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Marine spatial planning for connectivity and conservation through ecological corridors between marine protected areas and other effective area-based conservation measures

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Maritime Spatial Planning (MSP) promotes the sustainable human activities development and uses in the marine space, playing a role in their effective management. The enhancement of connectivity is crucial for the conservation of biodiversity and landscape planning. Ecological Corridors (ECs) are an important type of connectivity for biodiversity conservation in fragmented habitats. The EU Biodiversity Strategy 2030 includes ECs into the network of protected areas and allows for the creation of additional protected areas. MSP studies considering ECs remain still lacking, especially for the design of networks between Marine Protected Areas (MPAs) and Other Effective area-based Conservation Measures (OECMs). In this paper, knowledge, and tools for investigating marine ECs were reviewed, with a systematic bibliometric analysis to summarize the current scientific research. Previous studies integrating ecological connectivity into planning for marine conservation have focused on models of larval dispersal, adult movements, and dispersal of single species by using benthic habitat proxies. Few studies were found on ECs in marine environments: in the coral Caribbean reef systems in the Gulf of Mexico; within benthic habitats along the Pacific coast of Canada; between MPAs in British Columbia (Canada); and by analyzing migratory species in the Yangtze estuary (China). Commonly used approaches to project and map ECs in marine environments are least-cost and circuit theories allowing to incorporate movement with cost or resistance to movement, depending on species and preferred habitats. The systematic bibliometric analysis returned 25 studies, most of which were from North America (40%) and European countries (36%) and the largest share of papers (68%) from 2018 to 2022. This review pinpointed the need of integrating different disciplines to investigate connectivity and the need by policymakers and practitioners to recognize the importance of ecological connectivity, even there are significant challenges for integrating connectivity into policies, planning, and conservation.

KEYWORDS

ecological corridors, connectivity, maritime spatial planning, marine protected areas, other effective area-based conservation measures, conservation

1 Introduction

Maritime Spatial Planning (MSP) is a strategy defined by the EU Directive 2014/89/EU as an integrative public process that establish a framework whereby authorities in relevant Member States allocate human activity in maritime space. MSP goals include fostering the long-term expansion of the maritime economy, the development of marine regions, and the exploitation of marine resources by integrating ecological, economic, and social objectives (e.g.: Gilliland and Laffoley, 2008; Halpern et al., 2008; Stelzenmüller et al., 2010; Micheli et al., 2013; Kelly et al., 2014; Halpern et al., 2015; Da Luz Fernandes et al., 2018). MSP outcomes can result in plans, permits, strategies, planning concepts, guidelines, governance principles, and other administrative decisions about the spatiotemporal allocation of present and future human activities and uses in maritime space (https://maritime-spatial-planning.ec.europa.eu/ msp-eu/introduction-msp¹). Furthermore, MSP promotes the reduction of conflicts and the creation of synergies and cooperation between sectors and EU countries, and the creation of protected area networks to safeguard and maintain the environment by recognizing the effects and opportunities for space utilization, raising stakeholder awareness (https://maritimespatial-planning.ec.europa.eu/msp-eu/introduction-msp1). MSP necessitates spatial information regarding marine resources, biodiversity, habitat, ecosystems, and human activities to effectively manage them (Ban et al., 2010; Da Luz Fernandes et al., 2018; Margules and Pressey, 2000; Pressey et al., 2007; Muñoz et al., 2017).

In this context, the protection and enhancement of natural connectivity is a challenging topic for biodiversity conservation and landscape planning (Ersoy et al., 2018; Fang et al., 2018; Pereira, 2018; Guzmán-Colón et al., 2020; Tulloch et al., 2021). Despite its ecological importance, connectivity in marine environments is challenging to assess due to limited data and the fact that it encompasses several ecological processes such as dispersal (by larvae, juveniles, and adults), oceanographic conditions, ontogenetic shifts, migration, nutrient flow, invasive species, anthropogenic impacts, or diseases (Gillanders et al., 2003; Robinson et al., 2005; Blowes and Connolly, 2012; Friesen et al., 2019).

