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A model-based assessment of reef larvae dispersal in the Western Indian Ocean reveals regional connectivity patterns — Potential implications for conservation policies

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ABSTRACT

Marine resources are under increasing pressure from a wide variety of threats such as overfishing, offshore energy development, and climate change. As marine ecosystems degrade, so do the well-being and livelihoods of humans that depend directly on the ecosystem goods and services they provide. Marine protected areas have been proposed to protect biodiversity, restore damaged ecosystems, sustain fisheries, and rebuild overexploited stocks. The effectiveness of marine protected areas depends in part on their effectiveness as connected networks, linked over large areas by ecological processes such as larval dispersal. Here, we applied a biophysical model driven by ocean currents derived from satellite altimetry to evaluate connectivity between Western Indian Ocean reefs. We applied graph-theoretic analysis, including clustering and a betweenness centrality metric. Our results show high interconnectivity within several regions (Mozambique Channel, Mascarene archipelago) and lower connectivity across the WIO region. We compared the results with the current MPA network, and proposed sites/reefs that should be considered priority sites for MPA implementation: Pebane, Cosmoledo, Majunga, Masoarivo, Platte Island, Farquhar, Agalega and Geyser bank. Our results are timely, considering the oil and gas exploration that is ongoing in the region. We discuss implications for transboundary marine policies and regional cooperation in the Western Indian Ocean, and advocate the creation of a regional-scale organization to structure interactions among the different actors.

1. Introduction

The world's coastal resources are being fundamentally altered by the combined effects of climate change, overfishing, pollution, and disease (Hughes et al., 2003; Hoegh-Guldberg et al., 2007; Srinivasan et al., 2012). Nineteen percent of the global extent of coral reefs has already been lost, with a further 35% under threat of loss within the next 20–40 years (Wilkinson, 2008). This will have significant impacts on the well-being and livelihoods of over 500 million people worldwide who depend directly on the ecosystem goods and services they provide (Moberg and Folke, 1999). Managing these ecosystems and associated resources effectively is crucial, from both social and ecological perspectives. This paper focuses on the assessment of coral reef connectivity patterns at broad scale (100–1000 km) and on using this information to improve marine protected areas (MPA) management and design in the broader framework of marine spatial planning (MSP).

The importance of an integrated ecosystem approach to the management of the ocean has been recognized (Lester et al., 2009; Foley et al., 2010), and environmental tools such as MPAs

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are a cornerstone of conservation strategy. MPAs have been implemented to conserve or restore species, fisheries, habitats, ecosystems, and ecological functions (NRC, 2001; Russ et al., 2004; Mouillot et al., 2008; Guidetti et al., 2008; Lester et al., 2009; Pujolar et al., 2013; Bennett and Dearden, 2014; Costello, 2014; Rossiter and Levine, 2014). They have a potential positive impact on poverty alleviation (Gjertsen, 2005) and could contribute to climate change mitigation and adaptation (McLeod et al., 2008). The Convention on Biological Diversity (CBD), through the Aichi Target 11, has committed countries to establish an "effectively and equitably managed, ecologically representative and well-connected systems of protected areas" covering 10% of the global ocean area in 2020 (COP10: www.cbd.int/cop10; Toropova et al., 2010). Although MPAs are expanding rapidly (Gray, unpublished), they currently cover only about 2.3% of the world's oceans (Spalding et al., 2013).

The effectiveness of MPAs depends in part on the maintenance of demographic and genetic connections through processes such as the dispersal of larvae, to support population replenishment, persistence, and gene flow within protected areas, between protected areas, and with adjacent habitats (García-Charton et al., 2008; Botsford et al., 2009). Many recent studies investigate how networks of MPAs can be designed to better protect and secure natural patterns of connectivity (Lubchenco et al., 2003; Cowen et al., 2007; Jones et al., 2007; Almany et al., 2009; Jones et al., 2009; McCook et al., 2009). Conservation organizations also recognized the importance of incorporating spatially-explicit connectivity knowledge into MPA design (Salm and Coles, 2001; Laffoley, 2008; Conservation International, 2009; Roberts et al., 2010a; Green et al., 2014). Determining whether protected areas are ecologically connected as a network, as well as where new MPAs should be established to promote network functions, requires information on the connectivity of biological populations across large areas (Fenberg et al., 2012).

Larval dispersal is an important process connecting marine populations but assessing the larval connectivity between distant populations is very challenging, and must consider both the physical processes of hydrodynamic transport (horizontally and vertically) and the biological traits of larvae. Many marine species have a bipartite life cycle and experience pelagic larval stage of certain duration, the pelagic larval duration (PLD), which may last from days to months. During development, larvae may acquire swimming and sensory capabilities that enable them to control aspects of their dispersal (Leis, 2002; Kingsford et al., 2002). Larval dispersal is notoriously difficult to study empirically due to the small size of larvae and long dispersal distances of up to hundreds of kilometers (Leis, 1984; Victor, 1987), and the dynamics of dispersal may vary greatly among species. By and large, these patterns remain a critical gap in the scientific knowledge required for the effective management of marine systems (Sale et al., 2005; Cowen and Sponaugle, 2009; Foley et al., 2010; Wilson et al., 2010).

