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Aligning marine spatial conservation priorities with functional connectivity across maritime jurisdictions

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Abstract

Globally, maritime boundaries on oceans form the basis of governance and management of natural resources, yet the fish, and other marine resources neither conform nor confine to these artificial boundaries. As goods and services from marine life continue to retrogress under the intense human exploitation and changing global environment, resilience could be supported through establishment of a functionally connected network of marine reserves across maritime jurisdictions. While the establishment of protected areas within the exclusive economic zones (EEZ) is expanding, mechanisms that would allow governments to conserve marine areas beyond national jurisdictions are currently inadequate. Consequently, implementing marine reserves is largely confined within territorial waters, high connectivity among contiguous maritime zones notwithstanding. As the global focus shifts toward achieving sustainable development goals for the oceans, there is a need for region-specific approaches to area-based biodiversity conservation that extends the scope of protection to areas in the high seas beyond the EEZ. Using simulations of functional connectivity and seafloor geomorphology, we present and apply in the Western Indian Ocean (WIO) region a contextual approach to regional marine conservation planning to inform a more effective regional marine conservation across maritime zones.

KEYWORDS

areas beyond national jurisdiction, fisheries management, functional connectivity, high seas, larval dispersal, marine conservation planning, marine protected areas, ocean governance, regional MPA, seafloor geomorphic habitats, Western Indian Ocean

1 | INTRODUCTION

The health of marine and coastal ecosystems is in serious decline from multiple human pressures, compromising the provision of essential goods and services for human persistence (Hicks et al., 2019; Myers & Worm, 2003). In addition to rapidly growing coastal populations, the expansion of existing uses of the ocean, and the addition of emerging uses such as renewable energy, large-scale aquaculture, oil and gas extraction and mining, will further exacerbate the decline of marine ecosystems (Cinner et al., 2018; Jones et al., 2018; Kroodsma et al., 2018; McCauley et al., 2015). While the consequences of marine and coastal environmental changes are often felt locally, nations have long acknowledged the need for global and regional management actions to transcend national jurisdictions (De Santo, 2018).

In the Western Indian Ocean (WIO)—under the stewardship of the Nairobi convention—regional efforts to implement ocean governance strategies, including the establishment of regional network of MPAs' within the framework of the existing global targets, are currently underway (i.e., Aichi target 11 protection targets and Sustainable Development Goals 14 on protection targets by 2020) (CBD, 2010). As the push for expanded protection targets intensifies, focusing on 2020 targets (10% of marine areas) for WIO can be a stepping-stone to moving toward larger protection targets such as 30% by 2030 (Luchansky, 2012). Furthermore, given governance of the WIO involves multiple countries, the establishment of MPA network in the WIO will need to consider among the main issues impacting on marine conservation in the region: the human use, knowledge gap and data scarcity, connectivity, and differential competencies and motivation among countries.

To increase the likelihood that MPA or other types of management networks will be effectively implemented in the WIO, socio-economic and geopolitical considerations such as multiuser conflicts and distribution of fishing activities have become critical components of planning (Maina et al., 2015). Within the region, there is a high dependence of communities on marine resources, which means the costs of establishing MPA to local communities is particularly high in these poor countries. Most of the existing MPAs' in the WIO are located within 10 km from the shore, exposing them to pressures associated with the gravity of markets (Cinner et al., 2018). Striking a balance between locating closures in low versus high human impact areas is critical; low human impact closures are important for sustaining ecological functions like high-order predation, while reserves in high-impact areas can provide substantial conservation gains in fish biomass (Cinner et al., 2018; McClanahan, Maina, Graham, & Jones, 2016; McNeil et al., 2015).

An additional consideration for designing and implementing MPAs' in the WIO is the knowledge gaps of how the intricate ocean ecosystems function and are distributed, in particular for the far offshore regions. This makes it hard to design MPA for representation of ecosystems because data on habitat distributions is often nonexistent (Ward, Vanderklift, Nicholls, & Kenchington, 1999). This challenge can be overcome by finding a suitable biodiversity surrogate and adopting the precautionary principle in designing management closures (Ban, 2009), limitations of such technique notwithstanding (Dalleau et al., 2010; Rodrigues & Brooks, 2007). For example, linkages between heterogeneity of seafloor geomorphic habitats and biodiversity are well established in the literature (e.g., Burnett, August, Brown, & Killingbeck, 1998; Nichols, Killingbeck, & August, 1998). In the absence of biodiversity distribution maps, publicly available datasets of seafloor geomorphic features can be used as surrogate measures of biodiversity to guide MPA network design (Fischer, Bhakta, Macmillan-Lawler, & Harris, 2019).

The third consideration is the high functional connectivity, or exchange of individuals among marine populations, among maritime zones. Although the functional connectivity among maritime zones is well documented (e.g., Cowen, Paris, & Srinivasan, 2006; Cowen & Sponaugle, 2009; Weersing & Toonen, 2009), recent reports emphasize high functional connectivity among maritime zones and the significant contribution of the high seas to marine capture fisheries in nation's economic exclusive zones in the WIO (e.g., Popova et al., 2019). One way that countries can safeguard fisheries is through a regional planning approach using functional connectivity as a focus for identifying marine areas suitable for inclusion in the regional network of MPA (Roberts, 2012).

Lastly, different competencies and motivation among countries can lead to complex and slow process of planning and negotiations among stakeholders (Smith & Jabour, 2017). Ongoing efforts by the UN Environment Nairobi Convention regional sea are aimed at achieving a consensus on regional ocean governance strategies for WIO, including the establishment of a regional MPA network. Previously, through similar efforts, eight locations covering 27% of the WIO high seas were described as ecologically or biologically significant area (EBSA) (Figure 1). Placing protection within EBSA, and other areas that are globally recognized as important but do not currently have ascribed management (e.g., important bird areas (IBAs) and key biodiversity areas (KBAs))—could provide less contested avenues for protecting recognized biodiversity values (Edgar et al., 2008).