Conservation in Europe is carried out with regulatory frameworks such as the Birds and Habitats Directives and the Marine Strategy Framework Directive (Leontiou et al., 2022) resulting in the designation of the Natura 2000 network, which currently covers almost 10% of the entire EU maritime area (more than 3,150 marine Natura 2000 sites, over 550,000 km²) (https://ec. europa.eu/²). In addition, the rate of Marine Protected Areas (MPAs) is increasing worldwide as a response to the UN Convention on Biological Diversity (2004) to effectively protect and conserve at least 10% of marine ecoregions through MPAs that

are ecologically representative and well connected. Currently, a total of 18,384 MPAs and 818 Other Effective area-based Conservation Measures (OECMs) exist, covering the 8.26% of the world's oceans, and less than a third of these are adequately connected (Saura et al., 2018; UNEP-WCMC, 2023).

Despite the EU's concerted efforts in the identification of conservation zones, biodiversity loss continues at worrying rates (European Commission, 2021). At the European level, MPAs cover 12% of the seas, and only 1% are strictly protected. In this context, the action plan to foster the protection of EU marine ecosystem and reduce the impact of fishing activities was set through the new EU Biodiversity Strategy for 2030 (European Commission, 2021). This strategy established as main objective the protection of 30% of the EU seas, of which 10% strictly protected.

MPAs represent an important component for protecting ecosystems and endangered species, as well as for fisheries management, to ease anthropogenic stresses and guarantee the sustainable use of marine resources (Lubchenco et al., 2003; Lowry et al., 2009; Halpern et al., 2010). MPAs can help to reduce biodiversity loss by fostering population persistence, recovery, and expansion, as well as conserving community composition and the biological processes that control those ecosystems (Almany et al., 2009; Gaines et al., 2010; Speed et al., 2018). MPAs contribute significantly to climate change adaptation by improving ecosystem resilience and maintaining ecosystem services (Micheli et al., 2012; Carr et al., 2017). However, When MPA classification cannot be extended to key sites or when it is not in the best interests of local governments or landowners, these places can nevertheless be designated as OECMs (Diniz et al., 2022). An OECM is a geographically defined area, but not a protected area, governed and managed for biodiversity protection and conservation, and associated ecosystem services, as well as, when appropriate, cultural, spiritual, socioeconomic, and other important values (IUCN-WCPA, 2019). Moreover, OECMs can include a variety of players and governance types (for example, indigenous peoples, local communities, business actors, and governments) (IUCN-WCPA, 2019). Participation of these stakeholders in areabased conservation efforts is a necessary step toward achieving favorable socioeconomic and conservation outcomes (Maxwell et al., 2020). The potential role of OECMs in constructing ecologically representative and well-connected networks of MPAs is gaining traction (Woodley et al., 2012; Spalding et al., 2013; Borrini-Feyerabend et al., 2014; Jonas et al., 2014; Dunn et al., 2016; Laffoley et al., 2017; Diz et al., 2018; Rees et al., 2018).

1.1 The role of ecological corridors in the environmental conservation

Among the most well-known, prioritized, and historically implemented types of connectivity, Ecological Corridors (ECs) represent clearly defined geographical spaces (biological or physical strips), regulated throughout time in order to preserve or restore effective ecological connectivity allowing movement of species and related ecological processes such as energy and gene fluxes and nutrient cycles (Good, 1998; Benson et al., 2007; Van der

¹ https://maritime-spatial-planning.ec.europa.eu/msp-eu/introductionmsp

² https://ec.europa.eu/

Windt and Swart, 2008; Palmeri et al., 2017; Hilty et al., 2020; Velázquez et al., 2022).

According to the EU Biodiversity Strategy for 2030, Member States are called to create ECs between protected sites (European Commission, 2021). In addition, IUCN Guidelines for Conserving Connectivity through Ecological Networks and Corridors is meant to guide global connectivity conservation efforts to design, govern, and manage for effective ecological connectivity (Hilty et al., 2020; Zhao et al., 2022). The EU Biodiversity Strategy asks for ECs to be included in the network of protected areas as a method of creating a cohesive transboundary network of protected areas (Hilty et al., 2020). Ecologically, ECs play an important role in the reconnecting fragmented ecosystems, regulating climate (Pataki et al., 2011; Gratani and Varone, 2013) and water (Cettner et al., 2014; Nickel et al., 2014), and providing food (Barthel and Isendahl, 2013), with the common aim of fostering, protecting and conserving biodiversity, (Hilty et al., 2006; Kattwinkel et al., 2011; Klaus, 2013; Garmendia et al., 2016; Fung et al., 2017). From a sociocultural standpoint, ECs connect valuable locations, offer working and leisure areas, and cultivate a sense of place associated with cultural heritage, in addition to being key components in the growth of tourism (McHarg, 1969; Beger et al., 2015; Beyer et al., 2018; Hilty et al., 2020).

