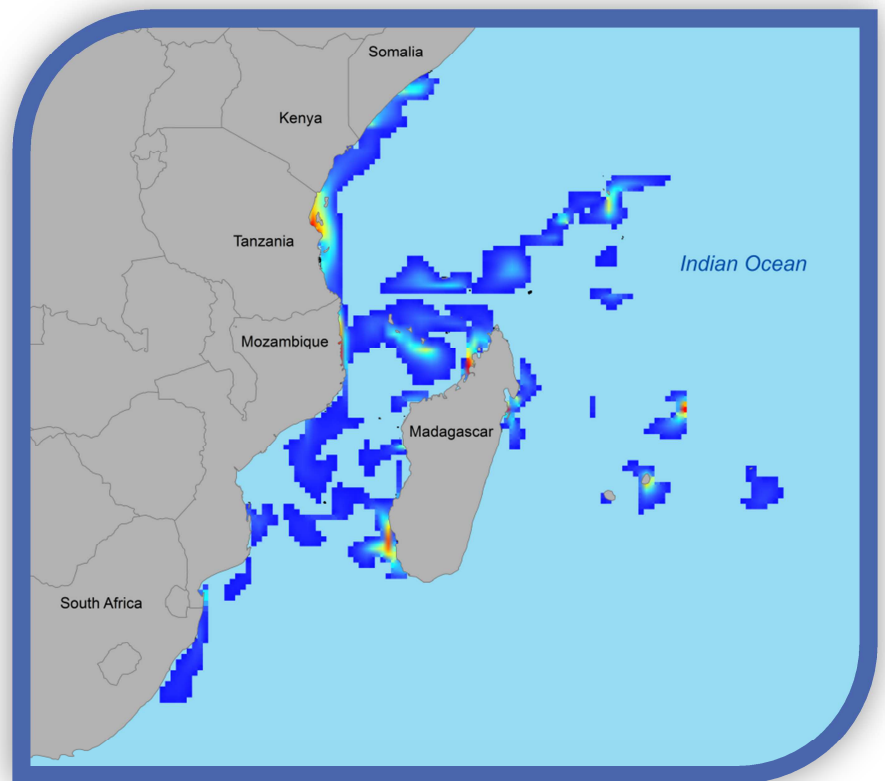# Fish larvae dispersal in the Western Indian Ocean and implications for marine spatial planning

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Contents

ASCLME project, general background

The Agulhas and Somali Current Large Marine Ecosystems (ASCLME) Project is part of a multi-project, multi-agency Programme (The Programme for the Agulhas and Somali Current Large Marine Ecosystems) to institutionalize cooperative and adaptive management of these LMEs. It is funded by the Global Environment Facility (GEF) and implemented by the United Nations Development Programme (UNDP) with the United Nations Office for Project Services (UNOPS) serving as the executing agency. A phased approach is planned that progressively builds the knowledge base and strengthens technical and management capabilities at the regional scale to address transboundary environmental concerns within the LMEs, builds political will to undertake threat abatement activities and leverages finances proportionate to management needs. In addition to the ASCLME Project, the Programme includes two parallel projects, one that addresses land-based sources of pollution (WIO-LaB, implemented by UNEP); and one that builds knowledge for the purposes of managing industrial fisheries (SWIOFP, implemented by the World Bank).

The activities within the ASCLME Project are focused on filling the significant coastal and offshore data and information gaps for these LMEs by capturing essential information relating to the dynamic ocean-atmosphere interface and other interactions that define the LMEs, along with critical data on artisanal fisheries, larval transport and nursery areas along the coast. The overall objective of this data capture will be to deliver national Marine Ecosystem Diagnostic Analyses (MEDAs) that feed into two Transboundary Diagnostic Analyses (TDAs), and two Strategic Action Programmes (SAPs), one for the Agulhas Current LME, and the other for southern part of the Somali Current LME (Kenya and Tanzania). The latter can be expanded when governance within the northern portion of the Somali LME, areas in Somalia, becomes more stable. The parallel UNEP and World Bank Projects will also feed pertinent information into the TDAs/SAPs formulation process, and identify policy, legal and institutional reforms and needed investments to address transboundary priorities. Collectively, the projects build foundational capacities at regional scale for management of the LMEs. Provision is made through the UNDP ASCLME Project for overall ASCLME Programme coordination.