Here we describe a regional marine conservation planning approach for prioritization across maritime zones of exclusive economic zones and the high seas in the WIO. In this approach, we apply functional connectivity as one of the conservation features guiding the identification of areas suitable for inclusion in transboundary MPA networks in the WIO. Using a larval dispersal model, we analyze connectivity patterns among existing MPAs', coral reefs, and seamounts at a large spatial scale to identify opportunities for maintaining functional connectivity in the WIO. To achieve our aim, we first apply graph theory to evaluate gradients of connectivity among marine features: MPA and biodiversity surrogates (corals, seamounts, and EBSAs). Using these results, we then conduct a preliminary marine spatial prioritization across the

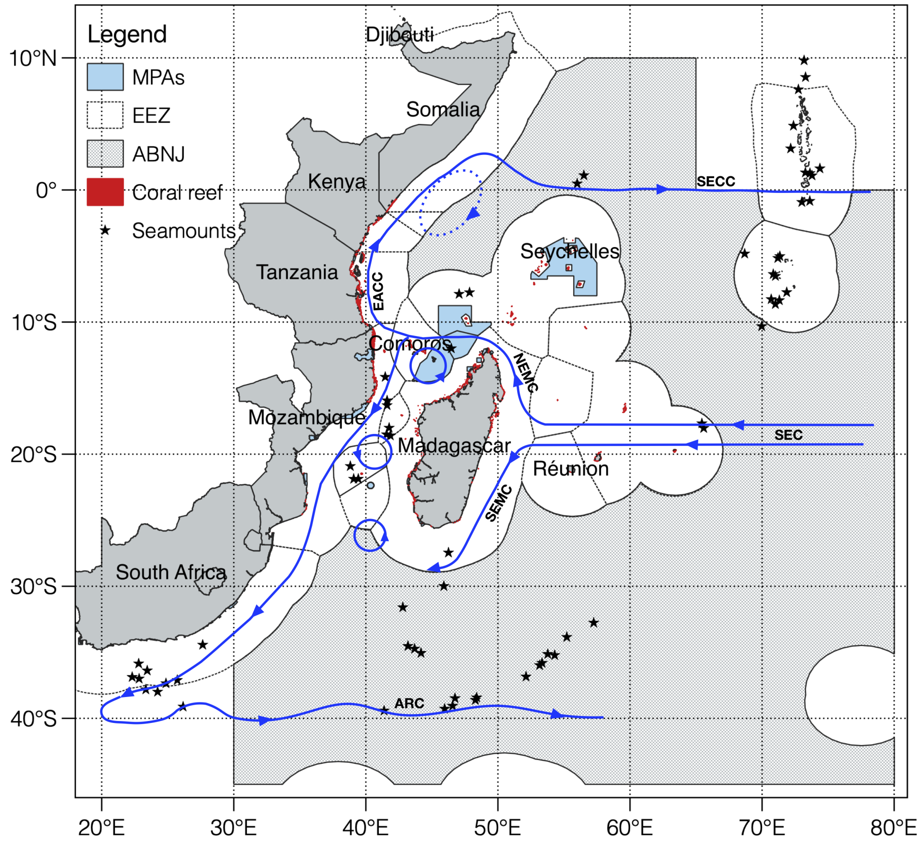

FIGURE 1 Map of the WIO showing the high seas, EEZ, MPA, seamounts, and the main oceanographic circulation in summer adapted from Schott, Xie, and McCreary (2009). Currents represented are: the South Equatorial Current (SEC), the North East Madagascar Current (NEMC), and the South East Madagascar Current (NEMC), the East African Coastal Current (EACC), Somalia Current (SC), the South Equatorial Counter Current (SECC). Further south is the Agulhas Current (AC) and the Agulhas Return Current (ARC)

WIO (both EEZ and high seas) in line with global protection targets that considers persistence of MPA networks and fisheries benefits.

2 | METHODS

2.1 | Regional geography

The WIO, one of the regional seas identified by the United Nations Environment Programme (UNEP, 2018), covers ~30 million square km of ocean off the coasts of eastern and southern African countries and covers ~8.1% of the global ocean surface. It comprises 10 countries—Comoros, France (overseas territories), Kenya, Madagascar, Mauritius, Mozambique, Seychelles, Somalia, South Africa, and Tanzania (Figure 1). Of these, five are mainland continental states on the eastern boundary of the WIO, four are small island states, and Madagascar, a large island, with EEZs covering over 6 million km^2 and a combined coastline of over 15,000 km (UNEP/Nairobi Convention Secretariat, 2009). For this study, we adopted WIO high seas region as an intersection of FAO fishing zone 51, and the Regional Fisheries Management Organization defined Southern Indian Ocean Fisheries agreement areas (SIOFA). Consequently, the eastern and the southernmost boundaries were set to 75°E and −44°S, enclosing a high seas region of ~15.5 million square km.

2.2 | Dispersal modeling

To estimate functional connectivity among key marine habitats (coral reefs, Seamounts), MPA, and marine jurisdiction zones (EEZ and the high seas), we modelled larval dispersal using *Itchyop* v 3.3, an individual-based model designed to study the effects of physical and biological factors on the dynamics of fish eggs and larvae (Lett et al., 2008; Lett et al., 2019). Models were run off-line using the daily (24 hr) velocity fields from the hydrodynamic model. Advection of the virtual larvae was simulated using a fourth order *Runge–Kutta* integration scheme and a random walk was applied using a dissipation rate of 1×10^{-9} m^2/s^3 for individual virtual larvae to account for turbulent motion not captured at the resolution of the oceanographic data (Lindemann, Aksnes, Flynn, & Menden-Deuer, 2017). We used Mercator Ocean's Global ocean physical reanalysis GLORYS2V1 (Ferry et al., 2012) at grid size of 1/4° and a temporal scope of daily from January 1, 2000 to December 31, 2010 as input to the model.

2.2.1 | Potential connectivity among MPAs′, coral reefs, and seamounts

Spatial data for WIO MPA was obtained from a recently constructed MPA database containing 120 MPA records (unpublished data). Coral reef data were obtained from the Millennium Coral Reef Mapping Project archived at UNEP-WCMC as Shapefile format at 500 m resolution and seamount data from global sea floor habitat database (Harris, Macmillan-Lawler, Rupp, & Baker, 2014). Because the Mercator ocean data has a spatial resolution of ~25 km, the coral reef layer was resampled to 25 km square grids. We used a subset of seamounts within the study area at depth range of 2–1,000 m. Grid centroids for MPAs′, coral reefs, and seamounts (N = 120, 242, and 67, respectively) were set as the release and settlement locations for virtual larvae. 1,000 virtual fish larvae were released from each centroid (at a variable depth for seamounts and coral reefs) for 11 years (2000–2010) from January to December. These were tracked for 30 days, the average Pelagic Larval Duration (PLD) of fishes, with a time step iteration of 6 hr (i.e., ~14 million virtual larvae released across all release; Andrello et al., 2017; Luiz et al., 2013).

