CHO Chapter 20

Aligning marine spatial conservation priorities with functional connectivity across maritime jurisdictions

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Key words: High Seas, ABNJ, Marine Spatial Planning, Western Indian Ocean, Geomorphic features, Marine connectivity, Marine conservation, Marine protected areas

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 or confine to these artificial boundaries. As goods and services from marine life continue to retrogress under intense human exploitation and climate change, resilience could be achieved through establishment of functionally connected network of marine reserves across maritime jurisdictions. Unfortunately, mechanisms that would allow governments to conserve the high seas are currently non-existent, while difficulties of non-spatial monitoring and data gaps obstruct conventional management and conservation planning approaches. Consequently, implementing marine reserves has been confined to within national jurisdictions, despite high connectivity among contiguous maritime zones. As the world focus shifts to developing mechanisms for governing the high seas, we present a novel approach, using simulations of functional connectivity and seafloor geomorphology, for cross-jurisdictional regional marine conservation planning. We apply this approach to the Western Indian Ocean to inform a more effective regional marine conservation.

Introduction

The health of global marine ecosystems is in serious decline from multiple pressures, including overfishing, pollution, invasive species, coastal development, and climate change, that compromise the ability of ocean and coastal ecosystems to support and sustain the essential goods and services for human persistence (Myers and Worm, 2003). Unregulated expansion of existing uses of the ocean, and the addition of emerging uses, such as renewable energy, large-scale aquaculture and mining, along with a rapidly growing coastal human population, are likely to further exacerbate the decline of marine ecosystem health (Cinner et al., 2018; Jones et al., 2018; Kroodsma et al., 2018; McCauley et al., 2015). As human populations continue to grow, and technologies continue to advance, a major challenge is to counteract ecosystems and biodiversity degradation across the Ocean, particularly in Areas Beyond National Jurisdiction (high seas, ABNJ) (Murawski, 2010).

The high seas make up two-thirds of Oceans and are largely unclaimed and ungoverned. In effect, there are no legal mechanisms for governments to create marine reserves in these largely ungoverned ecologically important areas. High seas are rare and fragile ecosystems, and are critical migration routes that help sustain species, which in turn support ecosystems and livelihoods around the world (Scovazzi, 2004). This notwithstanding, several human activities occur within ABNJ including commercial shipping and fishing (Heffernan, 2018). Globally ABNJ account for up to US$16 billion a year in fisheries catch (Sala et al., 2018) and are also prime territory for the discovery of valuable mineral deposits, potent pharmaceuticals and oil and gas reserves (Heffernan, 2018). At the same time, reciprocal legal obligations to protect the ABNJ are largely overlooked (Ardron et al., 2008). Yet, as destructive activities continue to unfold in the high seas, management actions are largely focused on coastal and inshore regions, where our understanding of marine ecosystems is best (Heffernan, 2018). Improving our understanding on marine ecosystems both within EEZ and in the high seas, and the foundational ecological process that functionally connect them is key to broadening conservation focus beyond territorial boundaries (Ardron et al., 2008).

Marine functional connectivity transcends maritime boundaries to support the most fundamental ecological function of connecting ecosystems, including the highly migratory species such as tuna, some sharks and long-lived species that move between the high seas and EEZs (Calich et al., 2018). Due to this highly migratory nature, these species tend to be intensely fished and overexploited (Campana, 2016). Oceanic sharks, of which 44% are threatened (Dulvy et al., 2014), spend a great deal of time in the high seas, where shark fishing is largely unregulated and unmonitored. As mechanisms that would allow governments to conserve the high seas, where non-spatial monitoring is difficult, and where data gaps obstruct conventional management approaches (Ardron et al., 2008), area-based planning across maritime boundaries, including marine spatial planning (MSP) and EBSAs is a practical way forward.

Marine Reserves, advocated as one of tools to preserve and maintain biodiversity and to mitigate negative effects of anthropogenic activities, have been implemented to a variable degree of success, including in the high seas where currently 12 Marine Protected Areas (MPA) exist (Smith and Jabour 2017; Roberts, 2012). However, MPA design and implementation in the high seas is complicated because (i) little is known about the intricate ocean ecosystems far offshore, and (ii) the complex, slow and challenging process of planning and negotiations involved (Smith and Jabour, 2017). An evidence-based approach to protecting the high seas will require massive amounts of research. For example, to get a better sense of the scale of the looming ocean crisis, scientists need to map deep-seabed habitats (eg Harris et al., 2014) and understand key processes such as physical and functional connectivity. In the meantime, suitable biodiversity surrogate, adoption of precautionary principle (Lauck et al., 1998), and functional connectivity could be used as the main focus of the conservation goals guiding the identification of areas suitable for inclusion in the high seas MPA (Álvarez-Romero et al., 2018).

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Functional connectivity, or the exchange of individuals among marine populations, is fundamental for ecological processes such as population dynamics, evolution, and community responses to climate change (Cowen et al., 2007). Connectivity facilitates recovery processes after disturbance, through spillover of mobile juveniles and adults from MPAs into adjacent unprotected habitat and seeding of unprotected sites with larvae spawned within MPAs (Roberts et al., 2017). Recovery through resettlement depends largely on maintaining the supply of larvae, underpinning the need for functionally connected networks of marine reserves. Consequently, the long-term persistence of marine ecosystems and ecosystem services they provide hinges on identifying mesoscale connectivity patterns to link marine reserves within networks across the maritime jurisdiction.