In this context, remains still lacking the volume in MSP scientific research on ECs, and in particular, into the design of networks between MPAs and OECMs, supporting connectivity of marine systems (Balbar and Metaxas, 2019). MPAs and OECMs as elements for the conservation of the biodiversity may not be enough for addressing threats, such as, for instance, global climate change (Bates et al., 2019). For this reason, further environmental attributes, such us connectivity through ECs, might be considered to achieve biodiversity protection goals.

The aim of this paper is to review the scientific literature to investigate the current approaches and tools applied for investigating marine ECs between MPAs and OECMs, in an MSP perspective, and to identify gaps and opportunities to improve ecological connectivity between current areas to promote marine ecosystem conservation.

2 An overview of bibliometric research of previous literature

Literature search was conducted in Scopus³ and checked in Google Scholar⁴ by using the searching terms: "ecological connectivity", OR "ecological corridor*", OR "ecological network", AND "marine protected area*, OR "Natura 2000", OR "Other effective area-based conservation measures", OR "OECM*", AND "marine", OR "ocean", OR "coastal water*", OR "offshore", OR "Mediterranean Sea". Only peer reviewed English language articles were included in the analysis. Abstracts were subsequently examined manually to select only papers that analyzed connectivity in terms of ECs at sea among MPAs and OECMs.

The bibliographic review was completed on April 2023. The search returned a total of 25 studies, excluding duplicates, made up of 24 research articles and 1 review (Table S1). Of these, the largest share (n = 17, 68% of the total) was concentrated in the latest five years (2018-2022), while the first article dates back to 2009. Most articles were produced in North America (USA: 6, Canada: 4; 40%), followed by European countries (9, 36%), and Asian countries (3, 12%), while remaining papers were developed in South America and Oceania (3, 12%).

To highlight the main keywords on which considered papers have been focused, a total of 294 author keywords from the 25 investigated papers were collected and analyzed for their frequency and then plotted in a keyword cloud (Figure 1). Furthermore, most relevant keywords, found at least in five studies, are summarized in Table 1. Keywords were selected with the aim of collecting information first on global scale and then specifically on a Mediterranean scale to identify the existence of studies on marine ECs at two different scales (global and local). Only few manuscripts, that have been highlighted in this review have dealt with the topic, easily providing overall information covering the global oceanic scale. Because scientific literature on marine ECs is actually scarce, the focus on the Mediterranean would provide new information in anticipation of future studies.

3 State of art of ECs connecting MPAs and OECMs: what do we know?

To maximize conservation effectiveness, the upcoming extension of MPAs needs the use of systematic conservation planning methodologies that account for connectivity (Balbar and Metaxas, 2019; Katsanevakis et al., 2020; Virtanen et al., 2020).



³ https://www.scopus.com

⁴ https://scholar.google.com/

TABLE 1 Authors keywords, number of articles in which keywords are included, and proportion of these on the total of considered articles (%).

Author keyword	n° articles (% of total)
Marine	18 (72%)
Conservation	16 (64%)
Connectivity	16 (64%)
Network	14 (56%)
Area	13 (52%)
Ecological	13 (52%)
Protected	12 (48%)
Plannin	10 (40%)
Spatial	6 (24%)
Habitat	5 (20%)

Previous research has established advanced techniques for incorporating ecological connectivity into the selection of marine conservation priorities (Magris et al., 2016; Weeks, 2017; Daigle et al., 2020).

In contrast to terrestrial systems, where the underlying habitat structure associated with ECs is often rather static, in marine systems ECs are constantly changing due to water movements caused by hydrological and meteorological processes (Hastie et al., 2016).

Based on the information obtained from the systematic review, we report here on the state of art approaches and methodologies used to study ecological connectivity at sea. In particular, this section describes existing studies focused on the ecological connectivity in terms of larval dispersal, adults' movement and migration, the importance of the tridimensional character of the marine environment, and common methodologies.