2.2.2 | Potential connectivity between the high seas, EEZ, and territorial waters

To estimate potential connectivity between EEZ and high seas, larvae were released and tracked from within each EEZ. High seas consisted of 16,515 grids, where larvae were released every 6-hrs over 10 years from January to December between 2000 and 2010 and tracked for 30 days (in total ~19 million virtual larvae). The EEZ dataset consisted of 21 EEZ features for the region and was obtained from the UNEP-WCMC website (www.unep-wcmc.org).

2.3 | Indicators of potential connectivity

The primary output of each simulation of larval dispersal was a connectivity matrix with estimates of total larvae transported between release and settlement sites including local retention. Using the connectivity matrix, we calculated a suite of connectivity metrics to characterize connectivity among spatial features. *Connection probability* $C(i,j)$ was the fraction of larvae originating from a release point of interest i that ended up in destination point of interest j (Adrello et al., 2017). To identify important stepping-stones that facilitate connectivity in a network, we calculated *betweenness centrality* (i.e., number of times a particular node served as a stepping-stone in the shortest paths between all other pairs of nodes in the network). The objective here was to prioritize planning units, which may act as important stepping-stones (high *betweenness centrality*) among other planning units. To determine the number of connections originating from and coming into each planning unit, we computed *in-degree* and *out-degree* metrics, respectively (Minor & Urban, 2008). *In-degree* indicates the number of connections coming into each planning unit (i.e., sink) (Minor & Urban, 2008). Areas with a high *in-degree* may have higher genetic and species diversity (Kahilainen, Puurtinen, & Kotiaho, 2014; Munguía-Vega et al., 2015) as a result of the high number of incoming connections. However, planning units with high *in-degree* may be susceptible to outbreaks and invasive species (e.g., Hock, Wolff, Condie, Anthony, & Mumby, 2014). The associated objective was to prioritize for planning units that have a high number of connections going out to other planning units. *Out-degree* indicates the number of connections originating from each planning unit (i.e., source) (Minor & Urban, 2008). The associated objective was to prioritize for planning units, which have a high number of connections going out to other planning units.

2.4 | Designing a network of MPA across maritime jurisdiction

To select priority areas for marine conservation, first, we defined four broad conservation goals as follows: (a) to represent 21 seafloor geomorphic habitats (Fischer et al., 2019, S1) by protecting 10% of their current distribution across both EEZ and high seas (zone target of 5% for each zone, reflecting CBD Aichi Target 11 protection targets of 10%); (b) to promote the long-term population viability of marine populations by maintaining natural connections and connectivity corridors within marine reserves network and maritime zones mediated by larval dispersal (100% target for sources and sinks), (c) to preferentially meet targets within existing EBSA to align national and regional priorities with globally recognized areas (10% target for each EBSA), and (d) to minimize human pressure on ecosystems in the EEZs, while promoting consensus by selecting less fished areas in the high seas. We selected planning units of 25 km^2 (n = 7,685 planning units across the region) to reflect the resolution of our habitat data and to reflect that this is a regional prioritization. Within any one planning unit, further fine scale mapping might be required when moving from the spatial prioritization to on ground management planning.

As part of the regional wide prioritization process, we began by defining spatially consistent information on the habitat distributions across the planning domain. For conservation features, we used sea-floor habitat maps as they are found in varying proportions within and outside EEZ (Harris et al., 2014; S1), connectivity metrics as calculated in sections above, and EBSA (Fischer et al., 2019). We used *degree* and *betweenness centrality* connectivity metrics to inform selection of important areas for connectivity and reflecting best practice for planning for connected reserves (Álvarez-Romero et al., 2018; Magris et al., 2018; Magris, Pressey, Weeks, & Ban, 2014). Thus connectivity objectives were to prioritize features that receive input from a larger number of other features or are sinks (measured with *in-degree*), which have a high number of connections going out to other features or are sources (measured with *out-degree*), and which may act as important stepping stones among other features (those that have a high *betweenness centrality*). We set a 100% target for the connectivity measures to ensure that we designed a connected reserve system that would be self-sustaining.

Given that regional prioritization spans both EEZ and high seas maritime zones, we used Marxan with Zones to identify spatial priorities that meet conservation goals while differentiating between MPAs′ within EEZ and the high seas (Ball, Watts, & Possingham, 2009; Watts et al., 2009). Marxan with Zones is a multiple use planning version of Marxan used to identify configurations of land or water uses that achieve specified plan objectives while minimizing cost. Marxan is a spatial conservation planning decision support tool that uses a simulated annealing approach to return good solutions to the problem set (meeting stated objectives at minimum total cost) (Ball et al., 2009). We chose Marxan with zones for two reasons: (a) the types of governance arrangements needed to designate and enforce MPA are different between these two areas, therefore zoning them separately allows policy makers useful detail, (b) the types of human uses (and related cost measures) are different for these two regions and therefore to minimize the costs Marxan with zones allowed us to differentiate these costs.

To meet conservation targets while minimizing costs (Ban & Klein, 2009), within the EEZ zone, we set the cost as the gravity of markets, which is a proxy for human pressure on marine ecosystems (Cinner et al., 2016, 2018). For the high seas zone, we set the cost as the fishing effort based on Automatic Vessel Identification System data for 2016 (Kroodsma et al., 2018). This approach does not exclude areas of high fishing from selection for MPA, but instead searches for lower cost solutions where possible for meeting targets. Including spatially explicit costs within marxan with zones thus allowed us to meet our conservation targets while minimizing costs to fishers, reflecting spatial planning best practice (Ban & Klein, 2009; Watts et al., 2009).

To plan for spatially clumped reserves, we selected an optimal boundary length modifier value (0.007) using the calibration method of Stewart and Possingham (2005), which minimizes the trade-off in reduced boundaries and increased costs. We locked in all planning units with greater than 50% of their area overlapping existing MPA (Watts et al., 2009).

We ran Marxan with Zones for 100 runs. We present the Marxan with Zones "best" solution (i.e., a near-optimal configuration of zones that achieved objectives with the least amount of area).