In this paper, we evaluate marine connectivity and use it as one of the main focus of the conservation goals guiding the identification of areas suitable for inclusion in the high seas MPA. We assess connectivity patterns among existing MPAs, coral reefs and seamounts at large spatial scales to identify the gaps and opportunities for maintaining functional connectivity. Finally, we illustrate how regional scale prioritisation across maritime zones of Exclusive Economic Zones (EEZ) and ABNJ can be applied using area-based tools. Three goals to maximise conservation outcomes guided the identification of areas suitable for inclusion in the MPA network. These goals apply nationally, and they guide identification of representative marine reserves in all the marine regions. In the absence of comprehensive knowledge on high seas biodiversity, the planning goals were (i) to represent geomorphic sea floor habitats by protecting 10% of their current distribution; (ii) to promote the long-term population viability of focal species by maintaining natural connections and connectivity corridors within marine reserves network mediated by larval dispersal, and (iii) to minimize human pressure on ecosystems in the EEZs, while promoting consensus by selecting less fished areas in the high seas.

2. Methods

2.1 Study area

The WIO covers 30 million square km of ocean off the coasts of eastern and southern African countries, equivalent to 8.1 per cent of the global ocean surface (Figure 1). It comprises 10 countries – Comoros, France (overseas territories), Kenya, Madagascar, Mauritius, Mozambique, Seychelles, Somalia, South Africa and Tanzania. 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 km2 and a combined coastline of over 15,000km (UNEP/Nairobi Convention Secretariat, 2009). WIO is one of the regional seas identified by the United Nations Environment Programme (UNEP). The eastern limit of the WIO is not explicitly defined. For this study, we adopted WIO ABNJ region as an intersection of FAO fishing zone 51, and the Regional Fisheries Management Organisation (RFMO) defined Southern Indian Ocean Fisheries agreement areas (SIOFA) (Fig. 1). Consequently, the eastern and the southernmost boundaries were set to 75^{o}E and -44^{o}S, enclosing an ABNJ region of ~ 15.5 Million square km (Fig. 1). Eight locations, covering 27% of the WIO ABNJ are designated as ecologically or biologically significant area (EBSA).

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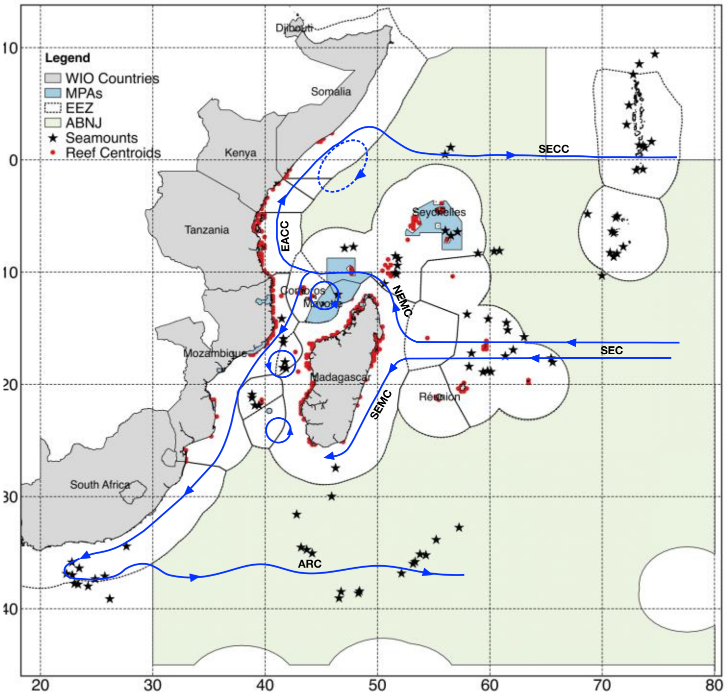

Figure 1. Map of the region showing the ABNJ, EEZ, MPA, geomorphic habitats and the main oceanographic circulation in summer adapted from Schott and McCreary (2001). The major currents illustrated include; the South Equatorial Current (SEC), the North East Madagascar Current (NEMC) and the South East 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).

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2.1.1 Regional fisheries

WIO ABNJ experience high intensity of fishing, with an estimated cumulative effort of 265,000 hours by 19 countries, with a net revenue $537 Million (Sala et al., 2018). Of the 19 countries that fished in FAO zone 51 in 2016, only four countries (Tanzania, Seychelles, Comoros and Maldives) were from the WIO region and earned ~$5 Million (Sala et al., 2018). According to the data from SeaAroundUs (USA, 2007), average fish landing within the EEZ from 2009-2014 was 682,265 tons/year with Tanzania, Mozambique, Madagascar and Somalia landing the highest amount. Industrial fishing, by comparison was relatively low (21%) compared to artisanal (61%). The low industrial landing (primarily from the high seas) does not reflect the importance of the ABNJ to the WIO countries. The high functional connectivity demonstrated in this and other studies suggest a high dependence between the EEZ and high seas. Consequently, the thought that WIO countries don't have control over exploitation of the adjacent high seas, an area with significant influence on fish stocks and fisheries of the 10+ WIO counties – and by extension socio-economics, is not equitable.

