controlling the assembly of local communities (Tosetto et al. 2022b).

The balance between the two archetypes is also expected to be reflected in the biodiversity structure of metacommunities (Suzuki and Economo 2021). Under species sorting, the landscape becomes a mosaic of locally well-adapted species, leading to low alpha diversity and high beta and gamma diversities. As dispersal and mass effect increase, more species reach local communities, leading to more homogenized communities (lower beta diversity). Until a certain point, local coexistence is possible and alpha diversity will increase in parallel

with dispersal. However, at very high dispersal rates, stronger regional competitors may overcome local selection and exclude the locally superior but regionally inferior species, reducing alpha and gamma diversities (Mouquet and Loreau 2002, Suzuki and Economo 2021). In this context, it is expected that metacommunities from assembling zones under higher species sorting control (e.g. 14, 1, 11 in Fig. 7) will exhibit higher gamma and beta diversities, while the ones where mass effect is intense (e.g. 5, 8, 10 in Fig. 7) will tend to be more homogenous. Within the recent effort in increasing knowledge on regional biodiversity in the Tropical Southwestern Atlantic (Tosetto et al. 2022b, Eduardo et al. 2022), this is a promising hypothesis to be tested in the future.

Regarding the physical environment, the assembling zones we identified were mostly shaped by the degree of exposure to western boundary currents and the presence or absence of mesoscale features (eddies, recirculation) resulting from the interaction between these currents and coastlines. The distribution and limits of the assembling zones generally followed the cross-shelf limits of the broad geomorphologic provinces we considered to classify the released particles (i.e. coast, outer shelf and slope). This outcome is due to the predominantly along-shore advection induced by the NBUC (Fig. 2, Dossa et al. 2021), which led to a large retention of particles within the geomorphologic province where they were released.

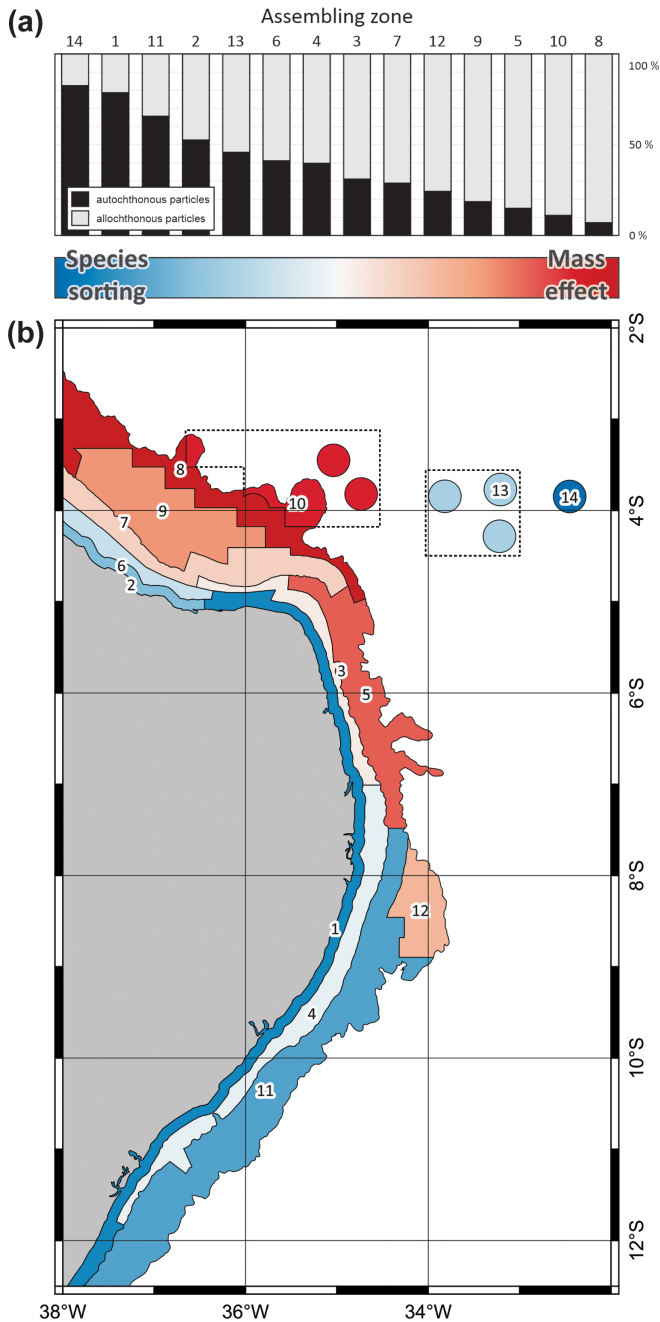


Figure 7. (a) Relative amount of autochthonous and allochthonous particle recruiting in each assembling zone. (b) Metacommunity archetypes expected to dominate in each assembling zone according to the proportion of autochthonous and allochthonous particles.