3 | RESULTS

3.1 | Connectivity between MPAs′, EEZ, and high seas

Madagascar, Mozambique, and Seychelles received (i.e., high *in-degree*) most of the larvae generated within MPAs′ (i.e., 19, 14, and 15% respectively; Figure 2a), while relatively fewer larvae settled in Kenya and Tanzania. Somalia, which has no MPA, received 5% of larvae emanating from MPAs′. Most of the larvae released from high seas settled in Mauritius, Seychelles and Madagascar EEZ, while Somalia and Mozambique received relatively high proportion in comparison to other continental countries (Figure 2b). Similarly, larvae released from seamounts in high seas settled in Mauritius, Seychelles, and Somalia EEZ (Figure 2c). Overall, 55% of larvae released from high seas settled within the EEZ, with the majority (10%) settling in Madagascar, 7.3% in Mozambique, 7.20% in Seychelles, 5.45% in South Africa and 4.86% in Reunion (Figure 2).

3.2 | How connected are the seamounts?

Seamounts are located in high seas and were found to be highly connected to other seamounts, coral reefs, and MPAs′. Approximately 34% of features identified as having a high regional connectivity value (i.e., 10th percentile of sources and sinks) were seamounts (Table 1 and Figures 3–5c). Long distance connection was also evident where seamounts within Chagos–Lacadive plateau were connected to those in the Mid-Indian Ridge (Figure 4c). Overall 15 (22%) seamounts were isolated, as they did not receive larvae

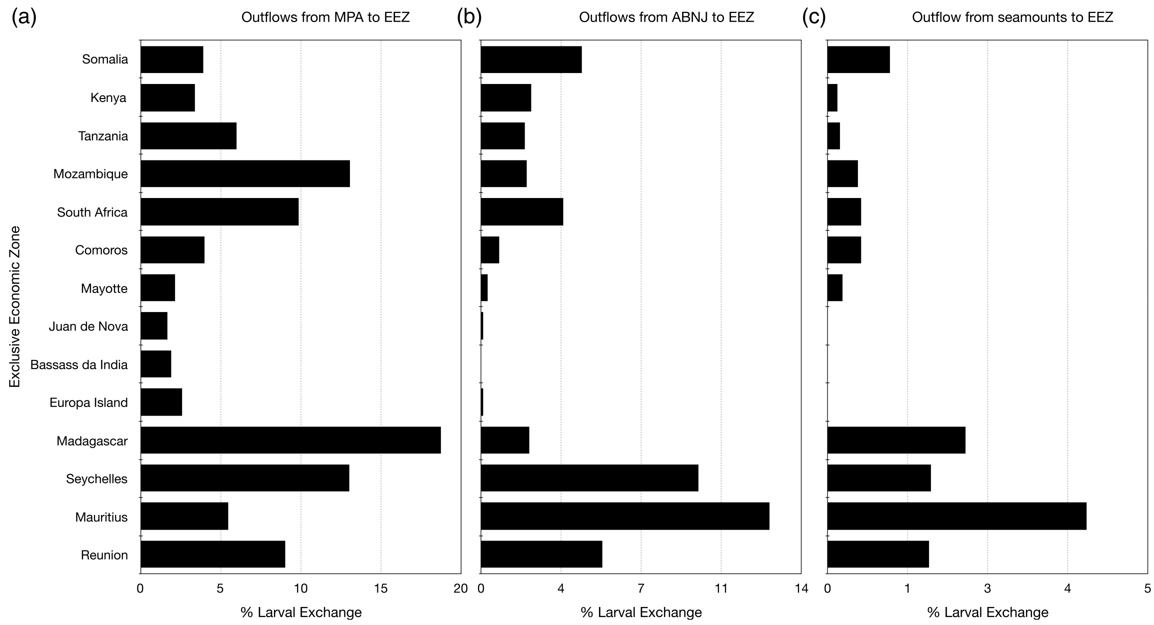

FIGURE 2 Bar graph indicating (a) proportion of larvae from MPA into exclusive economic zones (EEZ) (by country) and (b) proportion of larvae from high seas into EEZ and (c) proportion of larvae from Sea mounts into EEZ. Countries are sorted from North to South

TABLE 1 Percentage of features by habitat type and management that are among the most highly connected, that is, 90% percentile sources, sinks, and corridors

	Coral in fished	Coral in MPA	Noncoral in MPA	Seamount in fished	Seamounts in MPA
90th percentile source features	51	18	5	25	1
90th percentile sink features	37	15	11	7	0
90th percentile source/sink features	44	15	7	34	0
90th percentile corridors (i.e., betweenness)	68	12	4	16	0

Note: Each row equals 100%.

form other seamounts and 12 (18%) were nonseeding while seven (10%), located off South African coast along the path of the Aghulas current, were completely isolated (Figures 1 and 4c).

3.3 | Coral reef connectivity

Our results suggest that, ~ 44% of coral reefs identified as having the highest regional connectivity value (i.e., top 10th percentile of top sources/sinks and corridor reefs) are not protected by the current network of MPAs' (Table 1, Figures 3 and 5c, and S2). WIO coral reefs consist of clusters of connections (Figure 4a). For example, along the East African coast, the dominant connectivity pattern is south to north with Tanzania supplying coral larvae to Kenya, and Kenya supplying to Somalia coast along the northward flowing East African Coastal Current (Figure 4a). Madagascar reefs were the largest source of larvae and seeded reefs in Somalia, Kenya, Tanzania, Mozambique, Comoros, Mayotte, and Aldabra to the north. Madagascar reefs received less from other reefs except from Mozambican, Aldabra, Comoros, and Mayotte reefs. Reefs in the southeastern WIO (Agalega, Tromelin, St. Brandon, Mauritius, and Reunion) were completely isolated from the western part of the domain except for rare westward dispersal from Agalega and Tromelin to Alphonse, Bassas da Indian and into Madagascar reefs.

3.4 | How connected are WIO MPAs'?