2.2. Dispersal modeling

To simulate larval dispersal, we employed Mercator Ocean's Global ocean physical reanalysis GLORYS2V1 (Ferry et al., 2012), which covers the Western Indian Ocean region extent [11º N to 40º S and 20º E to 75º E]. The model's spatial resolution is 1/4º and the temporal scope was daily from January 1st, 2000 to December 31st, 2010. Larval dispersal simulations for coral reef, MPAs, ABNJ and seamounts were performed using Ichthyop (Lett et al., 2008) and run off-line using the daily (24 h) velocity fields from the hydrodynamic model. Advection of the virtual larvae was simulated using a 4th order *Runge-Kutta* integration scheme and a random walk was applied using a dissipation rate of 1 x 10−9 m^2/s^3 for individual virtual larvae to account for turbulent motion not captured at the resolution of the oceanographic data (Peliz et al., 2017).

2.3 Connectivity among MPA's, coral reefs, and sea mounts

Spatial data for MPAs for the WIO were obtained from a recently constructed WIO MPA comprehensive 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 at 1 km resolution. Because the Mercator ocean data has a spatial resolution of ~25 km, the coral reef layer was re-sampled to 25km square grids. Seamounts data was obtained from global sea floor habitat database (Harris et al., 2014). We used a subset of seamounts intersecting the study area at a depth range of 2-1000m (Fig. 1). Centroids from MPA, coral reefs and seamounts (N=120, 242, and 67 respectively) were set as the release and settlement locations of virtual larvae. One thousand virtual larvae were released from each centroid from January to December for 11 years (2000-2010), and tracked over 30 days, the average Pelagic Larval Duration (PLD) of fishes with a time step iteration of 6 hours (ie ~14 million virtual larvae released across all release) (Luiz et al., 2013; Andrello et al., 2017). The primary output of each simulation represented an estimate of the total amount of larvae transported between each of the 429 locations including local-retention.

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2.4 Connectivity between ABNJ and EEZ and territorial waters

The EEZ is an area beyond and adjacent to a coastal State's territorial sea to a limit of 200 nautical miles from the baseline prescribed by the United Nations Convention on the Law of the Sea (1982). To estimate connectivity between EEZ and the high seas, we released and tracked particles at every grid in both regions. ABNJ area consisted of 16,515 grids, where larvae were released every 6hrs 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 containing 21 EEZ features for the region was obtained from the UNEP-WCMC website (www.unep-wcmc.org) (Fig. 1). One thousand virtual larvae were released and tracked from within each EEZ from January to December between 2000–2010.

2.5 Connectivity indicators

Using connectivity matrix as the input, we defined the connectivity matrix *C* as the matrix formed by the connection probabilities *C(i,j)* (Andrello et al., 2017). We generated a suite of metric of connectivity among the four habitats (ie MPA's, Coral reefs, Sea mounts, and ABNJ-EEZ). *Connection probability* c(*i*,*j*) was the fraction of larvae originating in release point of interest i that ended up in destination point of interest *j* (Andrello et al., 2017). *Connectance* was defined as the fraction of connections with nonzero probability out of the total number of connections (i.e. the number of nonzero elements of *C* divided by the squared size of *C*). *Betweenness Centrality* was calculated by determining the number of times a particular node, in this context, a reef, MPA or a sea mount served as a stepping-stone in the shortest paths between all other pairs of nodes in the network. *Betweenness Centrality* measure can be used to identify important stepping-stones that facilitate connectivity in a network. We also computed *degree* metrics: *In-degree* indicates the number of connections coming into each planning unit, and *out degree*, which indicates the number of connections originating from each planning unit (Minor and Urban, 2008).

2.6 Designing a network of MPA's across maritime jurisdiction

The *Marxan* objective is to minimize the total *cost* of implementing the reserve network plan while ensuring the set conservation objectives are met. As part of the regional wide prioritization process, we begun by defining spatially consistent information on the habitat distributions across the planning domain. Given that we needed prioritize areas within both EEZ and the high seas, we used Marxan with zones in order to differentiate between MPAs within EEZ and within the ABNJ. We did this for two reasons: 1) the types of governance arrangements needed to designate and enforce MPAs are different between these two areas, therefore zoning for them separately allows policy makers useful detail, 2) 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. For conservation features, we used sea floor morphology habitat maps as they are found in varying proportions within and outside EEZ (Supplementary figures 1, 2). We defined three broad conservation goals as follows: (i) to represent geomorphic sea floor habitats by protecting 10% of their current distribution; (ii) to promote the long-term population viability of focal species by maintaining natural connections and connectivity corridors within marine reserves network mediated by larval dispersal, and (iii) to minimize human pressure on ecosystems in the EEZs, while promoting consensus by selecting less fished areas in the high seas. We used *Betweenness Centrality* and *Degree* connectivity metrics to inform selection of important areas for connectivity. We set a 100% target for the connectivity measures to ensure that we designed a connected reserve system that would be self-sustaining. For 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 ABNJ zone, we set the cost as the fishing effort based on automatic vessel identification system for 2016 (Kroodsma et al., 2018). We selected an optimal BLM 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 existing MPAS (Watts et al., 2009).

