



Evaluating the potential for transboundary management of marine biodiversity in the Western Indian Ocean

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ABSTRACT

The economic and socio-political interactions between countries can have major impacts on transboundary conservation decisions and outcomes. Here, we examined for 14 Western Indian Ocean (WIO) continental and island nations the extent of their marine coral reef species, fisheries and marine protected areas (MPAs), in the context of their geopolitical and socio-economic connections. We also examined the role of external countries and organisations in collaboration within the region. We found large variation between the different countries in their protected area size, and management, which result from different interests in establishing the MPAs, ranging from fisheries management, biodiversity conservation to asserting sovereignty claims. Seventy-four per cent of the 154 MPAs in the region belong to island nations; however, the largest MPAs in the WIO were established by European powers, and include Mayotte and Glorioso Islands (France) and Chagos (UK). While the majority of MPAs are managed by individual countries, between-country collaboration within and outside the region is key if the aim is to achieve effective conservation of ecosystems and species across the island and mainland nations in the region. This may be advanced by creating transboundary MPAs and by regional conservation investment by external powers that benefit from the region's resources.

KEYWORDS

Western Indian Ocean; island nations; cross-boundary conservation; international trade; coral reefs

Introduction

Effective conservation of ecosystems and species with spatial distributions that cross international boundaries often require coordinated plans and actions at both the regional and national scales (Beger et al. 2015; Kark et al. 2015; Sandwith et al. 2001). Coordinated efforts can potentially reduce costs of protecting biodiversity and improve the efficient

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allocation of limited conservation resources (Dallimer & Strange 2015; Kark et al. 2009; Mazor et al. 2013; Pouzols et al. 2014; Punt et al. 2012). When countries have good relations (e.g. economically), collaboration to address shared conservation issues may be easier and for achieving international treaty goals (Levin et al. 2013).

Successful transboundary conservation depends on meeting ecological and biodiversity objectives and enhancing the economic ties and necessary political cooperation and will (Levin et al. 2013; Sale 2015). Building on existing between-country and institutional ties may reduce transaction costs of planning and resource management (Guerrero et al. 2013; Levin et al. 2013). Therefore, coordinated conservation is expected to be most applicable, effective and likely to take place when partners both share biodiversity features, conservation targets and have sound political and economic interactions. A first step towards assessing the potential cost-benefit of regional conservation collaboration is to evaluate the shared biodiversity, administrative structures, and political and trade relations among neighbouring countries. The Western Indian Ocean (WIO) region, which includes five mainland countries and nine island countries and territories, is examined here to evaluate the potential for multi-lateral collaborative conservation of biodiversity in a region that historically has had a weak government and economic ties (Chircop et al. 2010; McClanahan et al. 2011a).

The coral reefs of the WIO region comprise a marine biodiversity hotspot that crosses international boundaries and several distinct ecoregions, such as the Mascarene Islands, which contain high numbers of endemic species (Allen 2008; McClanahan et al. 2011a; Obura 2012; Selig et al. 2014). WIO coral reefs support many people that rely primarily on natural resources, and this results in a range of intense human use and environmental impacts such as unsustainable fishing and sedimentation (Hicks 2011; Maina et al. 2013; Parravicini et al. 2014; UNEP-Nairobi Convention & WIOMSA 2015; van der Elst et al. 2005). Coral reefs are threatened by both oceanic and land-derived factors; thus, landsea connections play an important role in the sustainable use and biodiversity conservation (Klein et al. 2012). Most WIO nations are highly dependent on their fisheries (Allison et al. 2009), with about three million people in the region directly dependent on artisanal fishing for their livelihood (Tobey & Torell 2006; van der Elst et al. 2005). Per capita seafood consumption is much higher in WIO island states than in mainland states (Groeneveld 2015a). Several studies indicate that coral reef health, biodiversity, fish biomass and coral cover are in decline in the region (McClanahan et al. 2011b; Selig et al. 2014). While the region's economic situation often poses constraints on resource management, and economic security needs often receive precedence over biodiversity conservation (Hicks 2011), the high resource dependency and low functional redundancy among fish communities (Cinner et al. 2012a; Parravicini et al. 2014) underscores the need for strategies that increase the capacity of these poor economies to adapt to threats posed by fisheries (McClanahan & Cinner 2012; Worm & Branch 2012). In addition to direct human threats posed to coral reef biodiversity by fisheries, terrestrial land uses (e.g. deforestation) have been shown to clearly impact marine ecosystems (Klein et al. 2012).

Fisheries form an important component of the GDP of many island nations (Gillett & Lightfoot 2001); however, many coral reef fisheries are unsustainable (Newton et al. 2007). Many recent efforts have focused on local fisheries management, which may be important for sustainable fisheries (Cinner et al. 2012b; McClanahan 2012; Rocliffe et al. 2014) but many key species cross international boundaries and regional collaboration will be important for their long-term protection (Berg et al. 2002). Tracked sea turtles, for example, have been shown to migrate in 21 ± 16 days over distances of 1359 ± 832 km from their nesting site to their foraging grounds, going through two to seven exclusive economic zones (Obura 2015), and the tracks of seabirds that cross boundaries have been suggested as a tool for identifying candidate marine protected areas (MPAs) in the WIO (Le Corre et al. 2012). Transboundary MPAs are a mechanism by which such species can be protected efficiently and reduces the conservation burden of each country; but this requires coordination of national and regional conservation activities (Grilo et al. 2012; Guerreiro et al. 2011; Kark et al. 2015). It is within this context that we examined the challenges and opportunities for between-country collaboration among the 14 countries/territories composing the WIO. Between-country collaboration has also been identified as key for enhancing marine conservation in the recent Regional State of the Coast Report of the WIO (UNEP-Nairobi Convention & WIOMSA 2015).

