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Larval dispersal and physical connectivity of *Pheronema carpenteri* populations in the Azores

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The study of larval dispersal and connectivity between deep-sea populations is essential for the effective conservation and management of deep-sea environments and the design and implementation of Marine Protected Areas. Dense sponge aggregations, known as "sponge grounds", are a key component of marine benthic ecosystems, by increasing the structural complexity of the sea floor and providing structure and habitat for many other species. These aggregations are characteristic of the Azores deep-sea environment. These sessile organisms rely primarily on larval dispersal for their reproduction. Connectivity between specific *Pheronema carpenteri* sponge aggregations in the Azores was studied using a 3-D biophysical dispersal model. Different biological trait scenarios were analyzed, considering spawning seasonality and pelagic larval duration. Model results indicate that regional circulation patterns drive larval dispersion, shaping population connectivity of *P. carpenteri* sponge aggregations in the Azores, particularly among aggregations in the Central Group of Azorean islands. Some areas present high retention rates, receiving larvae from several sponge aggregations while also being important larval source aggregations. In contrast, aggregations from the Eastern Group may be isolated from the others. Larval dispersal and connectivity patterns were analyzed concerning the current configuration of Marine Protected Areas (MPAs) in the Azores. The results underscored the importance of maintaining protection efforts in existing MPAs and identified stepping-stone locations and specific sites where additional measures could enhance species connectivity in the Azores.

1 Introduction

Connectivity is a fundamental process driving the persistence of marine populations and influencing the ecosystems' structure, biodiversity, productivity, dynamics and resilience (Kenchington et al., 2019; Busch et al., 2021). In the deep-sea (the ocean below 200 meters depth), connectivity is a key element for spatial management and conservation plans including the establishment of Marine Protected Areas (MPAs) (Lima et al., 2020; Combes et al., 2021).

Many marine organisms rely on the larval phase as the primary means to colonize new areas, making this process crucial for individual survival as well as in population dynamics and persistence (Ross et al., 2020). Some species possess a pelagic larval phase, during which their larvae are transported by ocean currents, facilitating migration between geographically distant populations (Paris et al., 2013). However, despite the pivotal role of the planktonic larval stage and larval dispersal in understanding deep-sea population connectivity, knowledge gaps remain due to challenges in obtaining *in-situ* data (Kenchington et al., 2019). This pelagic larval dispersal phase contributes to (i) population exchanges that aid in the replenishment of populations, population connectivity and the maintenance of well-established communities, and to (ii) the colonization of new territories/habitats, possibly modifying existing communities and associated biodiversity (Adams et al., 2012).

Dense sponge aggregations, known as "sponge grounds", are a key component of marine benthic ecosystems, enhancing, along with corals, the local biodiversity, and acting as feeding, reproductive, nursery and refuge areas for many invertebrates and fish (Pham et al., 2015; Beazley et al., 2021). Deep-sea sponges are thought to play an important role in the deep-sea nutrient cycle, recycling the nutrients, through their capacity of filtering large quantities of water (Leis, 2020). By converting dissolved organic matter (DOM) into detritus, sponges are enable to transfer the energy and nutrients in DOM to higher trophic levels, the so-called sponge loop pathway (Rix et al., 2018). They also contribute to the biogeochemical cycling of dissolved nutrients, such as carbon and nitrogen, and silicate in the case of siliceous sponges like *P. carpenteri*, which belongs to the class of Hexactinella (Maldonado et al., 2016; Ross et al., 2016, 2019; Taranto, 2022).

These deep-sea organisms rely upon a planktonic larval stage for dispersal; thus, studying the environmental patterns responsible for their distribution is critical to inform and support the development of appropriate conservation measures (Maldonado and Young, 1999; Cowen and Sponaugle, 2009; Xavier et al., 2015; Wang et al., 2021).

Deep-sea sponges inhabit multiple areas of the deep-sea, particularly in the North Atlantic (Samuelsen et al., 2022). The hexactinellid *Pheronema carpenteri* forms extensive sponge aggregations, occurring from south of Iceland and west of Scotland, across the Porcupine Seabight, Azores, northern Spain, Portugal, Canary Islands, and off Morocco at 800–1,350 m depth (Maldonado et al., 2016). Some of them are reported to have persistent spicule skeletons (Maldonado et al., 2005). These spicule mats created by the senescence and death of hexactinellid sponges, provide an important substratum that hosts diverse faunal communities (Bett and Rice, 1992) forming biodiversity hotspots (Henry and Roberts, 2014), and may even function as reducers of sediment erosion in the deep-sea (Black et al., 2003). Sponges are also known for establishing complex microbial symbioses being a reservoir of exceptional microbial diversity and major contributors to the total microbial diversity of the world's oceans (Thomas et al., 2016).

P. carpenteri forms the most extensive Hexactinellid aggregations in the North-East Atlantic (Graves et al., 2023), and is a typical organisms of the deep-sea in the Azores (Pham et al., 2015). *P. carpenteri*, is a nest-shaped sponge that likely forms the most extensive sponge aggregations at temperate latitudes, with abundances up to 6 individuals m^{-2} (Maldonado et al., 2016). *P. carpenteri* has been recorded in the northeast Atlantic from the northern Rockall Trough at about 59°37'N north, through the Porcupine Seabight, Bay of Biscay, Portuguese coast and Moroccan coast to the Azores, at depths ranging from 650m to 1600 m (Rice et al., 1990; White, 2003; Howell et al., 2016; Creemers et al., 2019; Colaço et al., 2020; Vieira et al., 2020; Somoza et al., 2021; Taranto, 2022). In the Azores its density can vary between 2 to rarely 56 individuals per squares meter (Colaço pers. observ.).

In the Porcupine Sea Bight, this species occurs in areas with low currents but close to regions where enhanced bottom tidal currents are found (White, 2003). This corroborates the hypothesis of Rice et al. (1990), that these sponges do not tolerate enhanced currents, but may nevertheless be dependent upon the resuspended or undeposited organic matter carried to them from regions of increased tidal energy. In the Azores the same phenomena is observed, with the sponge grounds being present in areas with low intensity currents (Viegas, 2022).

The Azores deep-sea benthos includes a high diversity of sponges and cold-water corals which build rich communities (Pham et al., 2015; Gomes-Pereira et al., 2017; Creemers et al., 2019; Colaço et al., 2020; Morato et al., 2021). *P. carpenteri* is a common taxon in the Azores bathyal environment, forming large aggregations (Colaço et al., 2020) and is considered a vulnerable marine ecosystem (VME) since it meet several of the vulnerability criteria, such as fragility, slow growth rate and low recovery potential (FAO, 2008).

Available data about the biology of hexactinellids sponges results mainly from studies with shallow-water sponges (Barthel et al., 1996; Boury-Esnault et al., 1999), also arctic deep-sea populations (Leys and Lauzon, 1998), and other non-specific glass sponge's case studies (Bett and Rice, 1992; Boury-Esnault et al., 1999; Guillas et al., 2019). The reproductive strategy of *P. carpenteri* is currently unknown (Graves et al., 2023) but Hexactinellids are assumed to reproduce both asexually and sexually with lecithotrophic larvae (Leys and Ereskovsky, 2006; Teixidó et al., 2006). During their life cycle, after hatching, pelagic larvae drifts in the water column for a limited period (Pelagic Larval Duration, PLD), before settling on the seafloor, in a recruitment area, to become sessile juvenile sponges, if the environment conditions are suitable (Maldonado, 2006). Despite their deep-water habitat, hexactinellids sponges may experience seasonality that perhaps influences their reproductive period (Leys and Lauzon, 1998). For the deep-sea species *Geodia* the reproductive season spans from spring to Autumn (Koutsouveli et al., 2020).

The current understanding of deep-sea larval behavior for deep-sea sponges is extremely limited (Busch et al., 2021), mainly due to the inherent difficulty of assessing deep-water habitats (Lopes, 2005), and particularly by the difficulty of collecting larvae of deep-sea organisms. Available data from the shallow-water sponges indicate that most sponge larvae are anchiplanic, with a short planktonic larval duration of minutes to a few days (usually< 2 weeks) (Maldonado, 2006; Ross et al., 2019). However, this short PLD is only reported for shallow-water species and is believed to not be representative of deep-sea water taxa such as *P. carpenteri*. The glass sponge *V. pourtalesii* has an estimated maximum pelagic larval duration of 2 weeks (Wang et al., 2021). Hilário et al. (2015) calculated that the average known PLD of a deep-sea organism is 35 days, which is longer than for their shallow-water counterparts PLD. Wang et al. (2021) used modelling tools to study the fate of glass sponge larvae in the Gulf Stream, hypothesizing a 2-week maximum PLD for deep-sea glass sponge.

Furthermore, it is suggested that sponge larvae may remain in the water column for longer periods, perhaps months (Boury-Esnault et al., 1999; Maldonado, 2006). Environmental factors like seawater temperature can influence the duration of the reproductive period (Maldonado, 2006). Therefore, two different PLDs were tested in this study, a PLD of 15 days (similar as was estimated *V. pourtalesii*), and a PLD of 30 days (similar as was estimated in other deep-sea larvae dispersal studies (Hilário et al., 2015; Vic et al., 2018) (Table 1).

In this work, the potential larval dispersal of *P. carpenteri* deep-sea sponge aggregations in the Azores, it was modeled, as a proxy for the potential larval transport around Azores and evaluate the probability of the current MPAs to maintaining the connectivity of these benthic organism populations.

2 Methodology

2.1 Study area

The Azores archipelago is composed of nine islands, spanning 600 km in the Northeast Atlantic, between 23°W and 33°W and 37°N and 40°N (Figure 1) and divided into three geographical groups. The Mid Atlantic Ridge (MAR) crosses the archipelago. Two islands are located west of the MAR, on the American plate, forming the Western Group (WG), while the other islands are located on the Eurasian plate with 5 islands positioned in the Central Group (CG) of the Archipelago and two islands situated further east (Eastern Group: EG).