3. Results

3.1. How connected are WIO MPAs?

Out of 14,280 possible paired connections, 248 connections were found (ie a connectance of 0.02 of the possible 1). When MPAs were connected, the connection probability was always low to moderate (median 0.07, interquartile range 0.29) (Fig. 2b). Connectivity of MPAs along the East African coast was the strongest (0.5-1), amidst the overall weak MPA connectivity in the region. Based on the degree metric of the total number of incoming and outgoing connections (Minor and Urban, 2008), MPAs in Tanzania (Mnazi Bay, Tanga, and Zanzibar) had the highest number of connections, while Madagascar had the lowest. Half of the MPAs in the region are isolated, where 55 MPAs (46%) are not seeded by any other MPA (zero incoming connections) and 62 do not seed any other MPA (50%%) (Fig. 2b). Overall, 38 MPAs (28%) are completely isolated (zero incoming and outgoing connections). Closeness Centrality (how close a particular node is to the other nodes in the network) was overall very low (mean 0.00), reinforcing the finding that WIO MPA's are poorly connected. Betweenness centrality (identifies which MPAs act as gateways to larvae and gene transfer) was highest on the MPA's on the East Africa coast, with Menai bay in Zanzibar, Mombasa, Mnazi Bay-Ruvuma Estuary, Tanga Coelacanth, and Malindi-Watamu among the highest larvae corridor. Density maps of the larval flow indicate high density in Tanzania and Kenya, while in Zanzibar, in addition to self-seeding, MPA's tended to seed Tanzania mainland coast and Kenya (Fig. 2b).

3.2 Coral reef connectivity

Overall, WIO reefs are well connected, with a connectance of 0.05 (2,868 connections out of possible 57,840). However, most of the coral reefs that were connected did not intersect with MPAs, as majority of connection were outside MPAs. WIO reefs network consist of clusters which are densely connected themselves but sparsely connected to other modules, and others strongly connected to other modules (Fig. 1a). 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 (Fig. 2a). A north-south connection is also evident where reefs in Somalia seed the northern bank of Kenya during the reversal of Somali Current. Islands in the Comoros Basin (Comoros, Mayotte, Geyser Bank and Aldabra) and Madagascar act as corridors for potential recruits enroute to the continental East Africa in Mozambique, Tanzania, Kenya, and Somali. Self-recruitment (particles settling within their release location) dominated as illustrated along the diagonal line. Madagascar appears to have the most connected reefs, and primarily seeds Somalia, Kenya, Tanzania, Mozambique, Comoros, Mayotte and Aldabra to the north. At the same time, Madagascar receives less from other reefs except from Mozambican reefs. Reefs in the southeastern WIO (Agalega, Tromelin, St. Brandon, Mauritius and Reunion) are 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. There are two breaks/barriers to dispersal as illustrated in the connectivity matrix, where the first barrier is located north of Mozambique Channel where none or few particles cross into or out of the Mozambique Channel effectively cutting the Channel from the north (Figure 1). The central barrier separates Seychelles archipelago with the southern (Mauritius, Reunion) and western reefs (Madagascar, continental EA), therefore, the isolated reefs depends entirely on recruits from local sources (i.e. self-recruitment). The central barrier may be from South Equitorial Current (SEC) which forks northwards to create a barrier between Seychelles and Madagascar/continental EA, and southwards to create a barrier between Madagascar and SE reefs. Northern Mozambique channel is an important dispersal corridor for corals as it has dense networks (Fig. 1).

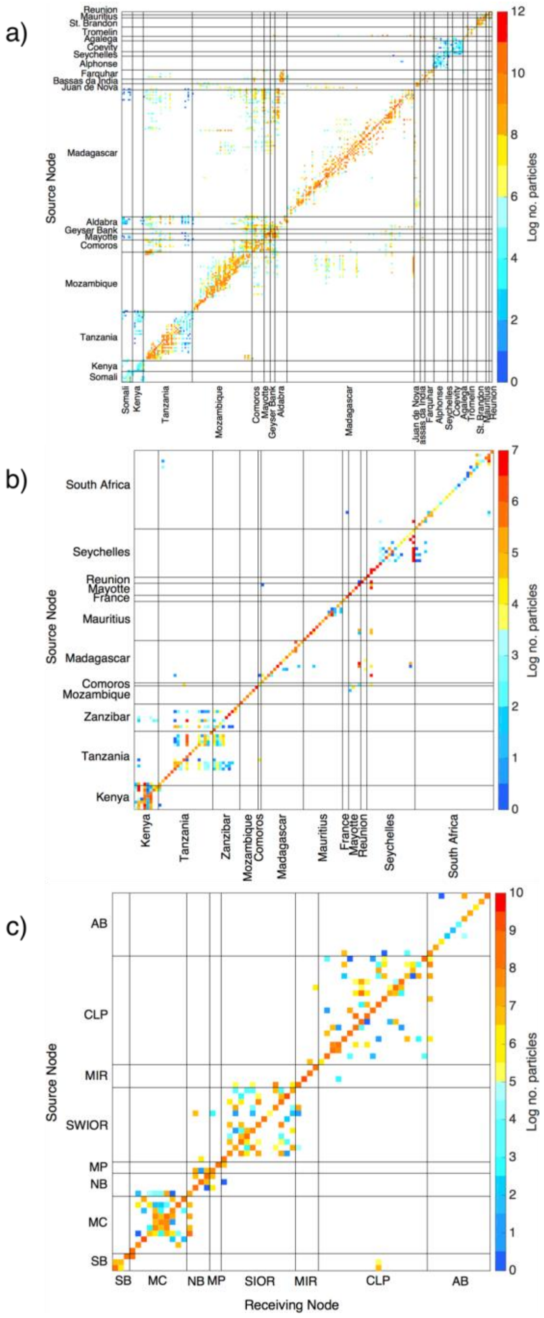a)
Reunion
Mauritius
St. Brandon
Tromelin
Agalega
Coevity
Seychelles
Alphonse
Farquhar
Bassas da India
Juan de Nova
Madagascar
Aldabra
Geyser Bank
Mayotte
Comoros
Mozambique
Tanzania
Kenya
Somali
Source Node
Somali
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Figure 2. Connectivity matrices indicating the exchange of virtual larvae originating from a location *k* to recruit in a settlement location *l* after completion of a 30-day Pelagic Larval Duration (a) illustrates coral reefs, (b) MPA' and (c) sea mounts. Self-seeding (recruits that settled into their origin habitats) follows the diagonal. The connectivity matrices are made of 243, 120 and 67 features of coral reefs, MPAs and sea mounts respectively in the Western Indian Ocean. The scale shows the log number of particles. Seamounts are grouped by Ocean Basins: SB = Somali Basin, MC = Mozambique Channel; MP = Madagascar Platue, NB = Natal Basin, SIOR = Southwest Indian Ocean Ridge, MIR=Mid Indian Ocean Ridge, CLR = Chagos-Lacadive plateau, and AG = Agulhas Bank. 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.