In this framework, we hypothesised that countries/territories with stronger existing political, trade and governance ties would have a greater incentive, opportunity and potential to collaborate (Kark et al. 2015; Levin et al. 2013; Mazor et al. 2013). We also hypothesised that given that the region's countries are relatively weak economically, external powers representing strong countries will have an important role to play in marine conservation efforts. We assess the distribution and overlap of key proxies for biodiversity and sociopolitical linkages among countries/territories, aiming to identify mismatches and priorities for multi-lateral conservation collaboration.

Methods

Study area

The WIO is defined by the SWIOFC as east of longitude 30°E and south of 10°N and includes 14 countries/territories (Figure 1). This includes a large island nation (Madagascar), a range of independent small island nations (Maldives, Seychelles, Mauritius and the Comoros) and four island entities under European sovereignty (The British Indian Ocean Territory, Mayotte, Reunion and the Îles Éparses) (the Scattered Islands, here termed as the French Southern Territories, to which they belong) and five African countries that have a coast on the western boundary of the Indian Ocean (Somalia, Kenya, Tanzania, Mozambique, South Africa). The three island entities belonging to France show large variation in each of their social-economic status, population density and geography. Considering that MPAs often have linked social and ecological dynamics (Pollnac et al. 2010), in our analyses we treated these three French entities independently.

Biodiversity and socio-economic data

To portray the characteristics of the WIO nations and their inter-relationships, we collated a database of biological, socio-economic and political features of all countries in the study area using a range of sources (Table 1). Data collected for each country included: biodiversity (marine fish and coral species range distributions), spatial conservation efforts (existing protected areas: Protected Planet 2017), demography (human population size),

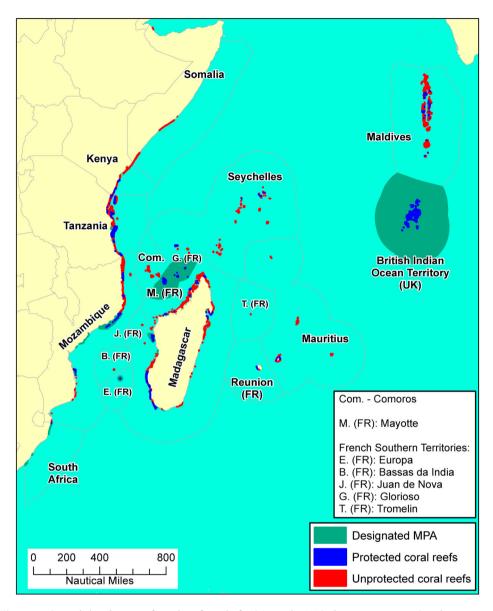


Figure 1. Spatial distribution of coral reefs and of MPAs in the WIO showing countries' exclusive economic zones.

governance (rule of law index: Kaufmann et al. 2011; multi-lateral and bilateral maritime and conservation agreements), economy (gross domestic product [GDP], trade, foreign aid), tourism (coastal tourism being highly important in the region, e.g. accounting for 60-70 per cent of the national tourism industry of Kenya; Odido 1998) and politics (history of conflicts, anti-shipping [piracy] activities) (Table 1).

After compiling these datasets, we calculated the magnitude of interactions among paired countries. These measures were then used as proxies for biodiversity linkages (number of shared fish and coral species between paired countries), trade (combined

Table 1. Datasets used in this study.

Variable group	Variable name	Reference					
Biodiversity and	Species range maps of marine fish	IUCN Red List of Threatened Species 2017					
conservation	Species range maps of corals	IUCN Red List of Threatened Species 2017					
	2010 Global Distribution of Coral Reefs	Ocean Data Viewer 2017					
		IMaRS-USF 2005; IMaRS-USF, IRD 2005;					
		Spalding et al. 2007; UNEP-WCMC et al. 2010					
	World database of protected areas	Protected Planet 2017					
Economic data	Gross domestic product (GDP)	World Bank Open Data 2014					
	Trade between countries	Trade Map 2014					
	Trade data for Reunion	Ministère de l'Economie et des Finances 2014					
	Pelagic fisheries	Indian Ocean Tuna Commission 2014					
	Tourism between countries	UNWTO 2013					
	Domestic and international tourist numbers	Bigano et al. 2007					
	Population size	World Bank Open Data 2014					
Political data	Global Maritime Boundaries Database	GMBD 2014					
	International and regional agreements	Southwest Indian Ocean Fisheries 2014					
	Rule of Law Index	World Bank Open Data 2014					
	(an index which captures perceptions of the extent to which agents have confidence in and abide by the rules of society)	Kaufmann et al. 2011					
	Military conflicts between and within countries	Uppsala Conflict Data Program 2014 Themnér and Wallensten 2013					
	Anti-shipping Activity Messages	Anti-shipping Activity Messages 2014					

Note: For each dataset, either a website or reference are provided.

annual import and export value), tourism (number of tourists) and governance (number of shared agreements). We created symmetric matrices of the values representing these linkages for each pair of countries. We used trade statistics from the Trade Map database covering 220 countries and territories and 5300 products of the Harmonised System (Trade Map 2014), which are based on statistics from the United Nations Commodity Trade Statistics Database (UN Comtrade Database 2017). We constructed matrices between countries for all commodity types as well as for trade only in marine products (including fish, crustaceans, molluscs, aquatic invertebrates; also from Trade Map). Total trade between countries is important as it indicates the strength of their economic ties. We tested the linkages among countries with a correlation analysis using Pearson's correlation coefficient. We also created matrix maps to visualise the level of shared biodiversity and the intensity of existing interactions.