2.1.1 *Pheronema carpenteri* in the Azores

The *P. carpenteri* sponge aggregations identified in the scope of the SPONGES Project, due to their frequent observations are the focus of this study. These *P. carpenteri* aggregations are located along the Azores Archipelago (Figure 1), in a bathymetric range from 630 to 1000 meters depth (Table 2). Specifically, they are found over the Mid-Atlantic Ridge (MAR) at Cavala Seamount (L#1) and Gigante Seamount (L#2); in the Central Group (CG), at the Princesa Alice (L#3), Açores Bank (L#4), in the South of Faial (L#6), South of Pico (L#7), and North of Pico (L#8); and in the Eastern Group (EG) L#9 in Mar da Prata, and L#10 in Formigas.

TABLE 1 Literature review for Pelagic larval duration, spawning seasonality, of deep-sea sponges, from different locations and depths, used/obtained in other studies.

Organism/Taxa	PLD	Spawning season	Organism location	Reference
Sponges (generic)	<14 days	n/a	n/a	1)
Sponges (generic)	n/a	phytoplankton blooms (March/autumn)	Several; northwest Atlantic	2)
Demosponge	14 days	After spring bloom	Cantabrian sea	3)
Demosponge (*Geodia barretti*)	n/a	Spring & autumn/phytoplankton blooms	Norwegian fjords, deep continental shelf	4); 5)
Hexactinellida	> 24h (<24h for shallow sponge)	–	North Atlantic	6)
Deep-sea species	Median: 10-310days		Deep-sea (Hydrothermal vents, cold seeps, food falls, Seamounts)	7)
Shallow species	Median: 0.17-293 days		Deep-sea (Hydrothermal vents, cold seeps, food falls, Seamounts)	7)
Hexactinellida	n/a	All year round/ phytoplankton blooms	Fiords, British Columbia	2)
Vazella pourtalesii (Hexactinellida)	2 weeks (value assumed for the model application)	All year round/	282 to 593 meters depth Eastern coast of North America	8)
Oopsacas minuta (Hexactinellida)	n/a	All year round	submarine cave, France	2)
Deep-sea organisms	30-180 days (estimated)	n/a	n/a	9)

1) Maldonado, 2006; 2) Kenchington et al., 2019; 3) Busch et al., 2021; 4) Spetland et al., 2007; 5) (Leys and Lauzon, 1998); 6) Ross et al., 2019; 7) Hilário et al., 2015; 8) Wang et al., 2021; 9) Vic et al., 2018; n/a, no information available or not applicable.
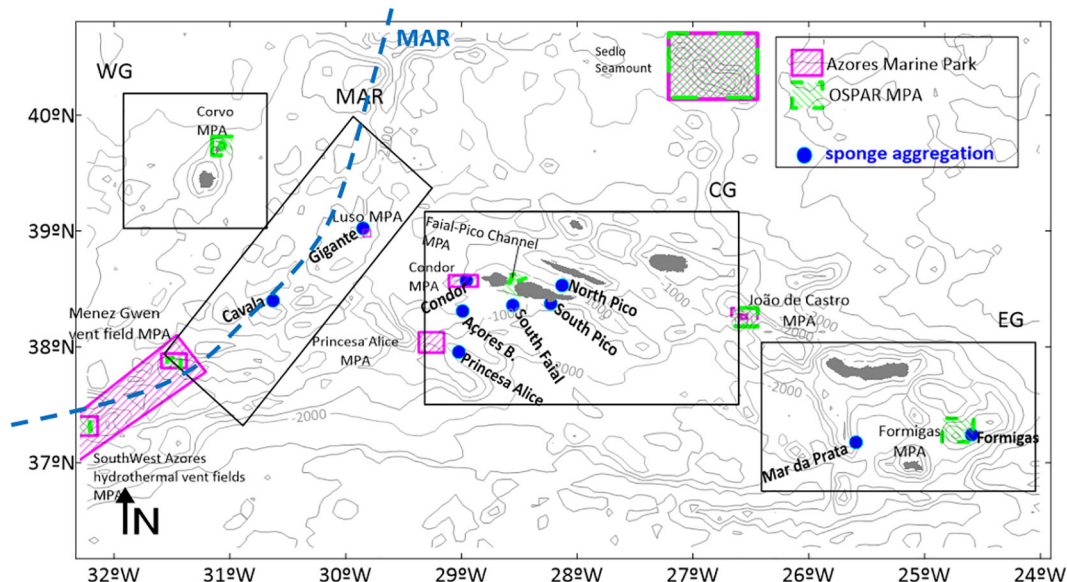
FIGURE 1

Bathymetry of the study area, with the representation of the Mid-Atlantic Ridge (MAR) with a blue dashed line, the 9 islands of the Azores archipelago in grey, the location of the *Pheronema carpenteri* sponge aggregations in the study with blue circles; black polygons depicts the groups in analysis: MAR Group (L#1 Cavala, L#2-Gigante), CG-Central Group (L#3-Princesa Alice, L#4-Açores Bank, L#5-Condor Seamount, L#6-South of Faial, L#7-South of Pico, L#8); EG- Eastern Group (L#9-Mar da Prata, and L#10-Formigas), and representation of the Azores Marine Park and OSPAR Marine Protected Areas, and the Western Group (Flores and Corvo islands), Central Group (Faial, Pico, São Jorge Terceira and Graciosa Islands), and the Eastern Group (São Miguel and Santa Maria islands).

For applying particle-tracking models to study larvae dispersal, it is essential to include information about their biological traits such as spawning seasonality, larval behavior, and pelagic larval duration (Busch et al., 2021). Empirical data about deep-sea sponges biology is very scarce, and specifically regarding *P. carpenteri* it is absent. Previous studies often assume that deep-sea sponges do not experience spawning seasonality, unlike their littoral relatives, because they are too deep to be influenced by light (Barthel et al., 1996). However, further studies pointed out that despite their deep-sea habitat, sponges experience seasonality, which influences their growth rate and perhaps reproductive period, which, in turn, may be regulated by patterns of primary production in the photic zone of the ocean and subsequent sinking of the generated production (Leys and Lauzon, 1998). A number of

TABLE 2 *Pheronema carpenteri* sponge aggregations in the study, their location, depth, source and name/location.

Location	Longitude (°W)	Latitude (°N)	Depth (m)	Name	Group	Source/project
L#1	-30.6701	38.3632	900	Cavala	MAR	emodnet[1]
L#2	-29.88809	38.98353	766	Gigante	MAR	Exp-Fund.Azul [2]
L#3	-29.06232	37.9183	900	Princess Alice	CG1	Biodiaz [3]
L#4	-29.02941	38.273	825	Açores Bank	CG2	Sponges-Observer_2017[4]
L#5	-28.99877	38.53281	775	Condor Seamount South	CG3	IMAR-DOP/UAz (CoralFish, Corazon, Condor) [5]
L#6	-28.59288	38.32531	630	South of Faial	CG4	Sponges-observer_2017[2]
L#7	-28.26657	38.33921	1000	South of Pico	CG5	Sponges-Lula[2]
L#8	-28.1735	38.49624	822	North of Pico	CG	Exp-Fund.Azul[2]
L#9	-25.63083	37.14111	780	Oeste West of São Miguel (Mar da Prata)	EG	IMAR-DOP/UAz (CoralFish, Corazon, Condor) [5]
L#10	-24.63	37.205	904	Formigas	EG	Colecta[6]

[1]http://ipt.vliz.be/eurobis/resource?r=imagedop_video_annotations; [2]Colaço et al., 2020; [3]Institute of Marine Research (IMAR-Azores), Portugal; [4]Department of Oceanography and Fisheries (DOP)-University of the Azores, Portugal, 2017. [5]ImageDOP Bentic Video http://www.vliz.be/en/imis?dasid=4492&doiid=304; [6]DOP/internal unpublished data.

deep-sea species display potential spawning that is linked to organic matter input during seasonal phytoplankton blooms (Mercier et al., 2011; Sun et al., 2011; Mercier et al., 2013; Baillon et al., 2014). In particular, for deep-sea corals, some gametogenic peaks coincided with periods marked by high surface productivity, in spring and autumn (Santos et al., 2013).

The information available regarding deep-sea larval behavior is scarce. Table 1 summarizes the literature review regarding the deep-sea larvae biological traits and specifically for deep-sea sponges larvae. Different scenarios were computed to study the larval dispersal in the Azores. It was considered a yearly release since no information on spawning was available, but since some deep-sea species are believed to experience spawning seasonality, seasonal scenarios were also performed. For the seasonal scenario, a release in March was simulated to represent the spring spawning season, and a release in October to represent the autumn spawning season (Santos et al., 2013). All the scenarios ran with different pelagic larval durations (PLD) of 15 and 30 days (Table 3).

2.1.2 3D Hydrodynamic model using Mohid

The 3-D hydrodynamic modelling system used was MOHID, developed at MARETEC (IST - University of Lisbon) which solves the 3D incompressible primitive equations built and developed using an object-oriented philosophy (IST, 2003; Braunschweig et al., 2004; Leitão et al., 2008). MOHID is an open-source model, available online at https://github.com/Mohid-Water-Modelling-System/Mohid. It is programmed in ANSI FORTRAN 95, following an object-oriented approach allowing the integration of different modules in implicit and explicit ways (IST, 2003). The hydrodynamic model simulates the currents and density fields, fundamental for the Lagrangian and Eulerian transports through advection and/or diffusion processes. The turbulence is solved by the General Ocean Turbulence Model (GOTM) module (Burchard

et al., 1999). Model configuration and boundary conditions are described in Table 4.