Conversely, boundaries between assembling zones along the shore were mostly shaped by three distinct types of interactions between western boundary currents and coastlines occurring along the domain. First, in the area under the influence of the seasonally variable bifurcation of the sSEC (northern limit of the bifurcation  $\sim 10^{\circ}\text{S}$ , Fig. 2), we identified assembling zones 4 and 11. The northern branch of the bifurcation, leading to the NBUC, remains relatively

distant from the shelf break until reaching the region of the Pernambuco Plateau ( $\sim 09^{\circ}\text{S}$ ; Dossa et al. 2021), where we observed the border between zones 11 and 12. In inner waters at this region, several cyclonic and anticyclonic eddies triggered by the interaction of the sSEC with the coast occur (Soutelino et al. 2011). Such features and the reduced exposition to the core of NBUC sustained a high exchange of particles between the coast, outer shelf and slope, and high retention within zones 4 and 11. Second, along the strong NBUC, whose core flows northward close and parallel to the shelf break (Dossa et al. 2021), we found assembling zones 3, 5 and 12. This fast-flowing current led to lower retention of particles when compared to the zones in the south. The region acts mostly as a narrow corridor with unidirectional northwards transport of particles from the south, and such bottlenecking led to recruitment in zones 3 and 5. Third, in the northwest of the study domain, there is a significant change in the direction of both the coastline and currents, leading to the formation of the Potiguar eddy at the subsurface (Fig. 2, Krelling et al. 2020, Dossa et al. 2021). Such configuration resulted in areas with different degrees of exposure to currents and recirculation that defined the boundaries of assembling zones: the more inshore (2 and 6), with reduced current speeds and high retention and recruitment; the area of the Potiguar eddy itself (7 and 9), where the recirculation leads to higher recruitment when compared to other areas over the slope; and the more offshore (8 and 10), exposed to currents and with lower retention and recruitment. Offshore, the islands and seamounts (assembling zones 13 and 14) are highly exposed to the westward cSEC (Silva et al. 2021), leading to lower retention of particles released there and reduced import from the inshore zones, particularly for the Fernando de Noronha Archipelago (zone 14), the furthest zone offshore.

Regarding the development of our approach, to simulate the diversity of marine fauna in the species pool (Fig. 1), we selected three planktonic life durations: 5, 15 and 30 days. These intervals encompass the larval duration of most meroplanktonic marine taxa (Bradbury et al. 2008) and the time until first reproduction in the case of holoplanktonic taxa. We also categorized the particles according to five broad geomorphologic provinces where they were spawned (coast, outer shelf, slope, seamounts and islands), assuming that the distinct habitats present in each province sustain particular lifeforms (Neumann-Leitão et al. 1999). By using 15 general categories resulting from the combination of these two traits in the model, we were able to represent most of the zooplanktonic community (Supporting information), which differs from usual Lagrangian simulations focusing on one or a few target species (Melià et al. 2016, Magris et al. 2016, Endo et al. 2019, Schilling et al. 2020).

Nevertheless, it is essential to recognize that these 15 categories are generalizations, and the particular life-story traits of species may also affect the range of their dispersal. For example, buoyancy and vertical migration influence the position of organisms in the water column and, consequently, their exposure to currents. Active swimming of organisms