Mapping connections between countries

Following the framework developed in our earlier work for the Mediterranean Sea (Levin et al. 2013), we evaluated the potential prospects for between-country collaboration in conservation based on the biodiversity, socio-economic and political variables collected. We used the exclusive economic zone (EEZ) boundaries to create a layer of Thiessen polygons (Thiessen 1911) representing 'areas of dual influence', using the ALLOCATE algorithm within Idrisi Selva 17.0 GIS software (Clark Labs, USA). Thiessen polygons define individual areas of influence around sets of points, defined by the EEZ boundaries. Using the Thiessen polygon layer of areas of dual influence, we allocated marine areas to the nearest boundary between two adjacent exclusive economic zones. We hypothesised that neighbouring countries sharing an EEZ boundary will collaborate more when they are geographically closer and share similar challenges. At the country level, we hypothesised that countries with more tourism, a higher GDP, a higher rule of law index and high fish exports will have higher incentive to establish MPAs. As these variables are essentially at the single country level, to calculate them for paired countries, we calculated the mean of these variables for each pair of countries (e.g. for GDP, we calculated the mean GDP of each pair of countries).

For pair-wise country connections, we hypothesised that the fundamentals (or indicators) for collaboration in conservation were: (1) shared marine species, (2) bilateral agreements and (3) strong trade relations, such that paired countries with more of these fundamentals were more likely to collaborate. We then ranked each of these indicators for each pair of neighbouring countries (from high to low, giving a rank of 1 for the strongest connection), and calculated a mean rank as a proxy for collaboration potential between the two countries. Ranking was done separately for the biodiversity variables and for the socio-economic-political variables, as there may be misfits between institutional and ecological networks (Treml et al. 2015). To examine the correspondence between those networks, we calculated the correlations between matrices of biological, commercial and political connections among the WIO countries.

Results

Shared coral reef species

Madagascar has the largest coral reef area (3773 km²; Table 2) and the highest coral species richness (348 species), while Mauritius has the highest fish richness (195 species, based on spatial data of the International Union for the Conservation of Nature - IUCN). Due to its high latitude, South Africa had the smallest area of coral reefs (3.2 km²), followed by Reunion (12 km²) (Table 2). Overall, coral reef area (16,000 km²) covered 0.2 per cent of the entire EEZ area in the region. The number of shared species (between paired countries) in the IUCN list for all WIO countries ranged between 78 and 338 for the coral species and between 108 and 185 for the fish species. The per cent of shared species (out of the total number of species) of each pair of WIO countries ranged between 26 per cent and 100 per cent for the coral species and between 52 per cent and 100 per cent for the fish species. South Africa was the least similar country to all others in the number of shared coral species, followed by the Maldives (Figure 2). The countries sharing the highest number of coral species (both in absolute numbers and in per cent shared species) were Madagascar and the French Southern Territories (338, 95 per cent, respectively), and Mayotte and the Comoros (317, 100 per cent, respectively) (Figure 2).

MPAs in the WIO

As of 2017, 154 MPAs have been designated in the WIO, covering a total area of 782,794 km² (9.3 per cent of the total EEZ of the region's countries; Table 2). However, there was considerable spatial variation among the countries in the size, distribution and coverage of their MPAs (Table 2, Figure 1). Of all WIO MPAs, 114 of 154 (74 per

 Table 2. General geographic, demographic, trade and conservation statistics for each of the WIO countries.

ladian Ossan	Area	Pop 2012	GDP 2012	GDP 2012 (per		Exports		Imports from Indian Ocean	Ocean	fish products	Foreign aid	No. of	EEZ area	No. of	Area of MPAs	Area of MPAs (% of	Coral areas
Indian Ocean	(1000 km ²)	(10^6)	(10 ⁹ \$)	capita)	(10 ⁹ \$)	(10 ⁹ \$)	(%)	(% of total)	(% of total)	(% of total)	(% of GDP)	agreements	(1000 km ⁻)	MPAs (1000 km²)	EEZ)	(km ²)
British Indian Ocean Territory	0.1	0.0	N/A	N/A	0.1	0.0	322	0	1	11.0	N/A	40	636	7	637.0	100	1923
The Comoros	1.7	0.7	0.6	831	0.2	0.1	355	14	3	2.1	9.4	27	164	0	0	0	221
French Southerr Territories	n 7.9	-	N/A	N/A	-	_	N/A	0	0		N/A	47	623	2	45.6	7.3	131
Kenya	593.3	43.2	40.7	943	15.1	5.2	291	7	13	1.7	4.9	41	111	9	0.5	0.49	506
Madagascar	590.3	22.3	10.0	447	2.7	1.2	217	10	8	6.0	5.2	36	1191	42	8.8	0.7	3773
Maldives	0.3	0.3	2.2	6567	1.6	0.2	962	0	0	0.0	2.7	23	915	42	0.5	0.05	2696
Mauritius	2.0	1.3	10.5	8120	5.8	2.3	256	9	22	3.4	1.4	41	1270	7	0.04	0.003	716
Mayotte (FR)	0.4	0.2	1.0	4484	0.4	0.0	1281	12	22	63.2	56.8	47	63	3	68.3	100	295
Mozambique	786.0	25.2	14.2	565	6.2	3.5	178	32	20	0.7	14.2	33	566	5	12.7	2.2	2090
Reunion (FR)	2.5	8.0	18.8	22,355	2.3	0.3	843	9	25	32.6	N/A	47	315	1	0.03	0.01	12
Seychelles	0.5	0.1	1.1	12,783	0.7	0.5	141	12	6	25.1	2.6	34	1329	10	0.2	0.02	1572
Somalia	632.7	10.2	5.9	578	1.3	0.2	777	0	0	0.5	13.6	18	665	0	0	0	248
South Africa	1220	52.3	384.3	7352	101.6	86.7	117	2	5	0.5	0.3	45	317	5	1.4	0.45	3
Tanzania	939.8	47.8	28.2	609	11.7	5.5	211	13	25	3.0	9.6	35	240	21	5.5	2.3	2413