A variety of approaches (genetics, microchemical fingerprinting, stable isotopes, otolith chemistry and otolith shape analysis) have been developed to assess patterns of larval dispersal and fish population connectivity in the marine environment. However many techniques have limited spatial and temporal coverage. Spatially-explicit numerical transport models have then been developed to infer pattern of larval dispersal (Schultz and Cowen, 1994; Roberts, 1997; Cowen et al., 2000; Treml et al., 2008; Mora et al., 2012) and are increasingly being used worldwide for the design of MPAs (Planes et al., 2009) and fisheries management (Gaines et al., 2010).

This paper outlines a model-based assessment of connectivity patterns between reef ecosystems of the Southwestern Indian Ocean (WIO). To infer these patterns, we use a hydrodynamic connectivity model (Treml et al., 2008) parameterized with altimetric data (2006–2010) and a gradient in pelagic larval duration implemented in the Marine Geospatial Ecology Tools software (Roberts et al., 2010b). In a second step, a set of connectivity matrix are derived and summarized over time. The properties of the resulting connectivity network are measured using cluster analysis and a centrality index. Focusing on the implications of the connectivity analysis for marine spatial planning, we compared the connectivity matrix with the current location of MPAs and identified key sites required to fill in notable gaps in the MPA constellation. Finally, we discuss implications for transboundary marine policies and regional cooperation in the Southwestern Indian Ocean.

2. Methods

2.1. Study area

The study area (Western Indian Ocean) lies between 2°N and 35°S and 25–70°E (Fig. 1). The climate of this region is tropical. Coastal and island coral reefs cover 45 425 km^2. The study area (Southwestern Indian Ocean) lies between 2°N and 35°S and 25–70°E (Fig. 1) and includes coastal and island reefs. Note that the method used (see below) treats the mainland fringing reef from northern Mozambique to Somalia as a single 'reef' so connectivity along this coastline and of different locations on this coastline to the other selected sites is not analyzed.

The South Equatorial Current flows east-to-west between 4°N and 20°S (Fig. 2), splitting north and south when it reaches Madagascar (Tomczak and Godfrey, 2003; Chapman et al., 2003). The southern flow, the East Madagascar Current, flows south along Madagascar's east coast and meets the Agulhas Current. The northern flow diverges again adjacent to the Comoros, with part of it flowing into the Mozambique Channel in a series of dynamic cyclonic and anticyclonic eddies that have a net southwards flow, and a part of it flowing north as the East African Coastal Current, and meeting the Somali Current at about 2°S.

During the northeast monsoon season (November–May), cyclones occur episodically, with variable trajectories but generally following a southwesterly direction (Ginis, 2002). They cause significant perturbations in marine ecosystems at varying spatial and temporal scales, occasionally affecting coral reef structure and communities (Harmelin-Vivien, 1994; Gardner et al., 2005).

The region covers about 40 degrees of latitude and hosts a high level of marine biodiversity (Tessema and Salm, 1998; Obura et al., 2004; WWF, 2004a,b). It is home to at least 350 species of coral (Obura, 2012), 11 species of mangrove, and 12 species of seagrass, together with 1500 species of fish, 3000 species of molluscs, 450 species of crabs, 300 species of echinoderm and five of the world's seven marine turtle species (WWF, 2004a,b; Guerreiro et al., 2010). However, despite the substantial value of its environmental assets, the WIO faces significant resource management and environmental challenges (Moffat et al., 1998). Four overarching threats to marine biodiversity have been identified: overexploitation of natural resources, habitat degradation, land-based sources of pollution, and marine pollution (WWF, 2004a,c,d; Borja et al., 2008; Billé and Rochette, 2010).

The first MPAs in the WIO were implemented in 1965 in Mozambique (IUCN, 2000). Madagascar and Kenya followed within three years (UNEP-WCMC, 2010). Early MPAs tended to be small ($<$10 km^2) and designed to protect a specific habitat. By the 1990s, the emphasis had shifted to larger, multiple-use sites, based on more participatory forms of management (Rocliffe et al., 2014). Today, all WIO countries host MPAs except Somalia where conservation is difficult to set up (IUCN, 2000; Barrow et al., 2007). Seventy five MPAs have been declared in the region with a total coverage of 183 975 km^2, but still covering less than 10% of the continental shelf in the region (Rocliffe et al., 2014). Sixty six