2.4.2 How connected are the sea mounts?

We explored possible preferential routes for larvae exchanges among seamounts to provide a comprehensive analysis of potential connectivity. Although less is known about patterns of connectivity of seamounts, model results show that overall WIO seamounts are moderately well connected, with a connectance of 0.05 (237 connections out of possible 4489). In pairwise comparisons, seamounts within the Mozambique Channel (MC), the South Indian Ocean Ridge (SIOR) and Chagos-Lacadive plateau (CLP) were connected with each other (Figure 2c). Long distance connection was also evident where seamounts within Chagos-Lacadive plateau were connected to those in the Mid-Indian Ridge (Fig. 2c). Similar to shallow populations along coastlines, stepping stone may be appropriate for many deep-sea species particularly those arranged linearly along mid-oceanic ridge or linear array of sea mounts. In contrast, open ocean that separate linear array of seamounts create an effective barrier to dispersal and connectivity decrease creating regionally isolated populations. This scenario is evident in Figure 2c. 15 seamounts were isolated, as they didn't receive larvae form other seamounts and 12 were non-seeding while seven, located off South African coast along the path of the Agulhas current, were completely isolated (Fig. 2c).

2.5 Connectivity between MPA, EEZ, and ABNJ

Madagascar, Mozambique and Seychelles receive most of larvae generated within MPA's, respectively 19, 14 and 15% (Fig. 3a), while relatively fewer larvae settled in Kenya and Tanzania. Somalia, which has no MPA, received larvae (5%) from MPAs from other countries EEZ's. Most of the larvae released from ABNJ settled in Mauritius, Seychelles and Madagascar EEZ, while Somalia and Mozambique received relatively high proportion in comparison to other continental countries (Fig. 3b). Similarly, larvae release from the seamounts in ABNJ settled in Mauritius, Seychelles and Somalia EEZ (Fig. 3c). Overall, 55% of larvae released from ABNJ settled within the EEZ, with majority (10%) settling in Madagascar, 7.3% in Mozambique, 7.20% in Seychelles, 5.45% in South Africa and 4.86% in Reunion (Fig. 4).

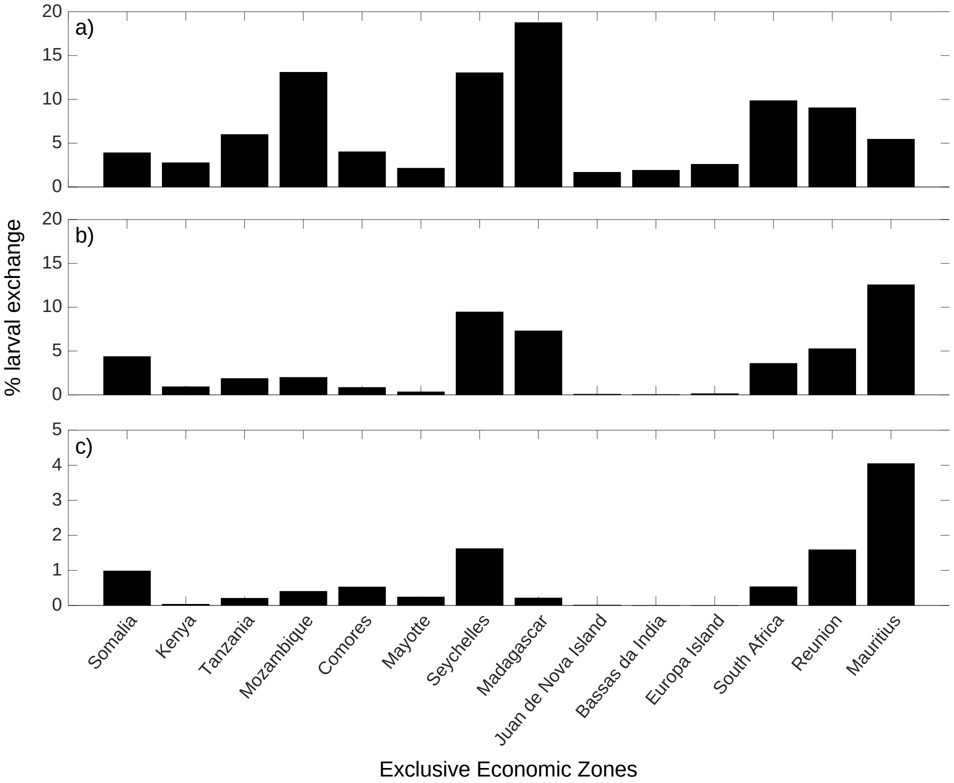

Figure 3. Bar graph indicating (a) proportion of larvae from MPA into EEZ (by country) and (b) proportion of larvae from ABNJ into EEZ and (c) proportion of larvae from Sea mounts into EEZ.