Note: Area and number of MPAs includes only designated MPAs within the WDPA database as of 2017.

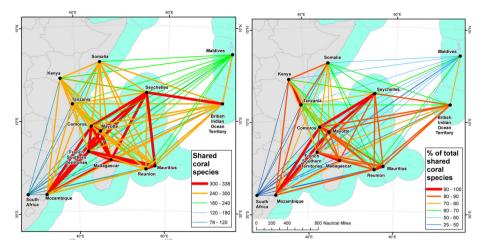


Figure 2. Shared coral species between WIO countries, in absolute numbers (left) and in percentages (right).

Note: Line thickness represents relative number of shared species between two countries. See colour version of this figure at www.tandfonline.com/tiem.

cent) were located within island nations covering 97 per cent of the total area of WIO MPAs. For example, in Mayotte and the British Indian Ocean Territory, the entire territorial waters and exclusive economic zones were designated as MPAs in 2010, whereas in the Glorioso Islands, the entire territorial waters and exclusive economic zones were designated as MPAs in 2012. Conversely, other countries in the region (Somalia and the Comoros) had no designated MPAs. In the remaining countries, the area declared as MPAs ranged between 0.003 per cent of the whole EEZ in Mauritius (40 km²), to 2.3 per cent in Tanzania (5564 km²). However, only a few of the existing MPAs offer notake protection, and in Somalia, Seychelles, Mauritius and Maldives, less than five per cent of their coral reefs were included within designated protected areas.

Trade connections within the region and beyond

In general, bilateral trade among WIO nations and territories was low compared with their international trade with partners outside the region (Figure 3). On average, the share of imports and exports among WIO nations was less than 13 per cent of their total trade. France, China and India were the three most important trade partners, each supplying on average 10 per cent of the imports to the WIO region in total (Figure 3, Table S1). France especially was found to be a key trade partner, receiving on average 11.7 per cent of the total export of WIO countries (Figure 3, Table S2).

South Africa was found to be the WIO's strongest economic power, with a total GDP of \$384 billion (as of 2012), 74 per cent of the total GDP of all the region's countries combined (Table 2; South Africa's GDP per capita was not the highest in the region, see Figure S1). South Africa was also the most important trade partner for most other WIO countries, especially with Mozambique and Tanzania (Figure 3).

WIO countries have strong economic ties with foreign countries and have a negative trade balance with imports for all countries' being greater than exports. The lowest

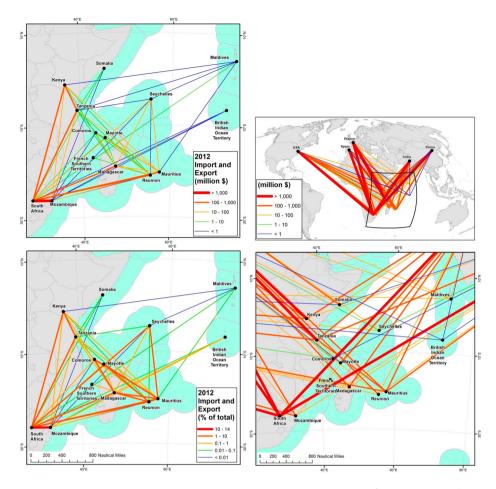


Figure 3. Trade connections (import, export) between (a) WIO countries, in \$ millions (top left) and in percent of total trade (bottom left) (as of 2012), and (b) between WIO countries and selected foreign countries, in \$ millions (as of 2012) (right).

import/export ratio was found in South Africa (117 per cent) and Seychelles (141 per cent) and the greatest import/export ratios were found in Mayotte (1281 per cent) and Maldives (962 per cent) (Figure S2, Table 2). Total foreign aid to WIO countries amounted to 1.9 per cent of their overall GDP. For some countries (e.g. Mayotte, Somalia and Mozambique) a substantial amount of their GDP (10 per cent or more) was from foreign aid (Figure S2, Table 2). Tourism is an important industry in most countries, with an annual average of over 500,000 tourists in each of six of the WIO countries, and over 0.4 tourists per person in the island states of Reunion (0.46), Mauritius (0.55), Seychelles (1.65) and Maldives (1.74) (Figure S2). Economically, income from international tourists is highly important in some of the island countries, being the largest revenue generator in the Maldives (about 80 per cent of the GDP), and a major source of revenue in Mauritius (about 16 per cent of the GDP).

Marine products are a large proportion of the total exports of Mayotte (63 per cent), Reunion (32 per cent) and Seychelles (25 per cent) (Table 2). The greatest fishing fleets



within WIO nations (by ship flag, on average between 2000 and 2013) belonged to the Maldives (241 vessels) and Seychelles (45 vessels). However, most fishing within the WIO (as defined by the IOTC boundaries) was by foreign countries, with only 23 per cent of the total catches by WIO nations themselves.