3.1 Larval dispersal

Research to investigate ecological connectivity in marine environments has focused mainly on models of larval dispersal by oceanic currents (Sanvicente-Añorve et al., 2014; Soria et al., 2014; Thomas Y. et al., 2014; Roberts et al., 2021), as a key driver of population connectivity (Treml et al., 2008; Andrello et al., 2015; Magris et al., 2016). Understanding dispersal trends between MPAs and OECMs is difficult since these phenomena are influenced by currents, season, time, and depth, all of which vary by area and species (Kinlan and Gaines, 2003; Basterretxea et al., 2012; Sayol et al., 2013). To deepen connectivity in seawaters by using larval dispersal, it is also important to use oceanographic data when addressing dispersion direction, since they constitute key variables for recruitment estimates (Schunter et al., 2011). Chemical tags (Hüssy et al., 2020), parentage analysis (Bode et al., 2019), or individual-based biophysical models are often used to evaluate larval, fragments or organisms' dispersion distance in coastal marine ecosystems (Lett et al., 2020; Mari et al., 2020; Cecino and Treml, 2021) providing a spatial representativeness needed for conservation planning more easier than other techniques (Beger et al., 2022).

3.2 Adults' movement and migration

In the past ten years, also adults' movement has received a novel attention. It is well understood that knowledge on adult-mediated population connection is crucial for understanding the complicated dynamics of connectivity (Frisk et al., 2014; Pittman et al., 2014; Brvan-Brown et al., 2017; Holyoak et al., 2020; Keeley et al., 2021; Jetz et al., 2022). Connectivity analysis combines information about, for example, adult habitat preferences, resistance to mobility within and across habitat types, influence of oceanic currents, density dependency, and interactions between species where speciesspecific data are available (Rocha et al., 2002; Gillanders et al., 2003; Treml et al., 2008; Baggio et al., 2011; Caldwell and Gergel, 2013; Pittman et al., 2014; Magris et al., 2016; Allan et al., 2021). The most interesting species for assessing connectedness are those with modest adult mobility distances since the movement of widely dispersed species may limit the efficacy of conservation interventions (e.g.: MPAs) (Moffitt et al., 2009; Green et al., 2014; Friesen et al., 2021). Even if species with low dispersion distances might be confined, for example, within single MPAs (Kaplan et al., 2009; Carr et al., 2017; Friesen et al., 2021).

Furthermore, it was found that narrow coastal channels effectively function as ECs for mobile marine species migration, and earlier research suggests that marine predators may seek these habitats for feeding (*e.g.: Tursiops truncatus* and *Phoca vitulina*) (Brown and Mate, 1983; Thompson et al., 1991; Suryan and Harvey, 1998; Hastie et al., 2004; Wilson et al., 2007; Hastie et al., 2016; Krost et al., 2018). This because narrow coastal channels are characterized by hydrographic features (*e.g.:* current direction and velocity, tide) have been demonstrated to alter nutrient availability and movement, plankton retention, and fish aggregation, as well as potentially give greater feeding chances for predators (Benjamins et al., 2015).

Technological advancements in microelectronics for telemetry, spatial analytical approaches, and marine remote sensing favor the possibility of filling substantial information gaps in marine animal migrations (Pittman et al., 2014). In all cases, tagging highly mobile marine organisms with acoustic transmitters is the most successful and widely used approach for studying their movements in time and space (Pittman and McAlpine, 2003; Heupel et al., 2006).

In contrast, it is unclear how connectivity patterns, discovered using benthic habitat as a proxy, match with the effective population connectivity of a single species. (Friesen et al., 2019). By combining landscape characteristics with knowledge about a species' capacity for dispersal (Calabrese and Fagan, 2004) or likelihood of dispersal between patches (Watson et al., 2010), this potential connectivity provides a more thorough understanding of species-specific connectivity patterns than a habitat proxy approach. However, connectivity is an important component in marine habitats, particularly for benthic species (Carr et al., 2003). Indeed, several physical drivers such as ocean currents are involved in connectivity (Brock et al., 2012). Surface currents can help to detect main Podda and Porporato

connections and ECs which should be considered in MSP (Muñoz et al., 2015) and MPA network design (Schill et al., 2015).