Out of 14,280 possible paired connections, 248 connections were found. When MPAs' were connected, the

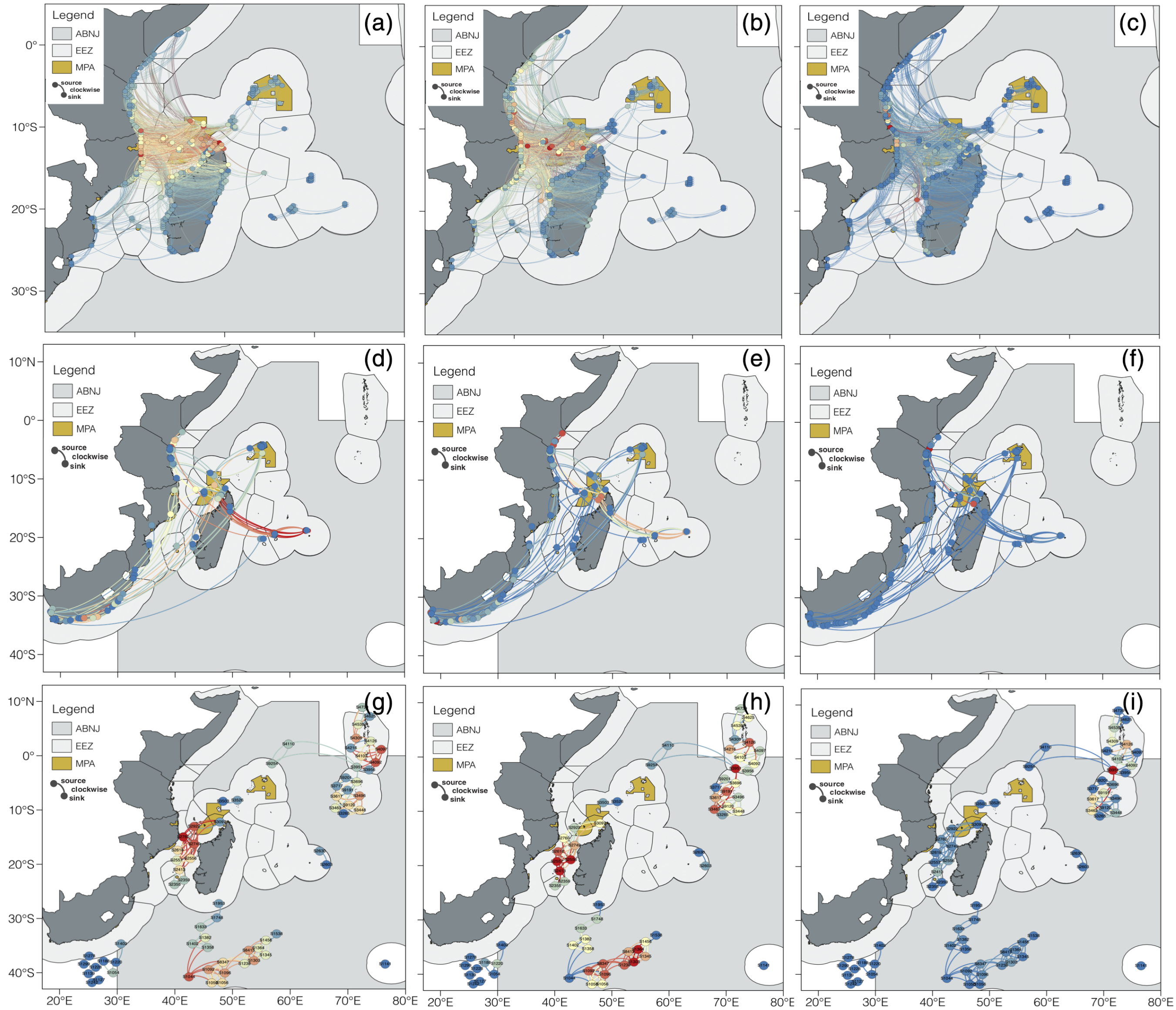

FIGURE 3 Map of larvae sources (*out-degree*), sinks (*in-degree*), and corridors (*betweenness centrality*) gradients in coral reefs (top panel), MPA (middle panel), and seamounts (bottom panel)

connection probability was always low to moderate (median 0.07, interquartile range 0.29; Figure 4b). Connectivity of MPAs' along the East African coast was the strongest (connection probability of 0.5–1), amidst the overall weak MPA connectivity in the region. MPAs' in Tanzania (Mnazi Bay, Tanga, and Zanzibar) had the highest number of incoming and outgoing connections, while Madagascar had the lowest. Half of the MPAs' in the region were isolated, where 55 MPAs' (46%) were not seeded by any other MPA and 62 did not disperse to other MPA (50%) (Figures 3 and 4b and S2). Overall, 38 MPAs' (28%) were completely isolated (zero incoming and outgoing connections) and for example, only 18% of the top sources were located in MPA (Table 1).

3.5 | Priority area selections

The Marxan scenario we used sought to protect 10% of each of the 21 seafloor geomorphic habitats (Fischer et al., 2019, S1) (within EEZ and high seas), while maintaining connections between and among coral reefs, sea mounts and the existing MPAs' (100% target). The best solution met all targets and required ~11% of the study region to be protected, which equated to 15% of EEZ areas and 9% of high seas. Habitats achieved a range of protection from 10 up to 90% (for smaller sea floor habitats such as Bridge and Sill; Figure 6). EBSAs achieved an average of 60% protection (ranged from 10 to 100%). Within the EEZ, a mix of offshore and coastal areas were selected including regions around existing