The model was implemented for the Azores region from 32.4721°N to 42.91211°N, -21.40775°W to -36.2878°W, for the years 2017 and 2018. It has a horizontal resolution of 1/16° horizontal resolution (6 km grid) and a vertical resolution of 50 vertical layers covering the entire water column from the surface to the sea floor (0 – 5940 meters). The first 10 meters of the water column are divided into 7 sigma layers, which change their size based on the tide level evolution. Below these, the water column is divided into 43 Cartesian layers, which are thinner in the upper layers (less than 2 meters in length) and larger in the bottom ones.

For the atmospheric forcing, the boundary conditions are obtained from the Global Forecast System (GFS model), provided by NOAA- America National Ocean and Atmospheric Administration, available at https://www.ncdc.noaa.gov/. This model has hourly fields of surface wind, temperature, relative humidity, pressure, and solar radiation.

Model validation of the selected parameters is detailed in Viegas (2022). Comparison between model results and tide gauge data reveals the capability of the model to accurately simulate sea water level, in the Azores region. Sea surface temperature was validated against remote sensing data and predicted sea water temperature and salinity were compared with *in situ* data from ARGOS floats. Model validation against the ARGO float data for vertical profiles of temperature and salinity showed Pearson correlation coefficients greater than 0.97, with the majority being 0.99 (Viegas, 2022). The outputs of the hydrodynamic model (horizontal and vertical components of the velocity, sea level, temperature, salinity, and density fields) were used to feed the CMS particle tracking model to simulate the plume-dispersal processes in offline mode.

TABLE 3 Scenarios considered in this study, with spawning date and pelagic larval duration and the release length (in days).

Scenario	PLD (days)	Release date	Release length (days)
PLD15_March_2017	15	March 2017	31
PLD15_October_2017	15	October 2017	31
PLD30_March_2017	30	March 2017	31
PLD30_October_2017	30	October 2017	31
PLD15_year_2017	15	January-December 2017	365
PLD30_year_2017	30	January-December 2017	365
PLD15_March_2018	15	March 2018	31
PLD15_October_2018	15	October 2018	31
PLD30_March_2018	30	March 2018	31
PLD30_October_2018	30	October 2018	31

TABLE 4 Hydrodynamic model configuration.

Parameter	MOHID hydrodynamic model
Model dimensions	3D – Baroclinic
Domain	32.472°N to 42.9121°N, and 21.4078°W to 36.288°W
Bathymetry	EMODNET (1/16arc-minutes) [a]
Horizontal solution	6km
Vertical resolution	50 vertical layers: 7 sigma layers + 43 cartesian layers
Tide	Tide: FES2014b)
Δt	120 seconds
Meteorological forcing	Global Forecast System model (GFS) 0.25° resolution c)
Hydrodynamical forcing	CMEMS Global Ocean Circulation Model (PSY4V3R1) 1/12°resolution [d]
Model output	3600 seconds
Simulation length	Jan/2017 – Dec/2018

[a]EMODnet Consortium, 2018; [b]Lyard et al., 2021; [c]National Centers for Environmental Prediction, et al., 2015; NOAA, 2015; [d]Lellouche et al., 2018; n/a, not applicable.

2.1.3 Particle tracking model

The CMS-Connectivity Modelling System is an open-source model, freely available online. It was created for the multi-scale tracking of biotic and abiotic particles in the ocean, based on a Lagrangian framework to study complex larval migrations (Paris et al., 2013). This model runs offline, over a 3D hydrodynamic model, applying its velocity fields (u, v, w) to each particle, using a 4th-order Runge–Kutta numerical discretization method (García-Martínez and Flores-Tovar, 1999) to differentiate particle positions through space and time. Modules distributed with the code include mortality, vertical migration, and a connectivity module designed to generate a connectivity matrix output from the source to the final destination of the particles. The model gives a probabilistic estimate of dispersion and oceanographic connectivity, transport and fate of Lagrangian phenomena. The model computes the probability of larval exchange (here in called connectivity), between source and recruitment areas, by dividing the number of larvae that reached each site by the total number of larvae release; mortality, and behavior; providing results over time including particles' location (x, y and depth), water properties, particle status (moving, dead, out of the domain or settled) and also the particles settlement location. For the purpose of the model, there is an assumption that the larvae that reach the recruitment site will settle. However, the successful development of the settled larvae into a new organism, depending on behavioral components and the suitable conditions (e.g., hydrodynamic, environmental conditions, biological and physical processes, competency or predation) (Pineda et al., 2010), is not estimated by the model.

The model can simulate particles settlement in defined recruitment locations (in this case the sponge aggregations in the study). These recruitment locations are defined by a polygon (longitude, latitude and depth). Particle settlement starts after the defined PLD.

In this study, each aggregation is defined by a polygon of 6x6 km (the model resolution). The initial positions for the drift trajectories of each population were the centroids of each one of these areas. Each population is defined by a release location, and Lagrangian tracers represent larvae. A position (longitude, latitude and depth), the number of particles released, the release frequency, and the date characterize each release location. Since there is no information about the fecundity, frequency and seasonality of larval emissions, a hypothetical number was defined (Cowen and Sponaugle, 2009). To standardize this approach, the same number of particles for all the locations was considered, assigning the same hypothetical relevance to all the release points, with the same release size and frequency. The model simulates a release of a total of 150,000 particles per month, in a time step of 1.5 hours, during the entire release period, for all the scenarios. In this study, all the aggregations are simulated with the same number of particles, not reflecting population abundances, size or reproduction rate. Larvae were simulated as passive particles, without any active swimming behavior, being just advected by the hydrodynamics. Model configurations are described in Table 5.

The number of particles was calibrated to provide accurate larvae dispersion results, considering the computational efficiency.

TABLE 5 Biophysical model configuration.

Model parameter	Parameter description
Hydrodynamic model resolution	6×6km
Model time step	720 seconds
Number of release points	10
Release depth	Sea bottom
Number of larvae per release	150000/month/release
Release time step	1.5 hours
Behaviour	Passive (Ross et al., 2019)
Mortality	Half-life (North et al., 2009)
Strata	600 to 1000m (*P.Carpenteri* bathymetric range)
Scenarios	Several considering PLD and seasonality
Simulation length	Jan/2017 – Dec/2018

This calibration was performed using two different methodologies (Viegas, 2022), the Particle Density Distribution, and the evaluation of the fraction of unexplained variation (Simons et al., 2013), and by the analysis of the dispersal pathlength distances saturation (Kough et al., 2013).

The model simulates the larvae dispersal, and larvae settlement after the precompetence period (the PLD). For connectivity studies the model allows defining suitable settlement locations, defined by a polygon (longitude, latitude and depth). In this case, to study connectivity between the sponge aggregations, each sponge aggregation is also a source location and a recruitment area, defined by a polygon of 6x6km (model resolution), and depth (700 to 1000 meters depth). The larvae exchange between different locations will represent connectivity between different sponge aggregations.

Alternatively, to study potential settlement location throughout the Azores region, another methodology was applied, assuming that larvae were able to settle at any location between 700 and 1000 meters depth.

Due to the many uncertainties about deep-sea larval biology, different scenarios were considered, with different pelagic larval durations (PLD), and seasonal scenarios to encompass different potential situations. This is one advantage of using modelling tools, allowing the study of different hypotheses and scenarios (Swearer et al., 2019; Wang and Qiao, 2020).

2.1.4 Data analysis

Larvae were represented by particles, and the model results were analyzed through dispersal maps, larvae positions and larvae exchange between different source and recruitment locations. Connectivity between the sponge aggregations in the study was represented by connectivity matrices, representing the percentage of particles that reach each site, which allows for the analysis of sink and source aggregations. In this study, each particle represents one larva. When

referring to settling particles, it means a particle has reached another location, representing a larva that has settled in a new location and potentially will develop successfully. Connectivity matrices also represent the percentage-recruitment levels. Connectivity between two locations was assumed when, at least, one modelled particle released from one location (source node) reach (also referred as settled in) another location (receiving node), after the PLD. When settling in the same location, it is considered self-recruitment. Source locations are represented as rows (j), and recruitment areas (receiving node) as columns (i), with self-recruitment in each location represented in the matrix diagonal. Colors represent the percentage of particles that reach each locations, calculated by dividing the total number of settled larvae from each source population that settled, at the end of the PLD, in each receiving population, by the total number of larvae released from the source population. Besides the connectivity analysis, the larvae settlement positions throughout the study area were analyzed, to identify other potential larvae settlement positions.

The particle density distribution (PDD) is represented in 2-D vertically integrated maps, where all particles are represented, and each domain grid cell (6km x 6km) correspond to the integrated number of tracers in the entire water column. In contrast, in the particle dispersal maps, particles are not integrated into the water column, and all the particles in each cell are graphed. Some particles can "mask" others, by overlapping. Travel distances were analyzed by the Shapiro-Wilk Normality Test (using Rstudio 2022.02.3), to test if they are normally distributed; and by using histograms to analyze potential travel distances from all the different release points for the different scenarios. These distances were calculated from individual particle trajectories as the sum of straight-line distances between each time step. Additionally, histograms of particle depths were used to analyze how particles are distributed along the water column.