Geopolitical and environmental relationships among WIO countries

The countries varied widely in their governance levels, ranging from Somalia, where effective central governance is absent, to the highly developed islands belonging to France. We found a positive correlation between the Rule of Law index and the number of international maritime and environmental agreements that countries signed (Figure S3). Most countries were signatories on general environmental treaties (92 per cent on average) and on wildlife/heritage conventions (70 per cent on average); however, only 56 per cent of the countries were signatories on general marine, marine pollution and shipping conventions, 50 per cent were signatories to regional conventions and 48 per cent on average were signatories to global fisheries conventions (Table S3). Somalia and the Maldives have signed the least number of international agreements and had the lowest numbers of shared international maritime and environmental agreements with other WIO countries (Tables 2, S3, Figure S4). There were very few cross-border armed conflicts among WIO nations, apart from cross-border conflicts in Somalia and Kenya. However, armed conflicts within countries' borders were abundant in Somalia and Kenya in the last decade (Figure S4). In addition, there were numerous anti-shipping activities (piracy), located within the EEZs of Somalia, Kenya, Tanzania and Seychelles and in high seas of the northern Indian Ocean (Figure S4). Disputed claims over maritime sovereignty were found between Somalia and Kenya, the Comoros and France (conflict over governance of Mayotte), France, Madagascar and Mauritius (over the French Southern Territories), the United Kingdom and Mauritius (over the Chagos islands) (Figure S4).

Congruence of international connections

The highest correlations between matrices of biological, commercial and political connections among countries (such as those shown in Figures 2-4) were found for numbers of shared fish species and numbers of shared coral species, and between the number of tourists and magnitude of import/export, as well as shared treaties (Figure 5). There was no correlation between the two human proxies: import/export and number of shared trade agreements. Numbers of shared fishes or corals were not correlated with any human socio-political proxies (Figure 5).

Identifying pairs of countries for potential collaboration in conservation

Ranks of dual influences based on the country-level and connection-level statistics using biodiversity and economic-political variables were not correlated (Figures S5, 6). The two mostly highly ranked countries in terms of their shared marine biodiversity and economic-political connections were Reunion and Mauritius (Figures S5, 6). Reunion and Mauritius, Madagascar and France (through its overseas territories), and Seychelles and Mauritius (Figures 6, S5) were among the country pairs with the highest dual influence rankings.

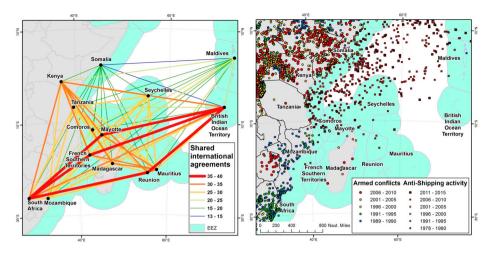


Figure 4. Shared international maritime and environmental agreements between WIO countries (left), armed conflicts within African countries and anti-shipping activities (right). See colour version of this figure at www.tandfonline.com/tjem.

Discussion

While conservation actions are very often planned and undertaken by individual countries independently of their neighbouring countries, cross-boundary collaborations and conflicts can be key in determining conservation outcomes (Kark et al. 2009, 2015; Mazor et al. 2013). This can be the case for both island and continental nations, yet the impact of collaboration on conservation planning and outcomes has not been examined for most areas around the world. Some of Earth's richest marine and coastal biodiversity is found in the WIO nations, especially around their coral reefs and coasts, which provide subsistence living for millions of people (Allison et al. 2009; Tobey & Torell 2006; van der Elst et al. 2005). Here, we identified and quantified for the first time the potential biodiversity, economic and political connectedness that might promote cross-country collaboration in marine resource management in the WIO region. In this region, nine of the countries are islands, ranging from very large ones (e.g. Madagascar) to small island nations and territories. We found the strongest bi-lateral relationships between Reunion and Mauritius, and Seychelles and Mauritius (Figure 6), which likely reflect their shared colonial histories with France and England.

Overall, there were stronger linkages in shared coral reef species between countries, compared to their social, political and economic linkages (Figure 5). Most countries showed stronger social linkages with their former colonial nations but also with emerging regional continental economies, such as India and China. Despite the weak history of socio-economic ties, a decision of the Nairobi Convention Conference of Parties indicated a willingness to establish a regional cohesive system of MPAs. There has, however, been little evidence to indicate specific recent actions (Chircop et al. 2010). Therefore, further socio-economic and political linkages may be required to develop the proposed cross-country management collaborations.

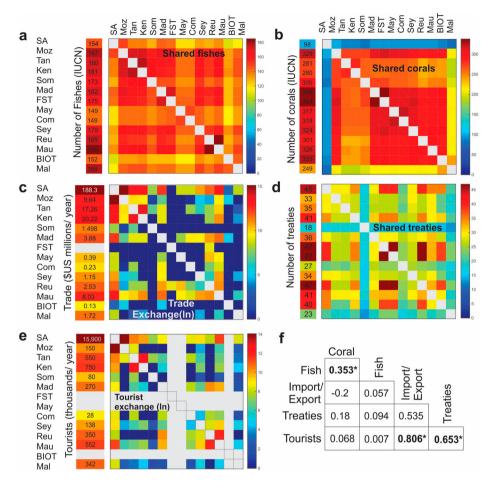


Figure 5. Matrix map of interactions among countries in the WIO: South Africa (SA), Mozambique (Moz), Tanzania (Tan), Kenya (Ken), Somalia (Som), Madagascar (Mad), French Southern Territories (FST), Mayotte (May), the Comoros (Com), Seychelles (Sey), Reunion (Reu), Mauritius (Mau), British Indian Ocean Territories (BIOT) and Maldives (Mal). Depicting interactions of (a) total and shared fish species, (b) total and shared coral species, (c) import and export, (d) total and shared environmental treaties and agreements, and (e) total and shared number of tourists. Pearson's correlation coefficient tests show substantial differences between ecological and socio-political interactions (f).