2.6 Priority area selections

The Marxan scenario sought to protect 10% of seafloor geomorphic habitats, while maintaining connections between and among coral reefs, sea mounts and the existing MPA (100% target)**.**
Within the EEZ, a mix of offshore and coastal areas selected include regions around existing MPAs of *Amirantes to Fortune Bank* in Seychelles (Fig. 4). New areas were also selected in Comoros and Gloriosso Islands, in Somali EEZ, offshore eastern Madagascar, Europa, Bassas da India, Mauritius and Reunion. ABNJ 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 at the cist here Marxan these areas were least priority for Marxan (Fig. 4).

Approximately 9.5% of the total area was selected within the EEZ, while 1.8% of the total area was from the ABNJ, significantly lower than overall EEZ selection, but relatively higher than the individual country EEZ selections except Seychelles. Of the EEZ selections, relatively large areas were selected form within Seychelles EEZ (3.2%) (Fig. 5). All other EEZs were <1% of the total area.

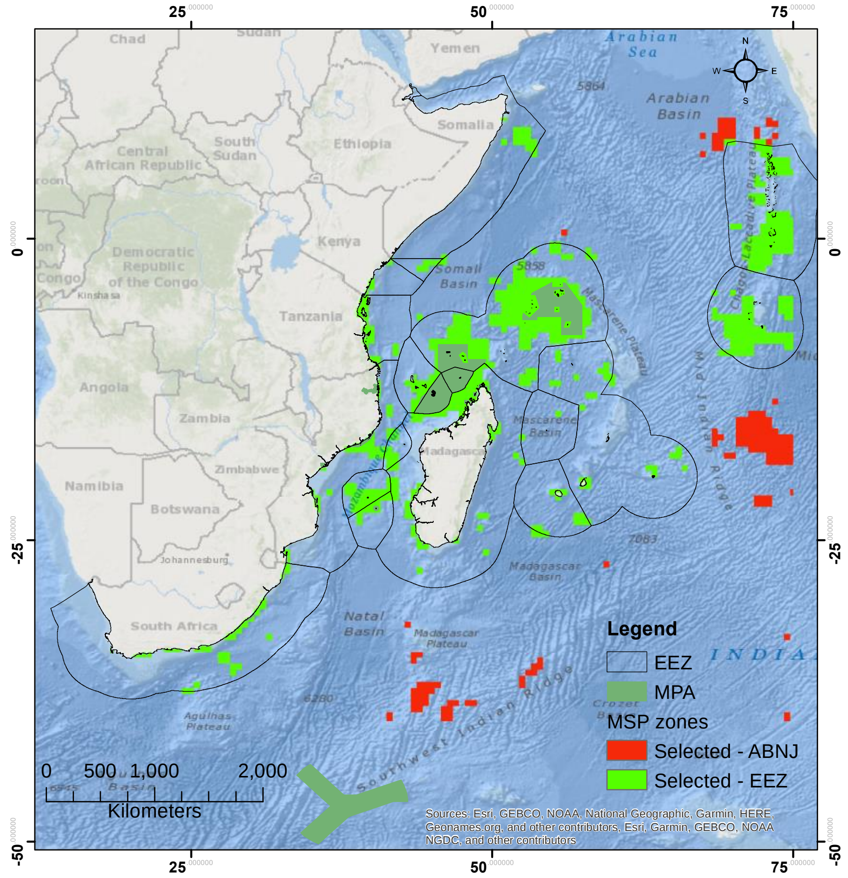

Figure 4. The best solution of priority area selection under the Marxan scenario.

4. Discussion

Ocean connectivity is critical for persistence of marine life, and the vast benefits that accrue from them. Understanding broad scale connectivity is crucial for the management of the oceans, both within and outside areas of national jurisdictions. In this study, we have analyzed regional scale connectivity among key habitats and maritime zones, and among marine protected areas in the

WIO region. As countries globally negotiate the mechanisms for managing the high seas, we present a case study in the WIO to apply functional connectivity to a regional spatial prioritization process across maritime boundaries. Three goals to maximise conservation outcomes guided the identification of areas suitable for inclusion in the MPA network: (i) representative area (10%) of sea floor geomorphic habitats, (ii) protect coral reef and seamounts that enhance and maintain connectivity across maritime jurisdiction, and (iii) reduce human pressure on ecosystems. Objective setting using sea floor geomorphic habitats, which are distributed in both EEZ and the high seas, and using marine functional connectivity, provides an opportunity to prioritise areas of ecological and economical significance for conservation across maritime jurisdictions.