3 Results

3.1 Passive particle drift trajectories

Larvae were simulated as passive particles, being advected by the hydrodynamic currents. The particle density distribution (PDD) illustrates the larval dispersal along the study area, (Figure 2),
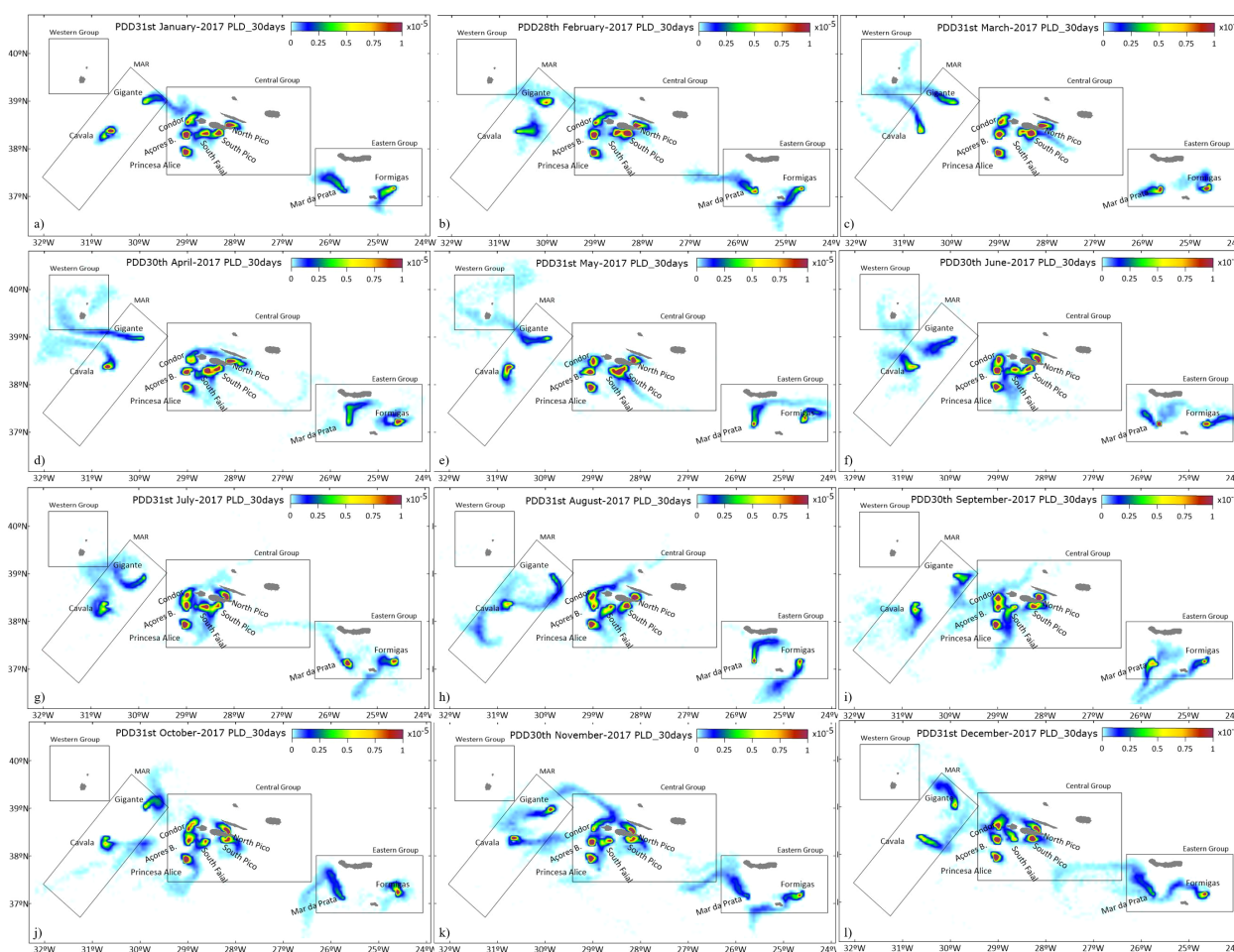

FIGURE 2
Particle density distribution for the annual release with a PLD of 30 days, for 31st January **(A)**: 28th February **(B)**; 31st March **(C)**; 30th April **(D)**; 31st May **(E)**; 30th June **(F)**; 31st July **(G)**; 31st August **(H)**; 30th September **(I)**; 31st October **(J)**; 30th November **(K)**; 31st December **(L)**. Black polygons represent the different location groups: MAR Group (L#1-Cavala, L#2-Gigante); Central Group (L#3-Princesa Alice, L#4-Açores Bank, L#5-Condor Seamount, L#6-South of Faial, L#7- South of Pico, L#8); Eastern Group (L#9)-Mar da Prata, and L#10-Formigas).

indicating the potential particle exchange between different locations. The results reveal a heterogeneous distribution depending on the spawning seasonality. Larvae from the MAR group can reach the Central Group (CG) only during the winter and autumn months (January, February, September, October, November and December). Larval dispersal plumes from the MAR can also reach the Western Group (WG), surrounding Flores and Corvo islands, during March, April, May and June months. Larvae exchange between CG and WG only occurs during July, November and December. However, the low PDD between these groups (Figure 2) indicates a low probability of particle exchange.

In March an eddy is formed between the Western Group and the MAR (Figure 3A), contributing to particle retention in this area. Larvae from the CG mostly remain around the islands. Nevertheless, the low current velocity, (Figure 3), is not sufficient to transport larvae from CG to the EG populations, given the PLD used in these scenarios.

Larvae from the Central Group populations, reach various sponge aggregations. Between the Central and Eastern Group, the hydrodynamic patterns go mainly in the eastward direction during March, Figure 3A, while in October there is a dominant current coming from the east and going westward (Figure 3B). In the northwest part of the study area, currents are stronger during October (Figure 3B) than during March (Figure 3A), and the
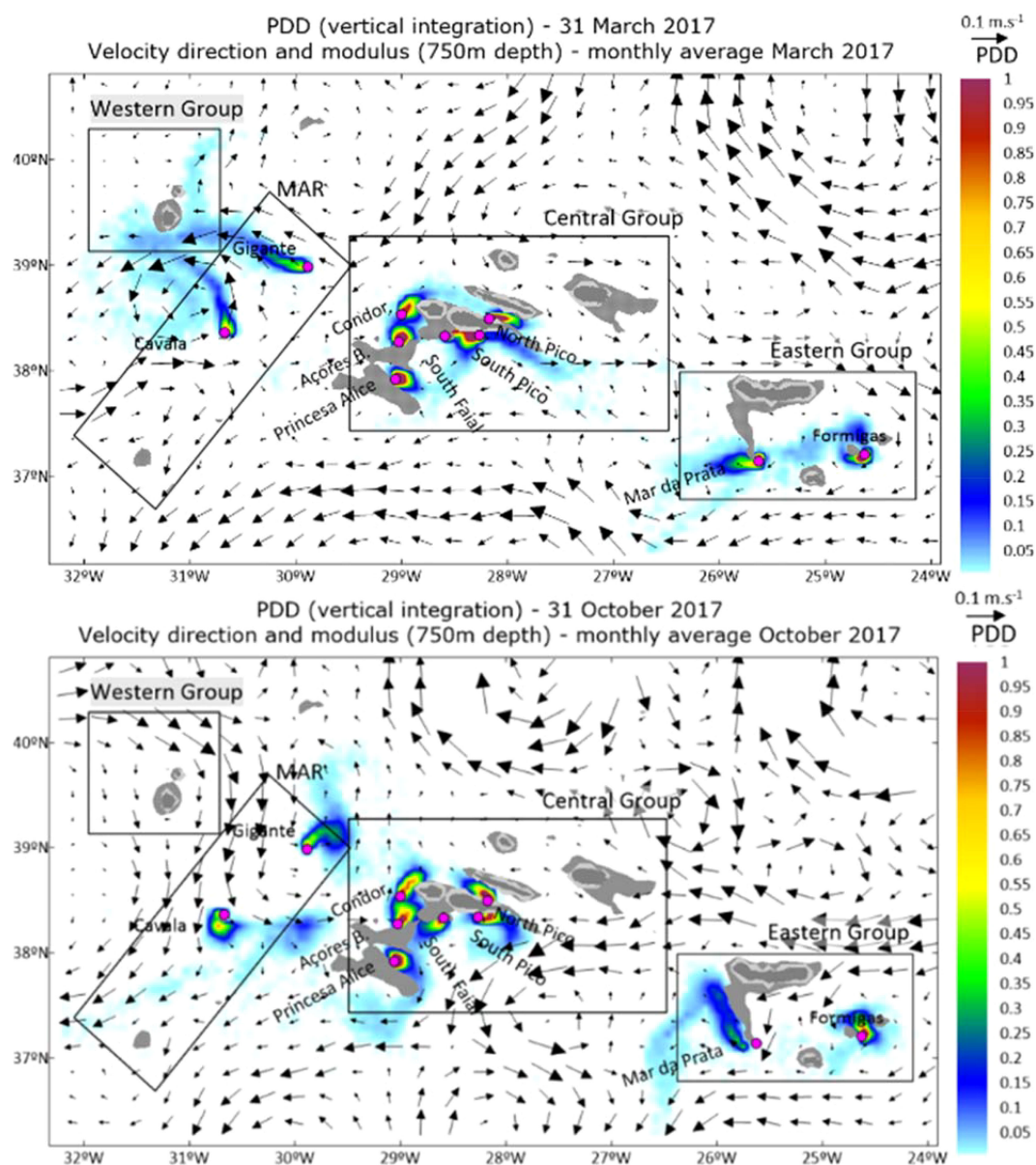

FIGURE 3
Particles density distribution integrated into the entire water column, like presented in Figure 2, with the representation of the velocity vectors at 750 meters depth, for 31 March 2017 (top), and 31 October 2017 (bottom). The PDD is represented with a color scale from blue to red, where 0 is white), vectors represent the monthly average of velocity modulus and direction at 750 meters depth.

major hydrodynamic fields present another pattern, where the higher velocity (>0.1m/s) matches the absence or reduced particle density, and the higher particle density occurs in locations with lower currents magnitude.