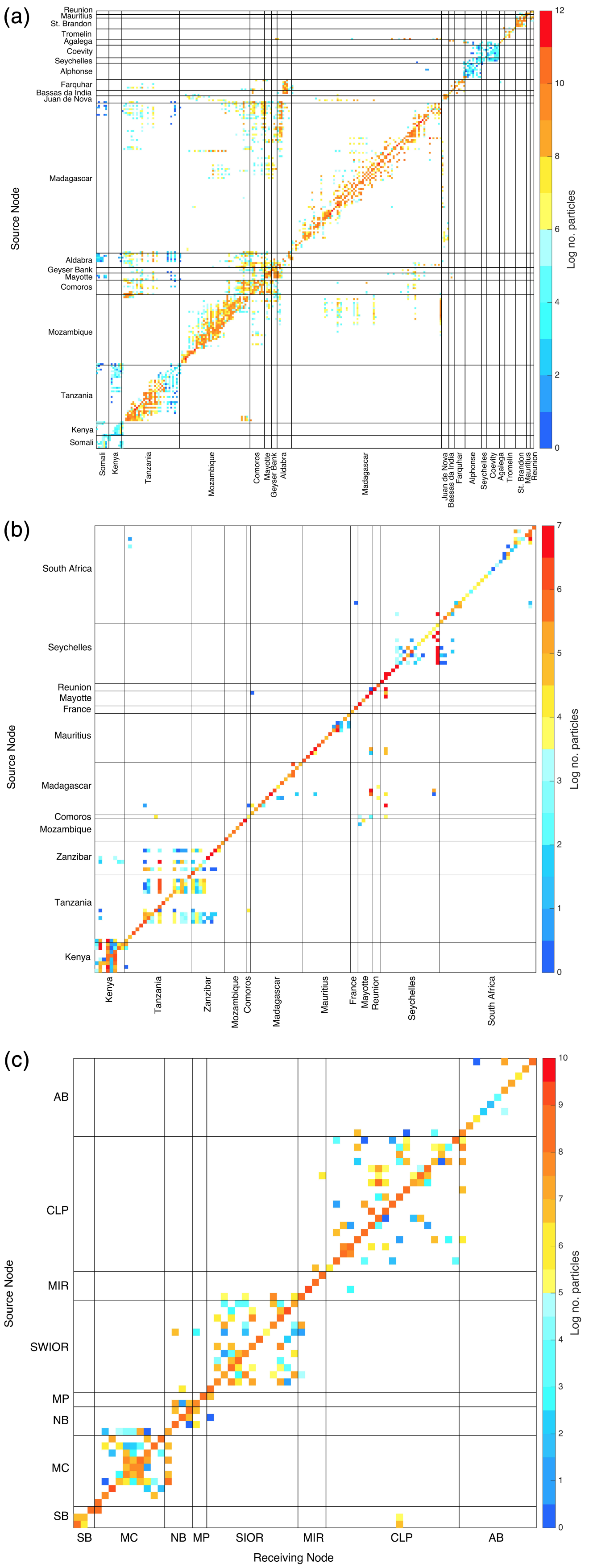

FIGURE 4 Legend on next column.

MPA of *Amirantes to Fortune Bank* in Seychelles (Figure 6). New areas were also selected in Comoros and Gloriosso Islands, in Somali EEZ, offshore eastern Madagascar, Europa, Bassas da India, Mauritius, and Reunion. High seas areas selected were off the Mauritius EEZ to the east and south. The Northern part of WIO ABNJ was not selected, due to the high fishing effort in these areas; given that fishing effort was used as a cost, Marxan avoided these areas where possible, meeting targets in lower fishing effort areas (Figure 6).

4 | DISCUSSION

The development of a regional conservation plan for the WIO, with functional connectivity as one of the factors guiding the identification of areas suitable for inclusion in MPA network, has been illustrated. Our results indicate that current arrangement of MPAs' does not adequately protect connections, with half of the MPAs' completely isolated. Approximately 44% of coral reefs of highest connectivity value are not protected by the current network of MPA (Table 1, Figures 3 and 5c, and S2). Our findings demonstrate a high connectivity between high seas and EEZ, with over half of the larvae released in the high seas settling within the EEZ and majority of these settling in Mauritius, Seychelles, and Madagascar. Regional patterns of connections were also described. Madagascar reefs serve as an important source for Somalia, Kenya, Tanzania, Mozambique, Comoros, Mayotte, and Aldabra. Reefs in the southeastern WIO were completely isolated from the western part of the domain due to barriers created by the oceanography patterns. We present one regional MPA solution for meeting protection targets, which selected ~11% of the study region, including 15% of EEZ areas and 9% of high seas (Figure 6

FIGURE 4 Connectivity matrices indicating the exchange of virtual larvae originating from a location k to recruit in a settlement location l after completion of a 30-day PLD, (a) illustrates coral reefs, (b) MPA, and (c) sea mounts. Self-seeding (recruits that settled into their origin habitats) follows the diagonal. The connectivity matrix represents 243, 120, and 67 coral reefs, MPA and sea mounts features in the Western Indian Ocean. The scale shows the log number of particles. Seamounts are grouped by Ocean Basins: AG = Agulhas Bank; CLR = Chagos–Lacadive plateau; MC = Mozambique Channel; MIR = Mid Indian Ocean Ridge; MP = Madagascar Platue; NB = Natal Basin; SB = Somali Basin; and SIOR = Southwest Indian Ocean Ridge. These are based on larval abundance at the end of a dispersal period. Consequently, the maps should be interpreted as potential larval export if larval production was constant across release locations and absent outside the release locations