Status of protected areas

Efforts to increase WIO's coral reef biodiversity conservation increased since the early 1980s, when only 15 coral reef MPAs were in Kenya, Mozambique and Seychelles (Rocliffe et al. 2014; Salm 1983; Wells et al. 2007). Most countries in the region have reached the *Convention on Biological Diversity 1993* target of protecting at least 10 per cent of marine areas for the coral reef habitat. In about half of the countries, 10 per cent of the continental shelf is covered by MPAs and by locally managed marine areas (Rocliffe et al. 2014). However, only three MPAs, one in Madagascar and three in the Seychelles, belong to categories of the highest level of protection (classes Ia ['Strict nature reserve']

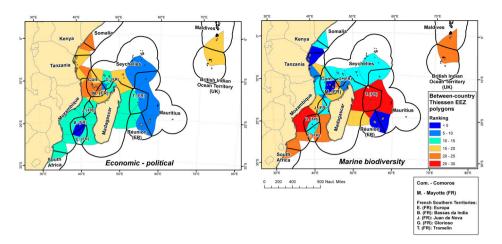


Figure 6. Thiessen polygons dividing the WIO area, based on the nearest exclusive economic zone boundary (shown in thick black lines). The colours of the Thiessen polygon were assigned based on the mean ranking of countries' characteristics. The mean ranking (left) is based on economic and political variables at the country level (tourism, GDP, rule of law, % of fish product exports) and between-country connections (shared international agreements and total trade). The mean ranking (right) is based on shared marine species (fish and corals, in both absolute numbers and percent shared species). EEZ areas adjacent to high seas areas are not included. Low values stand for high ranking (i.e. a value of 1 represents the strongest interaction).

and Ib ['Wilderness area']) of the IUCN classification of protected areas, and only 19 additional MPAs are in IUCN class II ('National Park'). Furthermore, as many as 40 per cent of the MPAs in the region have been classified as having low compliance in terms of their fisheries closures and others as allowing fishing, which reduces the fish resources and conservation value (McClanahan et al. 2015).

Weak governance and high subsistence fishing may explain the lack of MPAs in Somalia and the existence of just two proposed marine parks in the Comoros. In the Maldives, on the other hand, reef fisheries are not heavily exploited because the population largely eats pelagic tuna (McClanahan 2011; McClanahan et al. 2011b), but recent demand by tourist resorts for reef fish indicates an imminent change (Maria Beger, unpublished data). While 42 MPAs have been declared around key diving sites in the Maldives, there is little direct active management (Rajasuriya et al. 2004). In contrast to the large number of small MPAs in the Indian Ocean (<10 km²), two extensive marine reserves were established in 2010 in the Chagos (640,000 km²) and Mayotte (68,000 km²) (Kaplan et al. 2013; Pala 2013), and an additional extensive marine reserve was established in 2012 in the Glorioso Islands (45,000 km²). These new marine reserves are important as countries, extending the management of fisheries into open sea areas, may be better off in taking advantage of the new emerging 'Blue Economy' (Obura 2015). The Maldivian government pledged to make the whole country a UNESCO Biosphere Reserve by 2017 (Shakeela 2013). Similarly, plans for enlarging the protected areas by millions of hectares of land and marine areas have been developed in Madagascar (Allnutt et al. 2012) and in Seychelles (Kelleher 2015).

Two transboundary MPAs have been proposed in East Africa, one for the border area between Mozambique and South Africa (the Lubombo Ponta do Ouro-Kosi Bay Marine and Coastal Transfrontier Conservation and Resource Area, established in 2009 - the first transboundary MPA in Africa) and another between Mozambique and Tanzania (the future Ruvuma-Palma National Reserve; Grilo et al. 2012; Guerreiro et al. 2010). Indeed, as shown in the matrices (Figure 5), the trade and tourism connections between South Africa and Mozambique were higher than between any other pair of countries in the WIO. One of the main drivers for the transboundary MPA, established by these two countries, was to support tourism-driven economic development (Grilo et al. 2012) following the example of the terrestrial Great Limpopo Transfrontier Park (Wolmer 2003).

The potential for regional and international cooperation

While conservation actions are mostly taken at the national or local level, not all countries are equally inclined or able to designate, monitor and effectively manage marine conservation areas. Global conventions, such as the Convention on the Conservation of Migratory Species of Wild Animals 1983, seek to answer conservation challenges that relate to boundary crossing species. However, global guidelines may not meet regional issues and concerns, and it has been suggested by Prideaux (2001) that a regional agreement to protect small cetaceans should be implemented for the Indian Ocean, following successful examples such as the Agreement on the Conservation of Cetaceans of the Black Sea, Mediterranean Sea and Contiguous Atlantic Areas 1996, and regional initiatives enable the sharing of expertise among countries in the region, and improving management effectiveness (Francis et al. 2002). Several existing regional examples can be given in this respect. The region's fishery body is the Southwest Indian Ocean Fisheries Commission (SWIOFC), established in 2004 by the UN Food and Agriculture Organization. The main objective of the SWIOFC is to promote the sustainable utilisation of the living marine resources of the Southwest Indian Ocean region. The Western Indian Ocean Marine Science Association (WIOMSA), which has a membership of conservation professionals across the region, was formed along the regional political and economic setting (i.e. East African Community, and Southern African Development Community and the Small Islands Developing States; Western Indian Ocean Marine Science Association 2017). The UNDP (United Nations Development Programme) led initiative, the Agulhas and Somali Current Large Marine Ecosystems Project (ASCLME) has as its main objective to enhance and to facilitate the governments in the region to implement multi-lateral and bilateral agreements on the conservation of marine biodiversity (Vousden et al. 2008). Additionally, a regional Coral Reef Task Force has been attempting to coordinate reef adaptation programmes at the regional level.