3.2 Particles travel distance

Larvae can travel from a few kilometers to a maximum travelling distance of over 400km (Table 6). Travel distances are highly non-normal, confirmed by the Shapiro-Wilk Normality Test (using Rstudio 2022.02.3). Therefore, rather than considering the average values, the median and the 95th percentile are used for this analysis (Phelps, 2015). Maximum total travel distances are an order of magnitude larger than median distances. Across all March and October scenarios, the longer PLD causes higher travel distances. Median total travel distances for a PLD of 30 days are double the distances with a PLD of 15 days (Table 6). Larval travel distances vary both seasonally and spatially. During March, larvae from the MAR locations: L#1, and L#2, have higher travel distances than those from other locations (with a 95th percentile of 207 and 220 km respectively).

In the Central Group (CG, locations L#3 to L#8), the overall median particle distance in all tested scenarios is lower than in other groups, ranging from 8 to 20 km, which may contribute to higher self-recruitment levels. This lower travel distance is due to the lower current velocities in the region (Figure 3), in contrast to the MAR populations, which are situated in areas with stronger currents.

3.3 Particles depth

Simulated larvae mainly remain close to the bottom at the released bathymetry (Figures 4, 5), despite some travelling through different bathymetric ranges. Histograms of particles' depth along their trajectory are represented in Figure 4 for the March release and in Figure 5 for the October release. In all the locations, larvae remain mostly within the bathymetric range of the release (>40%). A longer PLD contributes to a wider distribution of particles along the water column. The results show no significant difference in particle depth between the March and October releases. This demersal larval dispersal can also lead to higher levels of particle retention at their source locations.

3.4 Connectivity between populations

Results show variation in the level of population connectivity depending on the PLD of 15 or 30 days. Connectivity between the different populations in the study is illustrated by connectivity matrices, and also by connectivity arrows represented on the maps (Figure 6). The matrices depict the percentage of larvae exchanged between different populations, indicating connectivity, or in the case of self-recruitment, the percentage of larvae that settled in the source population after the PLD. A PLD of 30 days enables more connectivity between the different sponge aggregations than a PLD of 15 days (Figure 6). Conversely, a shorter PLD, results in higher self-recruitment levels. There is no connectivity between the EG and the CG or WG, in both PLD scenarios. In the WG, connectivity between Formigas (L#10) and Mar da Prata Seamount (L#9) is unidirectional, with a PLD of 15 days, and bidirectional with a PLD of 30 days. Between the CG and the EG, the larvae exchange is minimal, with no significant larvae exchange among the different populations, as is represented in the connectivity matrices.

This yearly release allows for the analysis of different spawning and hydrodynamic scenarios. The hypothesis of a seasonal spawning release was studied, considering releases of one month in March and one month in October to cover spring and fall scenarios, respectively. The results indicate different connectivity patterns in terms of

TABLE 6 Particle travel distances for the different scenarios.

	Travel distances (kilometres)											
	PLD_15_March			PLD_30_March			PLD_15_October			PLD_30_October		
	max	med	P95	max	med	P95	max	med	P95	max	med	P95
Cavala #1	221	14	126	375	43	207	152	16	73	325	33	138
Gigante #2	285	18	107	462	44	220	179	15	77	334	32	195
Princesa Alice #3	75	8	36	146	16	58	97	7	34	192	15	51
Açores B.#4	83	8	39	186	15	53	132	10	43	314	18	71
Condor B.#5	128	10	55	326	19	80	158	10	61	359	26	168
South Faial #6	205	10	50	436	21	132	196	14	61	385	26	128
South Pico #7	127	9	40	254	20	87	108	9	42	341	20	98
North Pico #8	69	8	38	270	15	55	85	7	39	286	16	63
Mar da Prata #9	118	10	47	264	22	97	176	27	86	406	50	148
Formigas#10	113	11	59	218	24	96	168	11	55	345	23	162

Maximum distance (max); median distance (med) and percentile 95th.
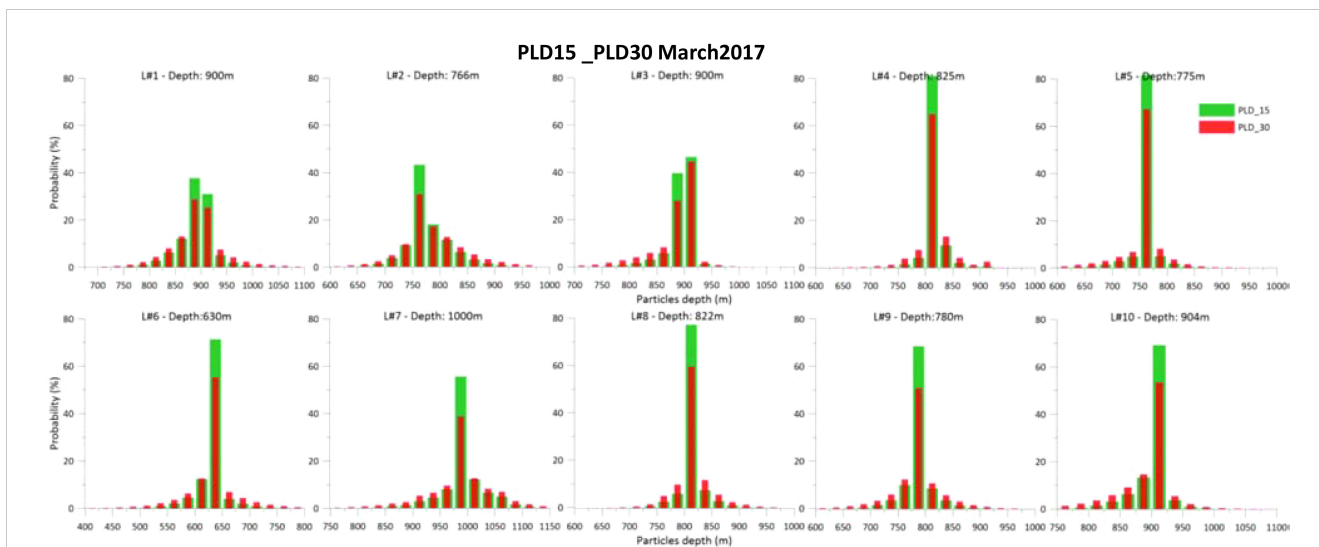
FIGURE 4
Histogram of particles' depth along their trajectory, for each location, for PLD15 and PLD30 days for March 2017 release. The depth of the respective release is detailed at the top of each graph.

seasonality. The October release (Figure 7), generates lower larvae exchange between the different sponge aggregations. Population connectivity between MAR and CG only occurs in the March_PLD_30_2018 scenario, namely between the Azores Bank (L#4) and the Cavala (L#1) and Gigante (L#2) Seamounts. In the other scenarios, there is no connectivity between the different groups. In the CG, the connectivity between different sponge aggregations reveals seasonality, with a higher number of connectivity relations in the March scenarios. The percentage of self-recruitment (Supplementary Tables A3–A6 in the Supplementary Material) is different from March to October, with the releases from CG revealing the highest self-recruitment percentage in October. In different situations, there is neither self-recruitment, nor connectivity

between Gigante Seamount (L#2) and any other populations. The same occurs in the Mar da Prata Seamount (L#9), which shows no self-recruitment in October_PLD30_2017.

3.5 Larvae settlement locations

Besides the sponge aggregations in the study, larvae can also settle in other regions of the domain. This study was performed within the defined bathymetric range of 600 to 1000 meters depth. Seasonal dynamics can induce different settlement positions. The yearly release considers all the monthly scenarios, and consequently more settled larvae along the Azores region (Figure 8). Considering
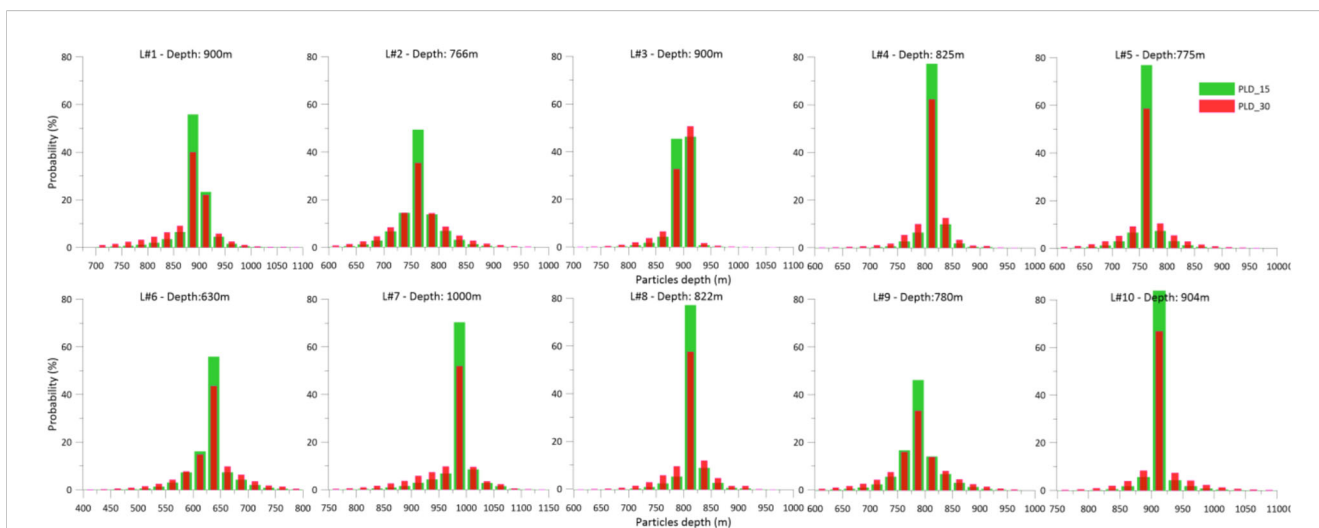