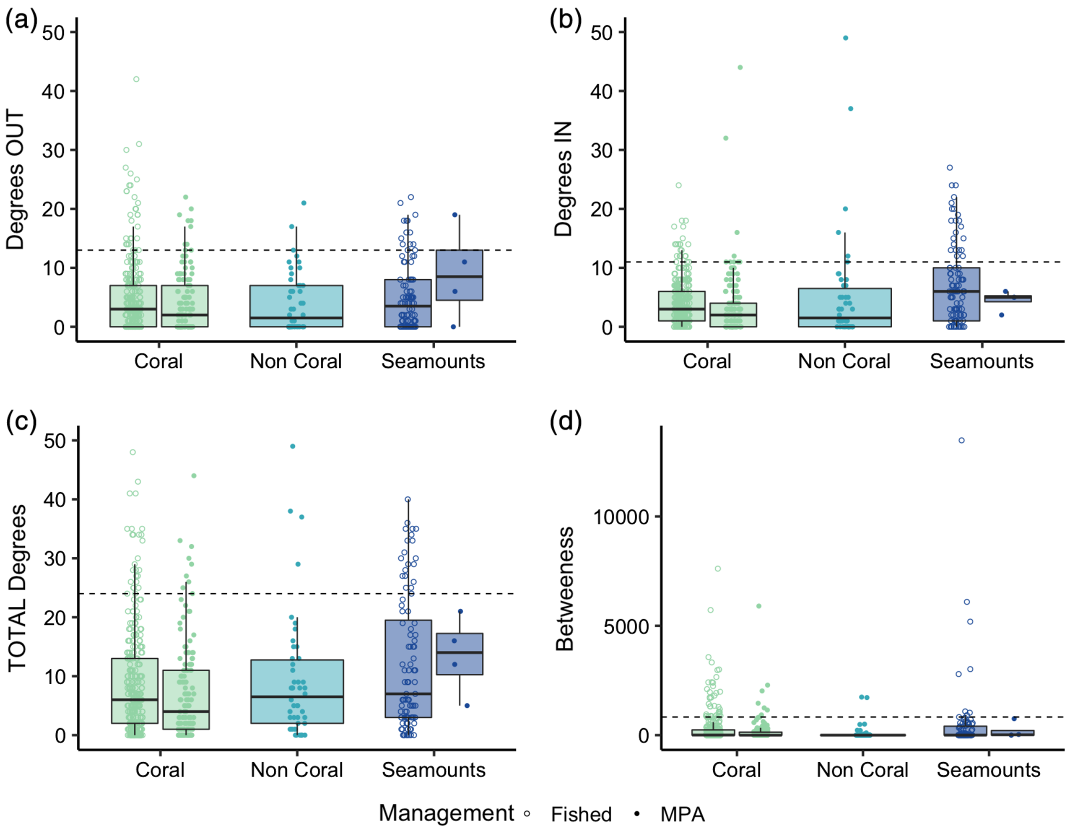

FIGURE 5 Distributions of connectivity metrics for each type of ecosystem: coral (green), noncoral (light blue), and seamounts (dark blue) in fished (open circles) and unfished (MPA) (filled circles). Metrics presented are (a) *out-degree* (i.e., number of connections originating from a feature, (b) the *in-degree* or the number of connections coming into a sink feature, (c) total *degrees* (the sum of out and *in-degrees*), and (d) the *betweenness centrality* or the number of times a cell acts as a bridge along the shortest path between two other features. The dotted line represents the 90th percentile value for each connectivity metric

and S3). This is one scenario of the possible many given that other goals and priorities not captured in our analyses may result in different spatial priorities.

4.1 | Aligning conservation areas to regional connectivity patterns

The current network of 120 MPAs', the majority of which are on the shallow (<100 m) areas of the western boundary of the WIO, is moderately connected. Connectivity as measured by *degree* and *centrality* metrics was high along the East–West direction and following the major ocean currents. Most of the these MPAs' were established to protect biodiversity on key biodiversity hotspots in the region, which was underpinned by the high connectivity among other factors. Opportunities exist for looking at other areas that are highly diverse and could serve as biodiversity hotpots in the future. Of the 243 reef locations, 103 are located within MPA, and do not include the most connected reefs. In effect, highly connected reefs in the region are not enclosed within the current protection arrangement. Earlier reports on MPA connectivity indicate poor connections among global MPA network (Andrello et al., 2017) and a mismatch between fishing dependency and larval supply from MPAs'. For the full benefits of protected areas to be realized, closures should enhance maintenance of connections within MPA networks and between MPA networks and fished areas across maritime zones (Álvarez-Romero et al., 2018).

The Marxan-with-Zones best solution presents one option for expanding protection within EEZs to 15 and 9% within high seas to meet biodiversity targets aligned with existing priority areas (EBSAs) and maintain connectivity by protecting connected reefs. Protection targets could be met largely within EBSAs (Figure 6). Establishment of MPA's may be more feasible within these areas that are globally recognized as important but do not currently have ascribed management; therefore placing protection within these areas may be less contested but also protect recognized biodiversity values. By including fishing pressure (gravity of markets and number of vessels)

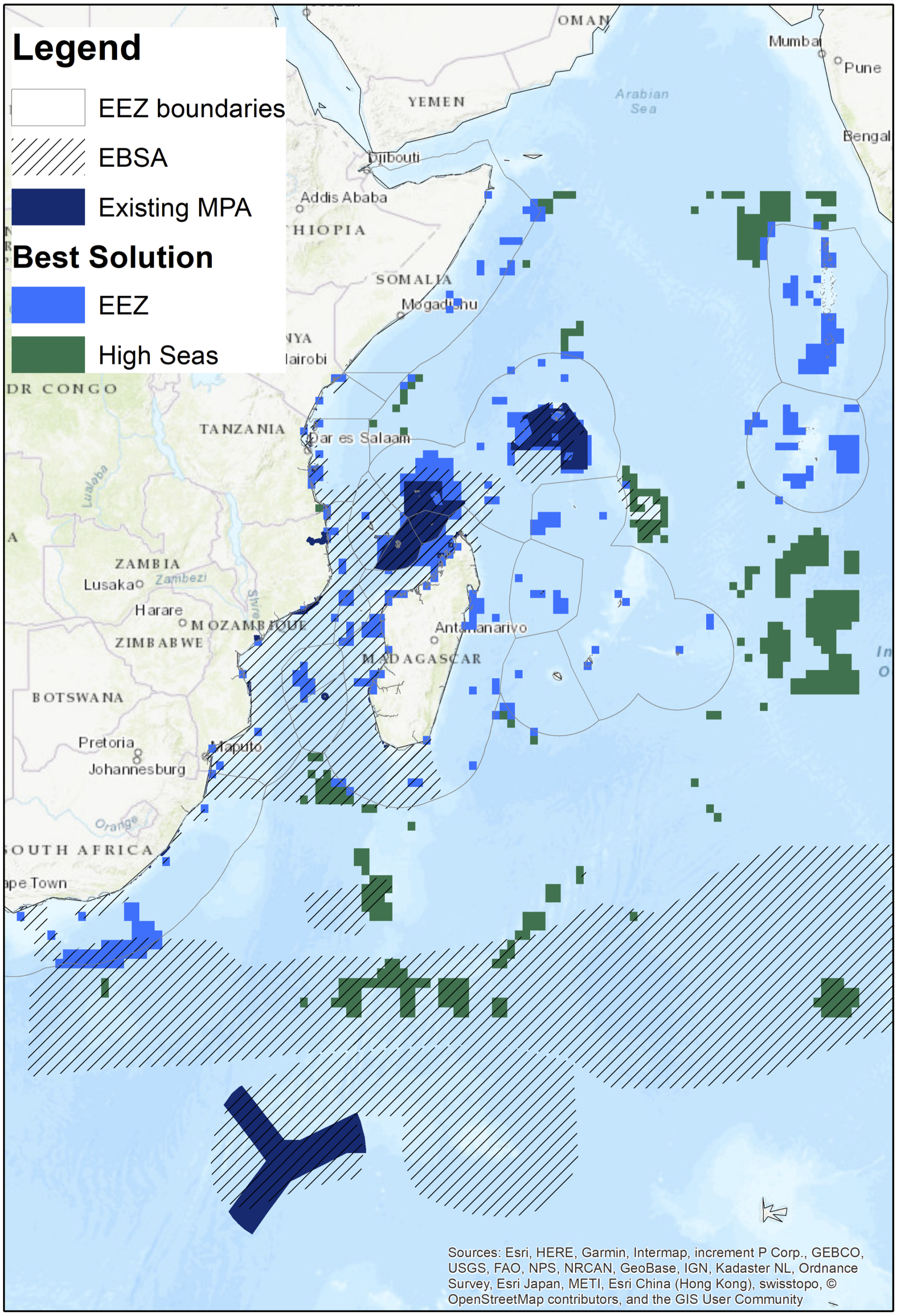

FIGURE 6 Marxan with zones best solution (indicating areas selected within exclusive economic zone [EEZ] and high seas zones). Country and associated EEZ boundaries are shown for context as well as existing MPA are also shown (locked into the Marxan with Zones solutions) and EBSAs (that were preferentially targeted in the best solution)