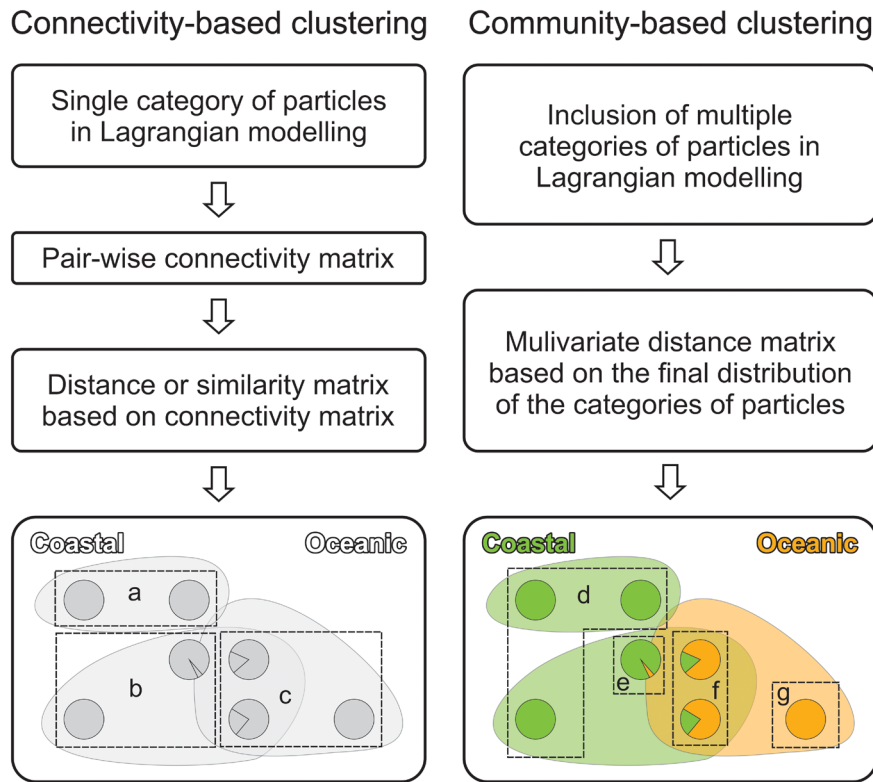


Figure 8. Comparison between the main aspects of the community-based clustering methodology proposed in the present study with the connectivity-based clustering approaches (Jacobi et al. 2012, Berline et al. 2014, Garavelli et al. 2014, Rossi et al. 2014). The diagrams represent simplified examples of possible results. The transparent polygons in the background represent the dispersal range of three hypothetical spawning spots. According to the release province, two categories of particles were defined (note that in our model we used 15 categories, the released habitats and pelagic life durations (PLDs)). The pie charts represent the relative number of particles received by seven distinct cells in the grid. Dashed rectangles indicate results of the clustering methods. Marks refer to in-text citations.

could also play a role on top of passive dispersal. Although it is possible to take into account these processes in the modelling platform that we used (Ichthyop; Lett et al. 2008), they are poorly known in our study region, and thus were disregarded in our simulations. With advances in biodiversity knowledge and computational processing capacity, the development of more complex models considering larger and more detailed species pools is a promising perspective. Additionally, we intentionally ignored species spawning and recruiting in the open ocean. Such species are generally widespread, and open ocean communities are quite similar at the scale of our study (Boltovskoy et al. 2002). Therefore, modelling the entire open ocean would have increased computational processing requirement and added noise to the obtained patterns in shallow water without markedly improving ecological outcomes. Still, the advection of oceanic species to shallow water systems likely contributes to the assembly of these communities. We considered the issue by including the region over the slope, which in the study domain, is mostly ocean-like (Tosetto et al. 2022b). We also restricted our scope to animal assemblages. Considering the short life cycle of cyanobacteria, the main primary producers across the study area (Farias et al. 2022), it is unlikely that their distribution is significantly governed by dispersal.

Furthermore, the distribution of primary production along the seascape can be assessed through satellite observation (European Union-Copernicus Marine Service 2019).

Traditional uses of Lagrangian simulations evaluate connectivity between user-defined (often quite small) spawning and recruitment areas. Our study differed by considering the possibility of spawning and recruitment over the entire study domain (except the open ocean), and we were able to identify the assembling zones according to the final position of the unique combination of categories of particles and investigate all possible connectivity pathways over the domain. A few other studies also used Lagrangian models to identify spatial subdivisions of marine systems (Jacobi et al. 2012, Berline et al. 2014, Garavelli et al. 2014, Rossi et al. 2014). However, their methodology and purposes were quite distinct from the method we used to investigate community assembly, as they aimed to identify areas hydrodynamically connected based on univariate metrics of direct exchange of particles. We have summarized the differences between these methods (that we name connectivity-based clustering) and our community-based approach in Fig. 8. The simplified diagrams represent the range of dispersal from three hypothetical spawning areas for two categories (coastal and oceanic) of particles defined according to the release province (note