FIGURE 5
Histogram of the particles' depth along their trajectory, for each location, for PLD15 days and a PLD30 for the October 2017 release. The depth of each respective release is detailed at the top of each graph.
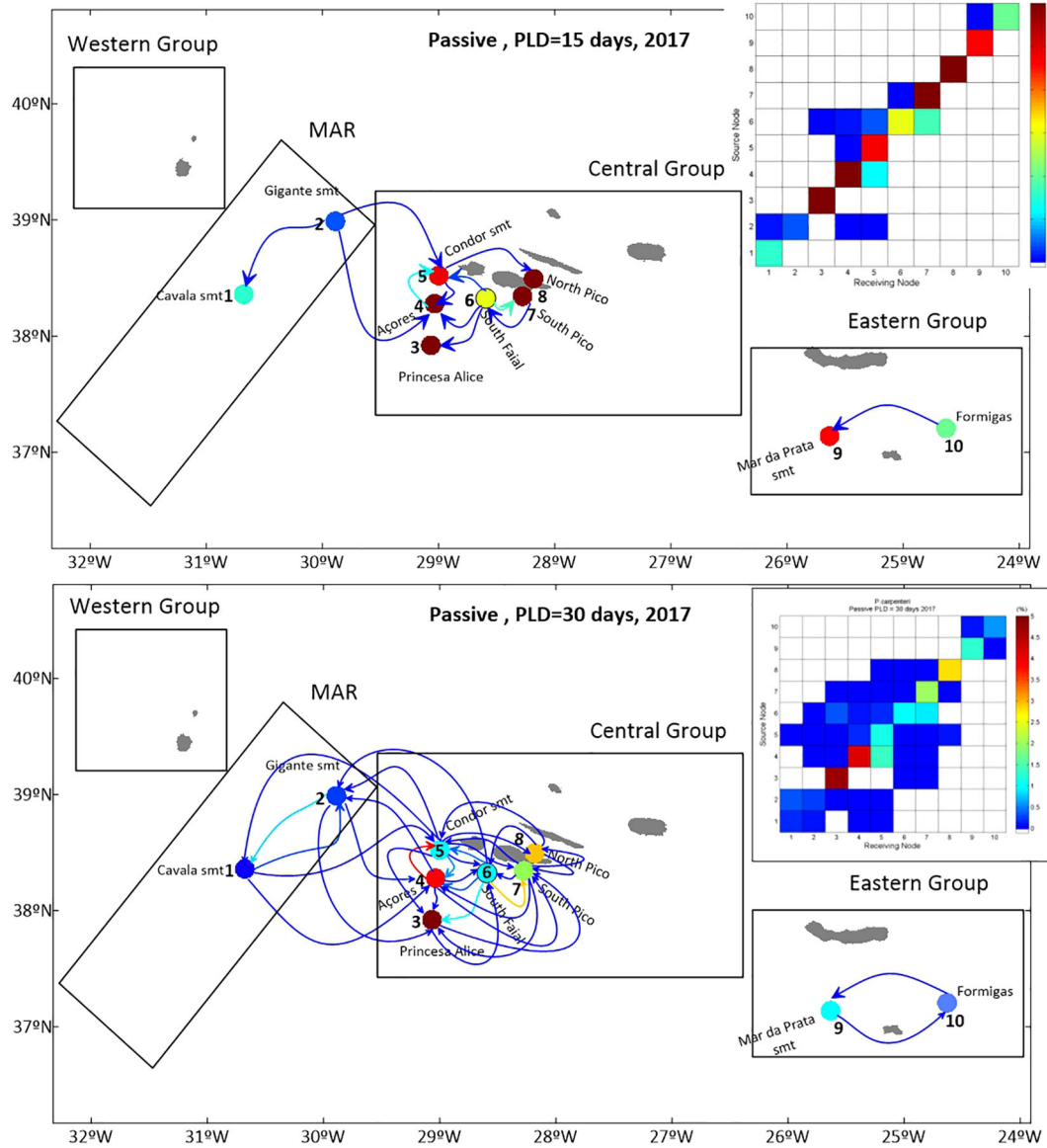
Map of connectivity relations, and respective connectivity matrix, for a yearly release (2017) with a PLD of 15 days (top), and PLD of 30 days (bottom), connectivity arrows and auto-recruitment circle colours represent the percentage of settled particles.

the bathymetric range from 600m to 1000m, larvae can settle around all the islands except Terceira island. Larvae settle along the MAR and on seamounts situated on its western and eastern flanks but also at different locations of the CG region'. The Central Group is an important recruitment area. This result highlights the potential connectivity between the populations in the Central Group. Major results show that during the yearly release, larvae from Cavala and Gigante seamounts, settle along the MAR, around Flores and Corvo islands, and along the west slope of the Central Group, but they hardly reach the East part of the Central Group. Gigante Seamount can receive larvae from different locations (Cavala (L#1), Gigante(L#2), Açores Bank (L#4), Condor (L#5), and South of Faial (L#6)), contrasting with the seasonal releases where larvae exchange occurs only during the October scenario, between Gigante (L#2) and Cavala (L#1) seamounts. The larvae

from South of Faial (L#6) are the ones with a wider range of settling locations; they can settle along MAR, in the WG, in the CG, in João de Castro bank, and in the EG, in the North of São Miguel (Figure 9F).

4 Discussion

This study aims to use specific sponge aggregations to study the dispersal of their larvae, and the potential connectivity among these different sponge grounds, considering spring and autumn spawning scenarios, and a yearly release, as a first approach to studying the dispersal of deep-sea larvae in the Azores. Given the many knowledge gaps in the reproductive and larval biology of deep-sea sponges, the use of models offers an advantage by allowing the study
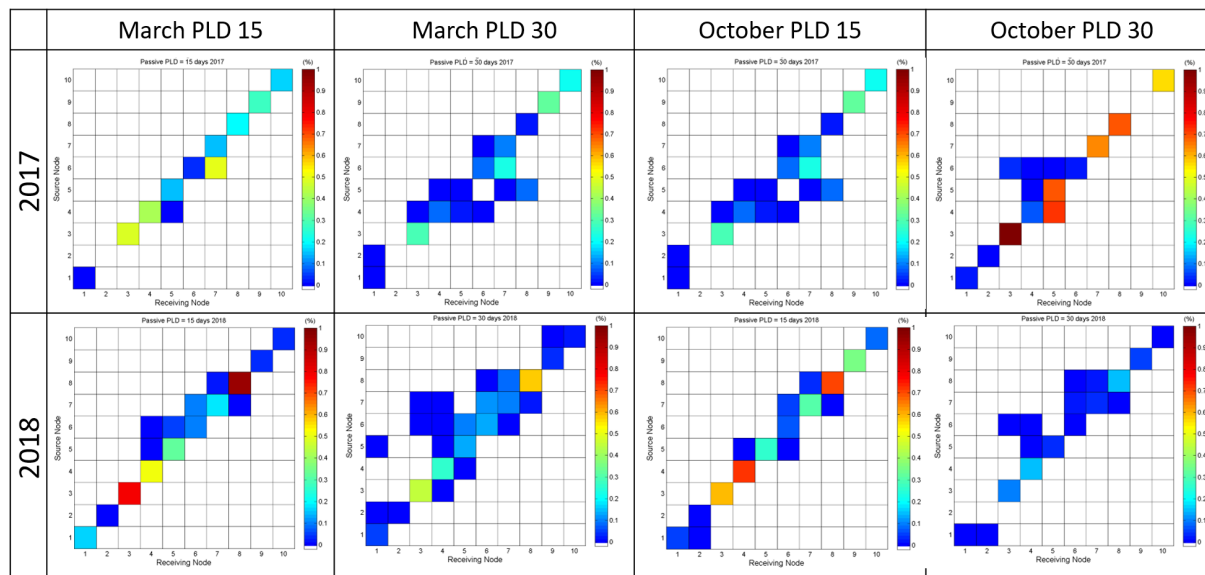
FIGURE 7
Connectivity matrices for the March_PLD15, March_PLD30, October_PLD15 and October_PLD30 for 2017 on top and 2018 on the bottom, connectivity and auto-recruitment colours represent the percentage of settled particles.

of different scenarios. *P. carpenteri* larvae were modelled as passive tracers, similar to other deep-sea sponge larval dispersal modelling studies (Kenchington et al., 2019; Swearer et al., 2019). The few studies of connectivity of sponge grounds in the deep sea in the Northeast Atlantic do not cover the Azores area, but they showed genetically a strong panmixia, and that the observed patterns were very well correlated with the physical drivers and the prevailing currents and topography (Taboada et al., 2023). In the Cantabrian sea, the same pattern emerged from the deep sea fan shaped sponges, where genetically a panmixia was present. However, when applying a virtual particle tracking model to assess oceanographic connectivity it showed a strong retention of larvae in the study area and a variable inter-annual connectivity highly correlated with the current regime (Busch et al., 2021).

Model results show that the hydrodynamic patterns have a strong influence on larval dispersal, causing different distribution patterns depending on the season. Larvae can be advected from a few kilometers to hundreds of kilometers, depending on the PLD and the hydrodynamic currents. The water-mass circulation in the Azores region is highly dynamic, and the influence of the different currents has seasonal effects on larval dispersal. The strong presence of hydrodynamic eddies (Caldeira and Reis, 2017) can contribute to particle retention in different areas, as is the case in March when an eddy forms between the Western Group and the MAR. These results show the importance of studying different spawning season scenarios for larval dispersal. Consequently, due to knowledge gaps in sponge reproductive traits, different seasonal scenarios and PLD were tested. Multiple connectivity relationships exist between the sponge aggregations in the CG, showing a redundancy in connectivity networks is a positive feature as it helps to mitigate recruitment failures by providing alternative connectivity pathways. These multiple connectivity relationships

may result from the proximity between these sponge aggregations, but also from the local hydrodynamic patterns characterized by lower velocities. This is in contrast to the strong hydrodynamic patterns that occur between the WG and the MAR in March, and between CG and EG in October.