as a cost, Marxan selected areas further from the shore and the least fished within high seas (i.e., to minimize costs) while meeting connectivity and sea floor habitat targets. In doing so this may also increase feasibility of implementing MPA's within areas beyond national jurisdiction as it promotes consensus by preventing loss of fishing ground, which is one of the issues that complicates country negotiations (Smith & Jabour, 2017). However, this may need to be balanced with ecological interests, for instance a scenario where thresholds of effort are set such that the algorithm prioritises both extremely fished and least fished in an inverted bell curve behavior pattern.

Balancing divergent interest among stakeholders may also be required. For example, investing in multi-objective hotspots alone, or areas where conservation benefits for multiple objectives coincide may go against the principle of a fair multilateral collaboration and equity in a transboundary setting (Beger et al., 2015). In addressing "burden" or equity issues one can either preformulate the solution to be "equitable" that is, every country puts in the same amount of protection, or as we have done here, assume that countries will negotiate outcomes as part of a process and that the final solution will reflect the burden they are willing or able to put in. Our marxan solution will become part of an ongoing conversation and negotiations where countries are expected to make choices on protecting more or less of their EEZ. Besides the amount of area protected by each country, another aspect of equity relates to potential impacts upon local communities including fishermen, addressed here by reducing costs (gravity measure). Therefore, regardless of total area in an EEZ protected, theoretically our solution avoided high impact areas effectively equalizing the "burden."

4.2 | Influence of oceanography on connectivity across ecosystems and maritime boundaries

Oceanic processes play a significant role at influencing larval dispersal and connectivity among populations. In the WIO, the westward flowing South Equatorial Current (SEC) connects the Indonesian region with the Indian Ocean between 10 and 20°S through a zonal flow, which creates a physical and functional connectivity barrier to dispersal between Seychelles and Mascarene islands (Figures 2 and 3). Similar findings were reported by Schott et al. (2009). On the east coast of Madagascar, the SEC accelerates past the tip of Madagascar as Northeast Madagascar Current (NEMC), in effect facilitating the observed larval dispersal from northeast tip of Madagascar into Comoros and further along the East African coast (Figures 1, 3, and 4). Instabilities in the current results in formation of Comoros eddies (Collins, Hermes, & Reason, 2014), which have important implications for connectivity as they entrap larvae released within the Comoros Basin. On reaching the East Africa mainland coast, the NEMC splits into the northward flowing East African Coastal Current (EACC) and southwards as eddies in the Mozambique Channel. The NEMC creates a connectivity barrier between the reefs north and further south in Mozambique Channel. Along the East African coast (Tanzania, Kenya and Somalia), the dominant pattern of connectivity is south to north, connecting coral reefs in Northern Kenya to Somalia (Figures 3 and 4).

4.3 | Management and policy recommendations

Area based tools, including MPA, are practical for protection of marine biodiversity in the WIO; however poor enforcement, lack of management plans, and significant data gaps can obstruct management effectiveness (Roberts et al., 2017). Adopting an evidence-based approach to biodiversity conservation of living marine resources and ecosystems, and improving the knowledge base for decision-making is of necessity (De Santo, 2018). Furthermore, studies on the feasibility, options, and scenarios for the establishment of marine protected areas in high seas, in consultation with the countries and relevant stakeholder involved is critical. This may involve partnerships with the International Maritime Organization and FAO, within the framework of the United Nations Convention on the Law of the Sea (UNCLOS), to facilitate identifying and designating area based management tools, which are of significance in terms of ecological, social, economic, or scientific criteria and are vulnerable to damage by fishing, mining, and international shipping among other destructive activities.

4.4 | Data and analysis caveats

In this study, we have used larval dispersal to represent potential functional connectivity. Yet, functional connectivity is more than larval dispersal as it includes animal movement, spawning aggregations, and other processes through which movement or exchange can be achieved. Consequently, elements of functional connectivity may be under or overrepresented in some areas. Furthermore, we did not attempt to model realistic numbers of dispersing larvae or specific spawning timings. Therefore, our models represent potential dispersal and connectivity level among habitats and marine jurisdiction zones. Furthermore, biological parameters of the model included passive larvae, which can lead to an overestimation of dispersal distances (Cowen & Sponaugle, 2009). Incorporating behavioral characteristics of larvae (such as orientational mechanism, mortality) into the model can change the patterns of larval dispersal and increase/decreases the chances of retention and recruitment. Thirdly, we used a constant PLD of 30 days for all larvae, however, PLD varies among fish taxa. Regional marine conservation planning is a complex process, often involving multiple stakeholders and negotiations on specific goals and priorities. We present one marine spatial planning scenario, recognizing that there are other goals and priorities not captured here that may result in different spatial priorities and that conservation of biodiversity is more than just connectivity. Our aim, however, is not to generate the best marine spatial plan, but to illustrate key elements, processes, and a framework that the ongoing WIO marine spatial planning process can build upon. Future studies using biodiversity occurrence data would allow selection based on species composition. Using high-resolution data can better estimate larval dispersal, considering that we have used here 25 km resolution grids that might be too coarse for some ecological features such as coral reefs.

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CONFLICT OF INTEREST

The authors have no conflict of interest.

AUTHOR CONTRIBUTIONS

D.W., J.B., J.F., and J.M. conceived and designed the study. J.M., V.A., S.D., and M.G. analyzed the data. J.M. led the manuscript with the help all authors.

DATA AVAILABILITY STATEMENT

All data are available on request by email to the corresponding author.

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