3.3 Tridimensionality of marine environments

Another factor to consider is the tridimensional character of pelagic ecosystems, as well as the fact that most MSP techniques do not take this third vertical dimension into account (Muñoz et al., 2017). In fact, vertical connectivity can be attributed to physical (upwelling, downwelling, particle settling) or biological mechanisms (migration) (Robinson et al., 2010). For instance, the upwelling from the thermocline to the photic zone may promote the growth of phytoplankton, a component which is the basis of the pelagic food web (Sarhan et al., 2000; Granata et al., 2004). The deposition of particulate organic carbon connects surface primary production to benthic secondary production (Pfannekuche, 1993). Zooplankton diel vertical migration (DVM) contributes to the biological pump as a driver of carbon fluxes (Hernández-Leon et al., 2010; Ochoa et al., 2013; Ariza et al., 2015). Horizontal or vertical connectivity in marine ecosystems is essential for MSP as well as potential risk assessment of marine activities and discharges, however, there is currently a scarcity of knowledge on connection in these ecosystems (Sutton, 2013; Muñoz et al., 2015; Muñoz et al., 2017). Furthermore, in terms of connectivity direction, studies have primarily focused on horizontal or vertical one, but not both at the same time (Sutton, 2013; Schill et al., 2015; Muñoz et al., 2017). MSP and risk assessment necessitate the simultaneous consideration of all types of connectivity (physical, biological, horizontal, and vertical) (Muñoz et al., 2017).

3.4 ECs projection and mapping

There are, to the best of our knowledge, relatively few studies about the presence of EC in marine environments and among MPAs, while none including OECMs. Specifically, Ortiz-Lozano et al. (2013) studied EC across three coral reef systems in the southwest Gulf of Mexico. This study pinpointed that the found heterogeneity at a biogeographical and habitat level represents one of the main criteria to establish MPAs networks (Ortiz-Lozano et al., 2013). Pittman et al. (2014) provided direct evidence of ecological connectivity throughout an MPAs network in Caribbean reefs, considering movements of fish populations by using telemetric data. Subsequently, Friesen and coauthors (2019) incorporated connectivity within benthic habitats, as a proxy of adult movement due to the lack of information on population or individual mobility, into MPA planning in a case study conducted on Canada's Pacific coast. In this paper, it was found a low interconnectedness among existing MPAs and the need to increase connectivity by prioritizing spaces that existing MPAs could use as steppingstones. In addition, Friesen et al. (2021) examined the ecological connectivity between MPAs considering two commercially important species in the Northern Shelf Bioregion in British Columbia (Canada). Lastly, even if not

among MPAs, He et al. (2022) examined the importance of ECs to migratory species in the Yangtze estuary, the largest estuary in China, based on the variance in temporal and spatial density of three top fishery species to identify migratory ECs connecting optimum habitats that may be important in preserving population or community connectivity.

Common methodologies and tools for projecting and mapping ECs in terrestrial conservation planning have been established (Fenu and Pau, 2018; Liang et al., 2018; Bergès et al., 2020; Hilty et al., 2020). However, to our knowledge, in marine environments only two of these approaches were applied: least-cost theory and circuit theory (e.g.: McRae et al., 2008; McRae and Kavanagh, 2011; Pittman et al., 2014; Thomas C. J. et al., 2014; Friesen et al., 2021; Weeks, 2017). The two methods consider costs or resistance to migration based on species or habitat preferences (McRae et al., 2008; Correa Ayram et al., 2016). To run the lowest cost path, organisms need to be familiar with the landscape and its costs (Adriaensen et al., 2003; McClure et al., 2016). In this regard, leastcost path analysis calculates the single route between two regions with the lowest aggregate cost. On the other hand, circuit theory includes random walk theory similarly to random exploratory individual movements, assuming that organisms have not priori knowledge on the landscape (McRae et al., 2008; Dickson et al., 2019). Furthermore, the circuit theory technique examines the probability contributions of all feasible pathways in the landscape, allowing for the assessment of path redundancy and movement bottlenecks (Carroll et al., 2012; Dickson et al., 2019).