A significant limitation of this and other deep-sea dispersal models is the lack of information on deep-sea species biological traits (Arellano et al., 2014; Hilário et al., 2015; Graves et al., 2023).

4.1 Connectivity between sponge aggregations and self-recruitment

There are no connectivity studies of benthic organisms in the Azores region. A retention particle study between 0 and 150 meters showed the potential of the different island groups of the Azores to retain particles, and their dependence on the current regime and topography (Sala et al., 2013). Close to the Azores a study of the physical connectivity between the NE Atlantic Seamounts showed self-recruitment abilities and great retention of particles on the seamounts (Lima et al., 2020).

This study shows larval dispersal between different sponge aggregations in the Azores, (Figure 9A–J) namely between the different sponge aggregations located in the same group (MAR, CG and EG), as well as between aggregations located in the MAR and the CG. However, there is no particle exchange between the CG and the EG. Moreover, these Eastern Group sponge aggregations do not exchange larvae with the other populations, and are the most isolated. Therefore, these populations may be spatially fragmented, similar to what was identified in other larval dispersal model studies for deep-sea populations (Hilário et al., 2015).
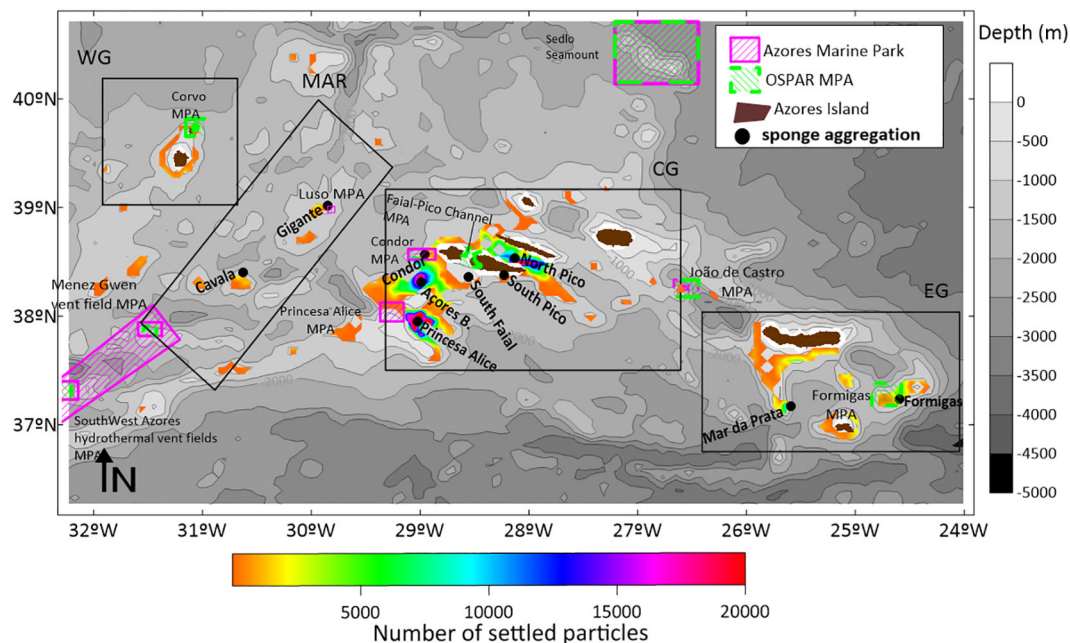
FIGURE 8
Location of settled particles along the domain, in the bathymetric range from 600 to 1000m depth, for the yearly release. Different colours represent number of settled larvae. Bathymetry is represented with a grey colour scale. The Azores islands are represented in dark brown, the Azores Marine Park in pink, and the OSPAR MPAs in green.

The results show that the local ocean currents shape the larval dispersal and connectivity, creating sub-regions not connected, given the studied scenarios. These kind of hydrodynamic barriers were also identified in other modelling approaches for deep-sea larval sponge dispersal on the east coast of North America (Wang et al., 2021). Moreover, this modelling approach also shows that the local eddies can supply and induce local retention of larvae, promoting connectivity and self-recruitment (Wang et al., 2021), as occurs in this case study in the Azores, namely between the WG and the MAR populations. A retention particle study in the Azores at 150 meters also showed the Eastern group isolation and the large capacity of the central area in the Azores to retain particles (Sala et al., 2016), which is coherent with the observed pattern in this study.

4.2 Larval dispersal patterns and connectivity for *P. carpenteri* in the Azores Marine Park

Connectivity among different benthic populations promotes the increase of their genetic diversity (Busch et al., 2021; Wang et al., 2021) and the resilience of the species (Bracco et al., 2019). It is an essential aspect in the development of management and conservation plans for marine ecosystems (Combes et al., 2021). Detailed knowledge of the hydrodynamic patterns and biological interactions that drive the transport of planktonic phases is crucial for improving the effectiveness of the MPAs (Stratoudakis et al., 2019). The model results of larval dispersal and larvae settlement positions for this target species in the Azores were analyzed considering the MPAs

from the Azores Marine Park. When MPAs are isolated from each other, they are more vulnerable to local extinction as they cannot be replenished by organisms or larvae from other locations (Stratoudakis et al., 2019). This is especially true for sessile organisms such as deep-sea sponges, which rely on larval dispersal to colonize new habitats (Metaxas and Saunders, 2009), and to support remote populations (Gary et al., 2020). Networks of marine protected areas arranged considering the larval dispersal patterns are considered ideal for the protection of marine species (Steneck et al., 2009). Therefore, studying larval dispersal patterns and identifying the main larval source and sink locations can contribute to the better implementation and management of conservation plans (Combes et al., 2021).

The study of larval dispersal and connectivity of these *P. carpenteri* aggregations serves as a pilot study for the connectivity of deep-sea benthic organisms in the Azores. The current regime and topography have been shown in other studies to be the main drivers of physical connectivity, explaining the genetic connectivity patterns (Busch et al., 2021; Taboada et al., 2023). Using *P. Carpenteri* as a proxy, we can discuss how effective the network of MPA from the Azores Marine Park is from the physical connectivity point of view. Among the 10 deep-sea sponge aggregations in the study, two are located in MPAs: Condor and Formigas populations. The Princesa Alice aggregation is located on the southern slope of the Princesa Alice Seamount, outside but adjacent to the MPA delimitation. Larval dispersal and connectivity results, indicate that Condor is an important source population, exchanging larvae with 8 of the 10 aggregations in the study (Figure 6). In addition, its larvae can achieve different locations in the Central Group, in the Western Group (around the islands of Flores and Corvo), and along the MAR: in the north, at 40.3°N (seamount south of the Kurchatov Fracture Zone); at 39°N in the
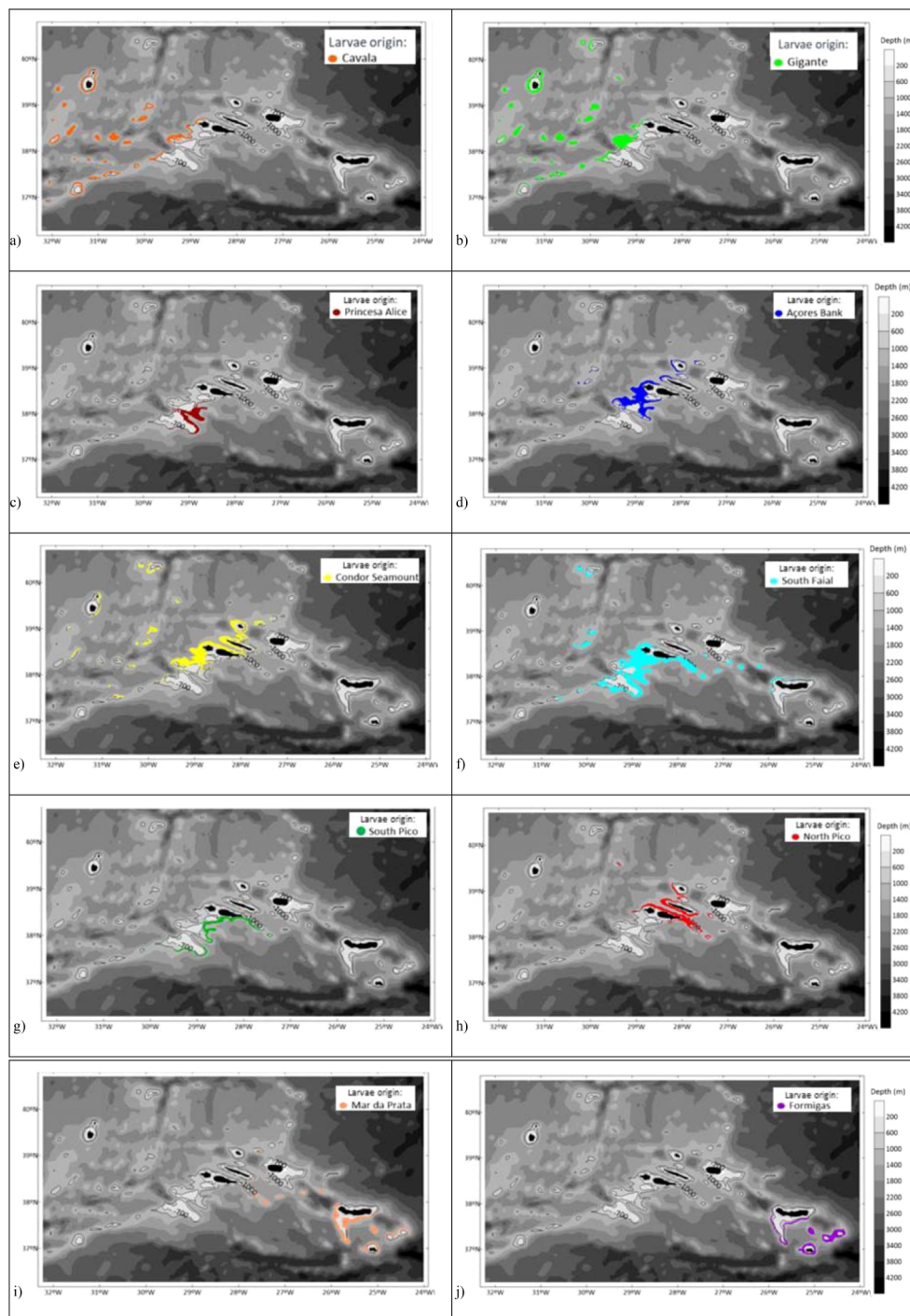
FIGURE 9
Location of settled particles, in the entire domain, in the bathymetric range from 600 to 1000m depth, for the yearly release of 2017 with a PLD of 30 days, for each origin. Different colours represent different releases: **(A)** Cavala; **(B)** Gigante; **(C)** Princesa Alice; **(D)** Açores Bank; **(E)** Condor Seamount; **(F)** South Faial; **(G)** South Pico; **(H)** North Pico, **(I)** Mar da Prata, **(J)** Formigas. Bathymetry is represented in a grey colour scale.