that we used 15 categories in our model, and not only 2). Connectivity-based clustering methods (which do not take categories into account) are particularly useful for defining boundaries between putative subpopulations (e.g. clusters a and b in Fig. 8; Jacobi et al. 2012, Garavelli et al. 2014). However, to understand the effects of dispersal in the process of community assembly, it is necessary to consider the characteristics of the transported particles (categories) in order to properly represent the diversity of animal assemblages. Indeed, if an area receives planktonic organisms from different origins, e.g. from both the coast and the open ocean, it is likely to result in a mixed community (Fig. 8; Neumann-Leitão et al. 1999, Tosetto et al. 2022b). Using the connectivity methods, these mixed cells would be clustered with the zone where most particles originate (clusters b and c in Fig. 8). In contrast, in our approach, these mixed zones are clustered together because they received a similar number of particles with similar traits. Thus, our method allows the identification of unique combinations of particles released into different environments that can potentially colonize and assemble communities in each cluster (cluster e and f in Fig. 8). Also, unlike in connectivity-based methods, if two areas received similar amounts of particles of the same categories, our approach groups them together, even if the two areas were not directly connected (e.g. cluster d in Fig. 8).

In conclusion, the identification of assembling zones obtained by coupling a community-based Lagrangian modelling approach with multivariate clustering has proven to be useful and appropriate for including dispersal patterns in the process of community assembly in marine systems. This approach contributes to understand the spatial distribution of animal communities (Box 1) and offers a broad view of the distribution of distinct communities and connectivity pathways along marine environments. It also provides a relevant basis for the formulation of ecological hypothesis in the metacommunity framework to be tested in situ, such as the balance between species sorting and mass effect assembling archetypes. However, dispersal patterns and assembling zones should be seen as one of several layers (e.g. geomorphology, thermohaline structure and distribution of primary productivity) interacting to shape local communities. Thus, crossing this layer with other physical, chemical and biological dimensions of the seascape, as well as quantifying the effects of interspecific interactions and ecosystem processes, is essential for a deeper understanding of the distribution of distinct communities and connectivity pathways along marine environments and their contribution to ecosystem functioning. Such knowledge can also be coupled with more general information such as habitat quality indexes and distribution of target habitats (Magris et al. 2016) in marine spatial planning, to build a functional and interconnected web of marine protected areas. With advances in knowledge of marine physical modelling and ecosystem functioning, as well as in computational processing capacity, integrating community-based Lagrangian dispersal modelling to other processes in broad metacommunity and meta-ecosystem models is a promising perspective for future research in seascape ecology.

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## Author contributions

**Everton Giachini Tosetto:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Validation (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (equal). **Christophe Lett:** Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Visualization (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Ariane Koch-Larrouy:** Methodology (equal); Validation (equal); Visualization (equal); Writing – review and editing (equal). **Alex Costa da Silva:** Methodology (equal); Visualization (equal); Writing – review and editing (equal). **Sigrid Neumann-Leitão:** Methodology (equal); Supervision (equal); Visualization (equal); Writing – review and editing (equal). **Miodeli Nogueira Junior:** Methodology (equal); Visualization (equal); Writing – review and editing (equal). **Nicolas Barrier:** Methodology (equal); Software (equal); Visualization (equal); Writing – review and editing (equal). **Alina Nathanael Dossa:** Methodology (equal); Validation (equal); Visualization (equal); Writing – review and editing (equal). **Michel Tchilibou:** Methodology (equal); Validation (equal); Writing – review and editing (equal). **Perrine Bauchot:** Methodology (equal); Validation (equal); Visualization (equal); Writing – review and editing (equal). **Guillaume Morvan:** Methodology (equal); Validation (equal); Visualization (equal); Writing – review and editing (equal). **Arnaud Bertrand:** Conceptualization (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing – original draft (supporting); Writing – review and editing (equal).

## Transparent peer review

The peer review history for this article is available at <https://publons.com/publon/10.1111/ecog.07110>.

## Data availability statement

The data underlying the results presented in the study are available in SEANOAE: <https://doi.org/10.17882/96778> (Tosetto et al. 2023)

## Supporting information

The Supporting information associated with this article is available with the online version.

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