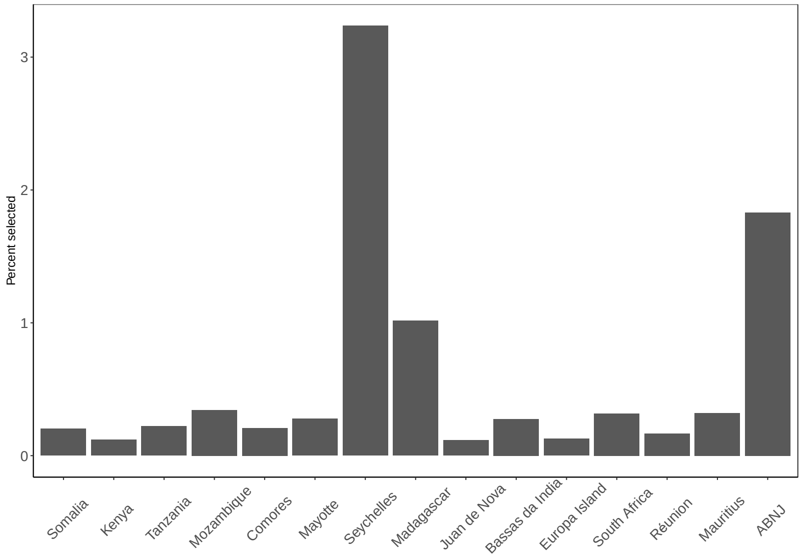

Figure 5. Proportion of area selected for protection within EEZ and ABNJ based on the Marxan scenario.

4.1 Connectivity between ABNJ and EEZ

The maritime boundaries between the exclusive economic zone (EEZ) and the ABNJ does not preclude a strong relationship between the High Seas and coastal states in practice. Many of these relationships have large economical value (Sala et al., 2018). Between 1970 and 2000, industrial marine fisheries catch in ABNJ increased by 10% (Pauly et al., 2002). In spatial terms, the greatest expansion of fishing effort took place primarily beyond the limits of the continental shelf and in ABNJ. With evidence of pelagic species and larvae moving across the ocean from ABNJ into EEZ (Fig. 3b), destruction of habitats in this area impacts on the adjoining EEZ’s. The dispersal model suggests that Island countries of WIO are more connected to the ABNJ than continental countries, with EEZs of Mauritius, Seychelles, Reunion and Madagascar being the destination for most of the larvae emanating from ABNJ. Among the continental countries, more larvae settle within Somalia EEZ than in any other continental country.

4.2 Aligning conservation areas to regional connectivity patterns

The current arrangement of 120 MPA's, majority of which are on the western boundary of the WIO are moderately connected, with connectance high along the East-West direction and following the major ocean currents. Most of the these MPAs were established to protect biodiversity on the biodiversity hotspots in the region, which was underpinned by the high connectivity. 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 MPAs, and do not include the most connected reefs. In effect, highly connected reefs, which could serve as stepping stones, or that could support seeding of other coral reefs, are not protected.

Priority selections were greatly influenced by the opportunity cost data. This is evident in the ABNJ where fewer areas were selected, as one of the Marxan objective was to select locations that are least fished within ABNJ (ie to minimize costs) while meeting connectivity and sea floor habitat targets. While the objective to minimize cost associated with loss of fishing ground may not select the most productive or frequented areas, this scenario is realistic as it promotes consensus by preventing loss of fishing ground which is one of the issues that complicates country negotiations (Smith and Jabour, 2017). However, this may need to be balanced with ecological interests, where for instance thresholds of effort is set such that the algorithm prioritises both extremely fished and least fished.

4.3 Influence of oceanography on connectivity across ecosystems and maritime boundaries

Our results elaborate how oceanic processes play an important role in larval dispersal and connectivity among populations. The westward flowing South Equatorial Current (SEC) carries waters from the Indonesian region across the Indian Ocean between 10–20◦S (Schott et al., 2009) (Fig. 1). This zonal flow creates a physical and functional connectivity barrier to dispersal between Seychelles and Mascarene islands. On east coast of Madagascar, the SEC accelerates past the tip of Madagascar as Northeast Madagascar Current (NEMC) while facilitating larval dispersal from northeast tip of Madagascar into Comoros and further along the East African coast. Instabilities in the current result in formation of the Comoros eddies (Collins et al., 2014). These eddies 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 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 connectivity for coral reefs. This is due to constant northward flow of the East African Coastal Current (EACC). It is also worth noting north to south (Somali to Kenya) connections mostly for reefs found in the northern banks of Kenya. This is because the northern region is seasonally influenced by the reversal of the Somali Current (from northward flowing current in southwest monsoon to southward flowing during northeast monsoon). Therefore, the strength in the amount of north to south connections depends on the strength of the reversing Somali Current. Further south, the northwest coast of Madagascar and Mozambique coast show high level of co the high seas, and spatially explicit considerations for maintaining or restoring habitat diversity and connectivity across maritime jurisdictions.

4.4 Management and policy recommendations

While this work is a preliminary exploration of regional scale connectivity patterns in the WIO, we have demonstrated the potential of using oceanographic modelling to estimate functional connectivity among zones of maritime jurisdictions. Our assessments indicate a well-connected marine areas and habitats, potentially with a significant impact on livelihoods, ecosystems and economies. Maintaining functional connectivity in the WIO, and the well-being of ocean ecosystems across all maritime jurisdiction, including the high seas, as well as their ability to provide ecological functions and essential ecosystem services for human populations, is a challenge because of the current assortment of complex and uncoordinated regulations governing use of coastal and the high seas (Dunn et al., 2014; Houghton, 2014). A sustainable future of marine areas in WIO, hinges on the formulation and implementation of a comprehensive governance framework that moves away from a within country, sector-by-sector management approaches to one that (i) incorporates appropriate ecological, socio-economic and geo-political perspectives across national and maritime boundaries; and (ii) supports management that is coordinated at the scale of ecosystems as well as political and maritime jurisdictions (Haque, 2015). These goals demand increased efforts to facilitate governing the high seas, and spatially explicit considerations for maintaining or restoring habitat diversity and connectivity across maritime jurisdictions. Consequently, regional institutions should explore options on ocean governance and conservation of marine biodiversity in adjacent ABNJ.