Gigante Seamount; and in the Voador Seamount at 37.5°N (Figure 9E). The MPAs of Princesa Alice and Condor may act as sink locations, once that larvae from different aggregations in the study achieve these locations. These results demonstrate the potential connectivity that sponge populations from Condor may have with different populations in the Azores region.

The Princesa Alice sponge aggregation in the study, adjacent to the limits of the MPA, demonstrates the importance of extending the limits of this MPA as it has the potential to retain larvae from multiple locations in the study: Cavala (Figure 9A), Gigante (Figure 9B) and Condor (Figure 9E) seamounts, and South of Faial (Figure 9F), aggregations.

The main results show a lack of larvae exchange between the EG and the other aggregations in the study (Figures 9I, J), mainly due to its distance from the remaining sponge grounds, but also as a consequence of the hydrodynamic patterns between the CG and the EG, impeding the larvae advection in the westward direction. No larvae exchange was identified between EG and the remaining sponge grounds. Therefore, the protection of an area in Mar da Prata will favor the maintenance of the sponge aggregations on the plateau south of São Miguel island, and both Mar da Prata and Formigas populations, which can be isolated from the remaining archipelago, due to their distance, but also restricted by the hydrodynamic patterns. The vulnerability of Formigas sponge grounds, which face several scenarios with no larvae exchange and the absence of self-recruitment, also reinforces the need to maintain the MPA of Formigas.

The João de Castro Bank MPA can receive larvae from the CG and from the Mar da Prata (in the EG) being an steppingstone location between the Central and the Eastern parts of the archipelago. Therefore, this site is very important for the longer-term protection of these aggregations, by promoting the establishment of a linkage between the CG and the EG. The Gigante Seamount, in the MAR, is a recruitment area for deep-sea sponges, retaining larvae from different sources from the CG (Condor, Açores Bank and South of Faial), as well as from Cavala and Gigante Seamount. The results of larval dispersal also show that larvae from the Gigante seamount can achieve the MAR region, up to seamounts located South of the Kurchatov Fracture Zone (north of the study area), and in seamounts west of the MAR like the Buchanon Seamount. On the other hand, larvae from aggregations of Voador Seamount will favor resilience along the MAR, and South of the Azores EEZ.

This study does not take into account the density of these sponge aggregations. Research by Graves et al. (2023) on the drivers of *P. carpenteri* density suggests that the available environmental data, combined with the scarcity of long-term time series for deep-sea environmental data, do not capture the key factors influencing this species' density. This limitation restricts the ability to model and identify areas where aggregations are likely to occur, particularly those with dense aggregations that could be considered VMEs. Increasing to a multi-year analysis would provide the opportunity to examine variability over the years and test other hypotheses, such as the average temperature variability, which has been identified as an important driver of *P. carpenteri* distribution (Graves et al., 2023).

The application of biological larvae traits and their parameterization in biophysical models presents a challenge (Hilário et al., 2015) even in well studied shallow-water systems (Metaxas and Saunders, 2009). When regarding these biophysical models for deep-sea dispersal, the application of biological traits is even more challenging due to the scarcity of data, and difficulty data collection, observation and model validation (Adams et al., 2012; Ross et al., 2016). So, these mode results can be used as a first approach to study the potential larval dispersal in the Azores, but always considering the associated uncertainties. However, models are always a simplification of the reality and despite all the uncertainty regarding the biological parameters (Simons et al., 2013), the validation of the physical circulation model used in this case study (Viegas, 2022) provides us with the guarantee of the correct physical model component, providing

a baseline to study different scenarios, and also to be used to study climate change scenarios hypothesis.

Furthermore, this modelling approach could be used in combination with the species distribution models (Beazley et al., 2021) to construct explicit spatial hypotheses for deep-sea populations connectivity following a seascape framework approach (Kenchington et al., 2006; Kavanaugh et al., 2014; Zeng et al., 2020; Swanborn et al., 2022), in this case for the Azores region. In the future, the possibility of collecting physical samples and performing a population genetic study, will contribute to a deeper knowledge of these populations connectivity (Kool et al., 2011; Selkoe and Toonen, 2011; Antonio Baeza et al., 2019; Wang et al., 2021), and will help to validate our hypothesis.

5 Conclusions and final remarks

The physical connectivity among different deep-sea *P. carpenteri* sponge aggregations in the Azores region was studied using a biophysical particle-tracking model. *P. carpenteri* larvae were modeled as passive tracers (Kenchington et al., 2019; Swearer et al., 2019) under pelagic larval duration (PLD) scenarios of 15 and 30 days and seasonal spawning, based on other deep-sea sponge studies (Kenchington et al., 2019; Ross et al., 2020; Wang et al., 2020, 2021). Model results indicate that PLD and spawning seasonality are crucial for larval dispersal and population connectivity in the Azores. Seasonal effects are mainly driven by the region's dynamic oceanographic conditions. Local hydrodynamic vortices can lead to larval retention, while stronger currents (exceeding 0.1 m/s) between the Western and Central Groups in spring, and between the Central and Western Groups in autumn, hinder larval exchange. Therefore, more information on the species' biological traits, including spawning seasonality, is crucial for understanding effective connectivity across the archipelago.

A PLD of 30 days would enhance population persistence and recovery after disturbances (Cowen and Sponaugle, 2009), whereas a shorter PLD of 15 days could increase population fragmentation. Connectivity and larval dispersal results were analyzed in relation to the current design of the Azores MPAs, demonstrating their effectiveness in promoting connectivity across the archipelago by protecting key sink and source locations. Stepping-stone sites, such as the João de Castro Bank, were identified as critical links between isolated populations of the Eastern Group and the central archipelago. Other locations along the Mid-Atlantic Ridge (MAR), including Gigante, Cavala, Ferradura, and Voador seamounts, also facilitate connectivity, serving as potential sink locations. These locations should be the target of greater protection measures in the design and implementation of protection plans.

This study also identifies potential areas for future exploration, such as João de Castro, Voador, Ferradura, and Buchanan banks, where larvae are predicted to settle. These locations are promising for studying not only *P. carpenteri* but also other deep-sea species cohabiting in these habitats.

This type of investigation highlights the utility of larval dispersal models in designing Marine Protected Areas (MPAs) (Lima et al., 2020), specifically their role in identifying source and

sink locations. It allows the identification of major larval dispersal and connectivity patterns among sponge aggregations in the Azores, providing a framework that can be extended to other deep-sea sponge and coral habitats.

Future studies should include more detailed biological and larval behavior data for deep-sea sponges. Integrating genetic connectivity studies will offer valuable insights into the behavioral dynamics and resilience mechanisms of these organisms within the Azores. Additionally, considering aggregation density and population size in models will provide a more precise quantification of recruitment efficiency. Novel insights into the biology, size, and density of sponge aggregations will be invaluable for understanding the dynamics of this species within the Azorean ecosystem.

Regardless of the lack of information about *P. carpenteri* biological traits, this dispersal modelling approach can provide an overall understanding of deep-sea larval transport in the Azores region, considering the studied PLD scenarios. Moreover, this modelling methodology can therefore be replicated for other species considering these or any other biological traits scenarios, or to study other hypothesis. These results can therefore be used to long-term conservation plans for deep-sea species, and support protection actions for local populations in the Azores.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

CV: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Writing – original draft, Writing – review & editing. MJ: Data curation, Methodology, Software, Supervision, Writing – original draft, Writing – review & editing. AC: Conceptualization, Funding acquisition, Investigation, Project administration, Resources, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2024.1393385/full#supplementary-material

SUPPLEMENTARY TABLE 1
Particle travel distances for the different scenarios. Maximum distance (max); median distance (med) and percentile 95th.

SUPPLEMENTARY TABLE 2
Connectivity tables detailing the percentage of particles released particles from each location (rows) that settled in each recruitment area (columns). For the scenario: Annual PLD15.

SUPPLEMENTARY TABLE 3
Connectivity tables detailing the percentage of particles released particles from each location (rows) that settled in each recruitment area (columns). For the scenario: Annual PLD30.

SUPPLEMENTARY TABLE 4
Connectivity tables detailing the percentage of particles released particles from each location (rows) that settled in each recruitment area (columns). For the scenario: March PLD15 2017.

SUPPLEMENTARY TABLE 5
Connectivity tables detailing the percentage of particles released particles from each location (rows) that settled in each recruitment area (columns). For the scenario: March PLD30 2017.

SUPPLEMENTARY TABLE 6
Connectivity tables detailing the percentage of particles released in each location (rows) that settled in each recruitment area (columns). For the scenario October PLD15 2017.

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