While there are very few cross-boundary management areas, regional bodies have promoted collaboration among research and biodiversity conservation institutions in WIO countries, including supporting multi-country research projects and policy harmonisation, which are some of the prerequisites for joint management actions (Table S4). Broadly, other efforts being led by the IUCN through the East Africa Community (EAC; Guerreiro et al. 2011) have seen the establishment of key institutions such as the Lake Victoria Basin Commission and the Lake Victoria Fisheries Organization for the protection of the Lake Victoria transboundary ecosystem. Similarly, the EAC is currently spearheading a process for the establishment of the first jointly managed MPA along Kenya-Tanzania border. Therefore, a continued support by the international community and conservation organisation is key for the realisation of these existing initiatives.

The economic-political ties among countries were not correlated with biological connectedness. McClanahan et al. (2016) found that regional collaboration can indeed reduce recovery times of fish in the WIO (compared with a no collaboration scenario). However, they also noted that in their modelled collaboration scenario, conservation responsibilities are unevenly distributed among countries, which might undermine collaboration. While the economic and political ties were found to be stronger in the southern part of the study area, species similarity was higher in the northern part of our study area (Figure 5). Whereas biodiversity similarity between countries is driven by the distance between countries as well as by environmental factors (Keil et al. 2012), socio-economic and political ties between countries are often shaped by history and by shared cultural values or economic interests (Matthews et al. 2016). As the designation of MPAs and their effectiveness depend on economic and political factors (such as governance and compliance; Edgar et al. 2014), these seem to be of key importance for determining areas for collaboration in marine conservation. Therefore, collaboration based on biological similarity and socioeconomics can require new political and socio-economic links that are historically weak in this region.

Areas of potential conflict between countries

Conflicts between countries hamper potential collaboration for common conservation goals (Hammill et al. 2016). Conflicts between citizens of neighbouring countries in East Africa are often associated with conflicts between national and migratory fishermen over limited marine resources (Crona & Rosendo 2011; McClanahan et al. 2013b; van der Elst et al. 2005; WIOMSA 2011). Armed conflicts are likely to have negative impacts on protected areas (Dudley et al. 2002; Hanson et al. 2009) due to the lack of rule of law during active conflicts. However, conflicting maritime boundary claims may sometimes have the opposite effect when countries chose to exercise their sovereignty (e.g. by designating an MPA in a contested area). Nonetheless, there have been relatively few armed conflicts between countries over marine resources in the Indian Ocean and such conflicts are not likely to be inhibiting regional collaboration (McDorman 1988). Conflicts over sovereignty and fishing rights of the Chagos Archipelago have continued between the British colony and Mauritius, and the establishment of the US Military base make this a strategic location (Dunne et al. 2014; Gifford & Dunne 2014). Mauritius claims the Chagos Archipelago and conflicts over fishing and the original inhabitants' rights continue with the no-take maritime reserve establishment (De Santo et al. 2011; Koldewey et al. 2010).

Mayotte's recent designation of a large marine reserve bares some similarities to the Chagos. Mayotte voted to separate from the Comoros Archipelago and remain under French sovereignty (Saint-Mézard 2013). While the Comoros and Mayotte share considerable amounts of marine biodiversity, their economic and conservation status are different due to different international socio-economic associations. The Comoros have stronger ties with Middle Eastern countries and do not recognise French sovereignty over

Mayotte (Yoon 2009). French designation of the entire EEZ of Mayotte as an MPA in 2010 was suggested to be a strategy of France to assert more control over the area. Consequently, large designated protected areas in this region have political incentives and repercussions that are expected to influence regional biodiversity collaborations.

Within the scattered islands of the French Southern Territories (where French sovereignty is challenged by neighbouring countries), France and Mauritius have agreed on the common management of the high sea fisheries and environmental protection at Tromelin Island in 2010 (Bouchard & Crumplin 2011). This agreement partly corresponds with our predicted ranking, in which France and Mauritius were highly ranked for their likelihood in collaborating in conservation. In addition, fishing was prohibited in December 2010 in the territorial sea of Bassas da India, Europa Island, Juan de Nova Island and the Glorioso Islands (making them all de-facto reserves, given their isolation and lack of permanent human populations). Europa Island is also being planned for marine park status (Bouchard & Crumplin 2011), and is also the focus of terrestrial conservation together with Glorioso Islands whose EEZ was designated as an MPA in 2012 (Russell & Le Corre 2009; Russell et al. 2016).