Area based tools, including Marine spatial planning as demonstrated here, is clearly a practical for protection of the high seas, where non-spatial monitoring is difficult, and where data gaps obstruct conventional management approaches. In adopting evidence-based approach to protecting the high seas, research on migratory patterns of critical species and biological processes in the high seas should be promoted. A connectivity study with a focus on coastal areas and spatially explicit linkages with ABNJ may help in the formulation of possible decisions on offsetting mechanisms where activities in the high seas are linked to impacts on coastal areas. Furthermore, studies on the feasibility, options and scenarios for the establishment of marine protected areas in ABNJ, in consultation with the countries involved is necessary. This may involve partnerships with the International Maritime Organization and UNCLOS, to facilitate identifying and designating as "particularly sensitive sea marine areas" which are of significance in terms of ecological, social, economic or scientific criteria and are vulnerable to damage by international shipping activities. Implementation of governance in the high seas may have to rely on effective satellite surveillance of fisheries activities on the open ocean. The International Maritime Organization (and Interpol) is already using vessel-monitoring technology to track ship movements and suspicious activity.

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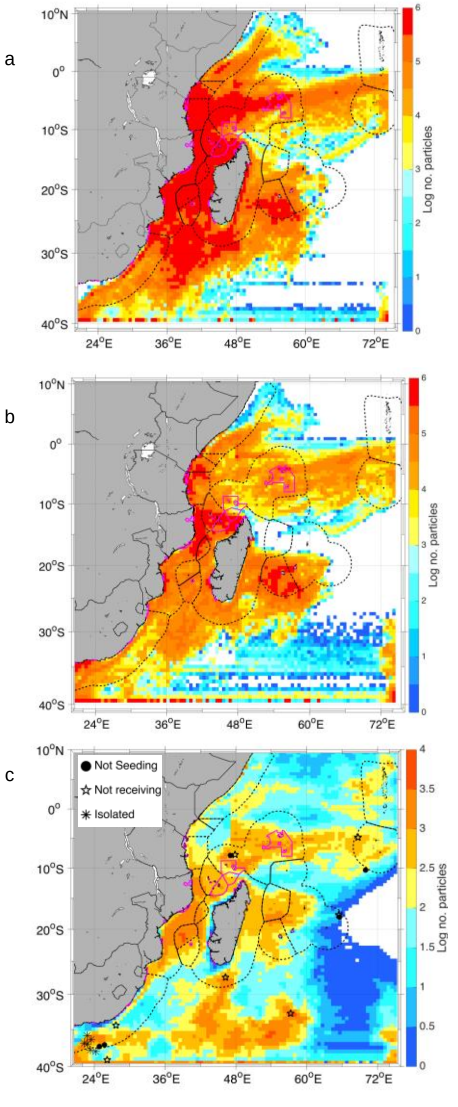
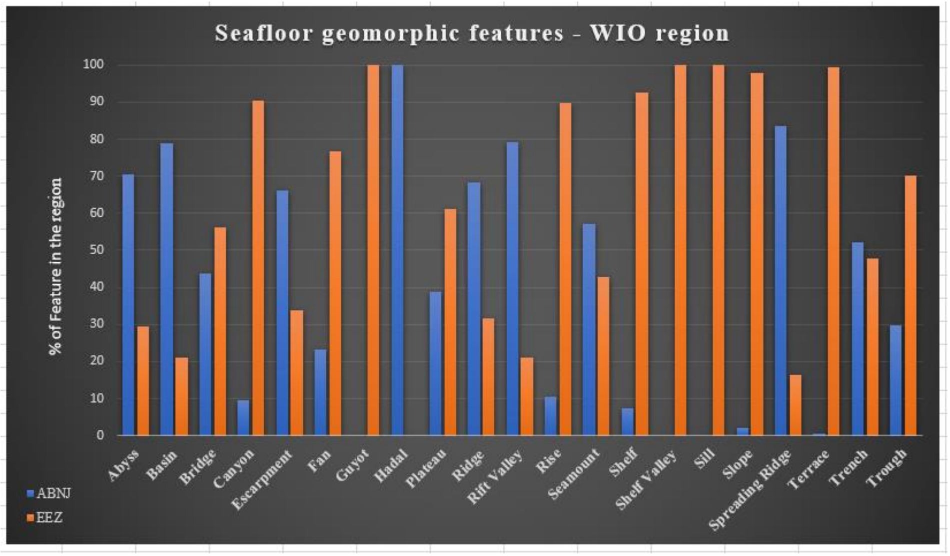
Supplementary information

Fig. 1- Density plots for (a) Coral reefs (b) MPA and (c) sea mounts. 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. Overlaid on the density plots are MPAs and EEZ.



Supplementary Figure 2: Relative proportion of sea floor habitat distribution within EEZ and ABNJ


Seafloor geomorphic features - WIO region
% of Feature in the region
100
90
80
70
60
50
40
30
20
10
0
Abyss
Basin
Bridge
Canyon
Escarpment
Fan
Guyot
Hadal
Plateau
Ridge
Rift Valley
Rise
Seamount
Shelf
Shelf Valley
Sill
Slope
Spreading Ridge
Terrace
Trench
Trough
ABNJ
EEZ