4 Discussion

4.1 Future perspectives and limitations of ECs connecting marine environments

MSP is one of the most significant processes for determining spatial priorities for the conservation through ecological connectivity (Beger et al., 2010). It is well understood that connectivity varies in space and time, making measurement and modeling difficult for conservation planning (Fahrig, 2003). Nevertheless, demographic growth and climate change present new problems and possibilities for incorporating connectivity into ecosystem-supportive planning (Simberloff, 1992; European Commission, 2015; Muñoz et al., 2017). Climate change is also expected to have a considerable influence on marine biological connectivity patterns (Harley et al., 2006; Andrello et al., 2015; Bruno et al., 2018; Friesen et al., 2021). Data on current and future ocean conditions, and the distribution of the species can be integrated to deepen how hotspots of connectivity as well as MPA networks interconnectedness may change over time (Heyman and Wright, 2011; Hooker et al., 2011; Piquer-Rodríguez et al., 2012; Friesen et al., 2019). Therefore, to integrate all available information on the ecological connectivity into MPAs planning is crucial (Carr et al., 2017). However, as stated earlier, direct integration of connectivity into MPA network planning is rare (Magris et al., 2014). To enhance connectivity between existing MPAs, planners should prioritize areas that can serve as steppingstones between

existing ones. Connectivity regards the spatial structure of a network of MPAs and the potential capacity of organisms to move within each MPA of the network and in other suitable habitats outside to maintain itself. In some cases, to evaluate connectivity, only habitat inside MPAs have been regarded (Allison et al., 1998; Jonsson et al., 2020).

Connectivity can also depend on the movement between habitat patches within an MPA during various life stages (Berkström et al., 2022). Furthermore, connectivity within MPAs is important for species with reduced dispersal ranges and living in fragmented habitats, while connectivity between MPAs and the surrounding area is important for dispersal and genetic exchange between populations for larger areas (Andersson et al., 2008). Therefore, if any climate refugia exist, locating and protecting them can assist to preserve sensitive ecosystems (Brito-Morales et al., 2018). In this context, future studies should examine shifts in connectivity patterns in relation to climate change (Magris et al., 2014; Andrello et al., 2015). To better understand connectivity patterns of species regarding possible climate change implications, studies should evaluate vulnerability and movements throughout all life stages (Moffitt et al., 2009; Álvarez-Romero et al., 2018; Friesen et al., 2021). For instance, it is known that climate change is predicted to modify larval dispersion patterns, whether owing to decreasing planktonic larval duration or larval sensitivity to changing environmental features (O'Connor et al., 2007).

To our knowledge, there are very few MSP research that include horizontal, vertical, physical, and biological connectivity (Muñoz et al., 2017). This might be due to the existence of barriers across disciplines (oceanography, biology, and management) as well as the difficulty of developing a sample strategy that allows to study physical and biological connectivity simultaneously (Muñoz et al., 2017). Typically, benthic habitat data may be the only information available in MSP procedures where data are scarce (Brooks et al., 2004). Because of limitations of time and resources, conservation planners frequently use limited data to guide their decisions (Ban et al., 2009; Hansen et al., 2011). The biology of ecologically significant species (spawning and nursery grounds, reproductive periods, migration patterns) should be deepened to determine potential connectivity and offer a firm foundation for reserve siting, planning, and zoning (Fraschetti et al., 2018).

Faced with a future of increasing susceptibility to human activities (Halpern et al., 2019), successful marine biodiversity conservation necessitates a strategic planning approach to identifying places where numerous anthropogenic hazards coexist with ecological components (Halpern et al., 2008; Crain et al., 2009; Micheli et al., 2013).

Investigating connectivity in a managed area is crucial for population management as well as possible pollutant spread derived from human activities (Muñoz et al., 2015). In this context, currents have a role in connecting coastal managed areas environmentally, but that result administratively disconnected because differently managed by various local governments or nations (Muñoz et al., 2015). In case good connectivity is found between areas resulting under the jurisdiction of different administrations and countries, MSP requires administrative cooperation in that area as well as connectivity estimation and identification of ECs and the time necessary to cross them (Muñoz et al., 2015). Lastly, encouraging is that policymakers and practitioners increasingly recognize the importance of ecological connectivity, even there are significant challenges for integrating connectivity into policies, planning, and conservation (Lausche, 2011; Keeley et al., 2019).

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

CP: conceptualization, data curation, validation, writing – original draft. EMDP: conceptualization, supervision, validation, 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.2023. 1271397/full#supplementary-material

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