Comparison with other regions

Regional Seas Programs have been established by UNEP (United Nations Environment Programme) (from 1974) to manage the seas as shared resources, and at present, almost 150 states across 18 regions participate in them (Rochette et al. 2015). Political and ecological regions outside the WIO show similar political complexities, where multiple countries, which are highly diverse socio-economically, share marine space and species. For example, the Mediterranean Sea has high diversity, is shared by 20 countries, and is subject to multiple anthropogenic threats (Coll et al. 2012). While both the Mediterranean Sea and the WIO incorporate many countries of varying economic power and political organisation, there are significant differences between the two regions. The GDP per capita of six of the WIO nations is lower than \$1000, whereas in the Mediterranean Basin, no country has a GDP per capita lower than \$2000 (Levin et al. 2013). Correspondingly, trade and commerce within the Mediterranean Sea are strong, whereas in the WIO the volume of trade among the region's countries is small, and there is a greater reliance on foreign capital.

The Pacific Islands area is an example of a region where the full implementation of conservation and management agreements is constrained by limited financial and technical resources (Wright et al. 2006). Precedents of international collaboration for the conservation of natural resources exist and represent powerful initiatives that have improved regional conservation outcomes and awareness. For example, the Micronesia Challenge (2017) is a union of Micronesian countries working towards the sustainable management and effective conservation of marine and terrestrial areas (Goldberg et al. 2008), driven by each country within the regional goals of effectively managing 30 per cent of their marine and 20 per cent of the terrestrial estate (Baker et al. 2011). The Coral Triangle Initiative (CTI; 2017) for Coral Reefs, Fisheries and Food Security (shared by six countries: Indonesia, Malaysia, Papua New Guinea, Philippines, Solomon Islands and Timor Leste) aims to co-ordinate efforts on the conservation and sustainable use of coral reef ecosystems and resources (Beger et al. 2015; Walton et al. 2014). The CTI has developed specific regional



goals to achieve their vision of improved coral reef biodiversity, sustainable fisheries and food security, and regional priority areas can provide guidance for nations and provinces to integrate national needs with a regional goal (Beger et al. 2015).

The role of foreign aid in collaborative conservation

MPAs in least-developed countries require local to national taxes (on fisheries and tourism) as well as serial donor support (McClanahan 1999). Further, reports indicate that increased management effectiveness in Kenya, Tanzania and Mozambique is paralleled by major donor investments (Wells et al. 2007). Large-scale fisheries in the Indian Ocean is an area of concern for the international community (Worm & Branch 2012). Considering that large-scale fisheries of Europe and North America are fully or overly developed, these countries have become more dependent on developing countries for wild-caught fish. Fishing effort has recently shifted towards developing nations in the South, including Africa (McClanahan & Cinner 2012; Worm et al. 2009). Indeed, the total catch (reported landings) has significantly increased in the south WIO between 1985 and 2012, with an increase in large pelagic fish landings in Seychelles after 1997, due to the development of its fishing port as a centre for the international tuna industry (Groeneveld 2015b). Therefore, developed countries ought to support the formation of MPAs, promote sustainable fisheries and food security in the WIO (McClanahan et al. 2013a).

The World Bank's Global Environmental Facility (GEF) is one of the largest public funders of environmental projects globally, and has also funded transfrontier conservation areas in southern Africa (Duffy 2006). Within the WIO, funding of marine environmental projects is given by the GEF to 20 national projects at a total budget of \$78 million (with co-financing of \$387 million; Table S4), and to 32 regional projects (including the ASCLME, for example) at a total budget of \$269 million (with co-financing of \$1481 million; Table S5) (Global Environmental Facility 2017) (Table S5). This funding by the GEF (and there are many non-GEF projects as well, such as WIOMSA) demonstrates a funding bias towards regional projects, thus favouring between-country collaboration.

Because of France's colonial history in the region, its administrated areas in the WIO (Reunion, Mayotte and the scattered islands of the French Southern Territories) combined to cover 15 per cent of the total EEZ areas (and 32 per cent of the area of the EEZ areas of dual influence) and 79 per cent of all MPAs in the region (when excluding the British Indian Ocean Territories), as well as through its dominant place in trade and tourism (more than 800,000 French tourists a year), France could play a key role in advancing marine conservation in the WIO. Given the colonial past and economic ties, low levels of multi-national international governance bilateral agreements and transboundary MPAs are more likely to be the next modest step in collaboration (Guerreiro et al. 2011). Without local and stakeholder involvement, these transboundary agreements may be viewed as overly centralised and fail to benefit local resource users and garner their support (McClanahan & Abunge 2016; Yates & Schoeman 2015). Consequently, there is a need to create local involvement and incentives to collaborate with international planning to avoid many of the previous donor-driven conflicts and failures (Duffy 2006; Kamat 2014; Western 2003).



Conclusion

The WIO has several characteristics and challenges that make it unique and a global priority for conservation and sustainable management (Allen 2008; McClanahan & Cinner 2012; Parravicini et al. 2014; Worm & Branch 2012). This may be achieved by expanding the MPAs through international collaboration, but these plans need to be considered in the context of the challenges related to environmental change, subsistence economies, poor fisheries-dependent coastal populations and the international composition of the pelagic fisheries industry. Collaboration is expected to involve foreign stakeholders and to recognise the socio-economic and political factors that have created and sustained the current economies. Nevertheless, poor integration of socio-economic and political groups within and among countries is expected to continue producing low compliance with proposed MPA rules and regulations, which frequently arise from top-down planning in poor countries. Avoiding this disconnect requires a good understanding of the social-ecological context and creating context-appropriate management systems. We suggest that future work should examine in more detail the role of cross-boundary collaboration among countries and across districts, organisation and regions and the role of land-sea connectivity, as well as socio-economic, political connections in marine and coastal conservation for both island and mainland regions.

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