The Programme Coordination Unit (PCU) is located in Grahamstown, South Africa and will provide a coordination and management structure for implementation of the UNDP-GEF Project in accordance with the rules and procedures of UNDP as executed through the United Nations Office for Project Services (UNOPS), under the day-to-day direction of the Project Manager, and based on the general guidance provided by the Project Steering Committee (PSC).

Introduction

Many marine reef fish species have two distinct life stages: a larval pelagic stage lasting a few weeks followed by a benthic stage after recruitment (Dufour, 1992; Shima, 2001; McCormick et al., 2002; Lecchini & Galzin, 2003; Irisson et al., 2004). Larvae dispersal is a vital process for species evolution, genetic mixing and overall adaptation of reef fish populations (Caley et al., 1996; Shulman, 1998; Planes, 2002). Integrating ecological connectivity patterns into marine ecosystem management is important (Roberts, 1997; Mora & Sale, 2002) especially in a global context of severe fish stocks depletion (Jackson et al., 2001) and growing degradation of coral reefs (Wilkinson, 2004) due to the combined impacts of human activities and climate change (Roberts, 2002; Hughes et al., 2003). Indeed, if a fish population is replenished by its own recruits (i.e. self recruitment), the population should be managed locally to maintain the genetic pool. This assumption of self-recruitment is dominant in the literature (Jones et al., 1999; Bay, 2000; Cowen et al., 2000; Fowler et al., 2000; Kingsford, 2000; Ochavillo et al., 2000; Jones et al., 2005; Almany et al., 2007). However if there is substantial exchange between geographically distinct populations, those species should be managed at a broader scale (Botsford et al., 2003), for instance through larger single marine protected areas (MPAs) (Claudet et al., 2008) or spatial reserve networks (Lockwood, 2002).

Ocean currents are the most influential parameter of larvae movement during the pelagic stage (Masterson et al., 1997) even if larvae have swimming and sensory capabilities that enable them to control part of their dispersal (Sale & Cowen, 1998; Kingsford et al., 2002; Leis, 2002). Determining larvae dispersal patterns based on in situ observation has always been a major challenge due to the small size of larvae and long dispersal distances (up to hundreds of kilometers from their initial release site, Leis, 1984; Victor, 1987; Clarke, 1995). In response, a variety of approaches have been developed to assess patterns of larvae dispersal and fish population connectivity across the marine environment, including genetics (Shulman, 1998; Planes, 2002), tagging (Jones et al., 1999; Swearer et al., 1999), stable isotopes (Peterson et al., 1985; Schwarcz et al., 1998; Blamart et al., 2002), otolith chemistry (Fowler et al., 1995; Campana et al., 1997) and otolith shape analysis (Smith, 1992; Torres et al., 2000; Pothin et al., 2006). Given the limited feasibility of the abovementioned methods across large regions, numerical transport models have been developed to infer pattern of larval dispersal (Schultz & Cowen, 1994; Roberts, 1997; Cowen et al., 2000; Treml et al., 2008; Mora et al., 2011). These models are increasingly being used worldwide for the design of MPAs (Planes et al., 2009), fisheries management (Gaines et al., 2010) and disaster management (e.g. oil spills, tsunamis, cyclones, Allison et al., 2003).

In this study we model connectivity patterns inferred between reef ecosystems of the Western Indian Ocean (WIO) using a hydrodynamic connectivity model (Treml et al., 2008) implemented in the Marine Geospatial Ecology Tools - MGET software - (Roberts et al., 2010). The fish dispersal model integrates historical altimetry data and pelagic larval duration (PLD). After

presenting the study area, data and results, we further discuss model improvements and implications of this connectivity analysis in term of marine spatial management.

Materials and Methods

Study Area

The study area (Western Indian Ocean) lays between latitudes 2° North and 35° South and longitudes 25° and 70° East. It includes coastal and island reefs, coded as below (Figure 1, Table 1).
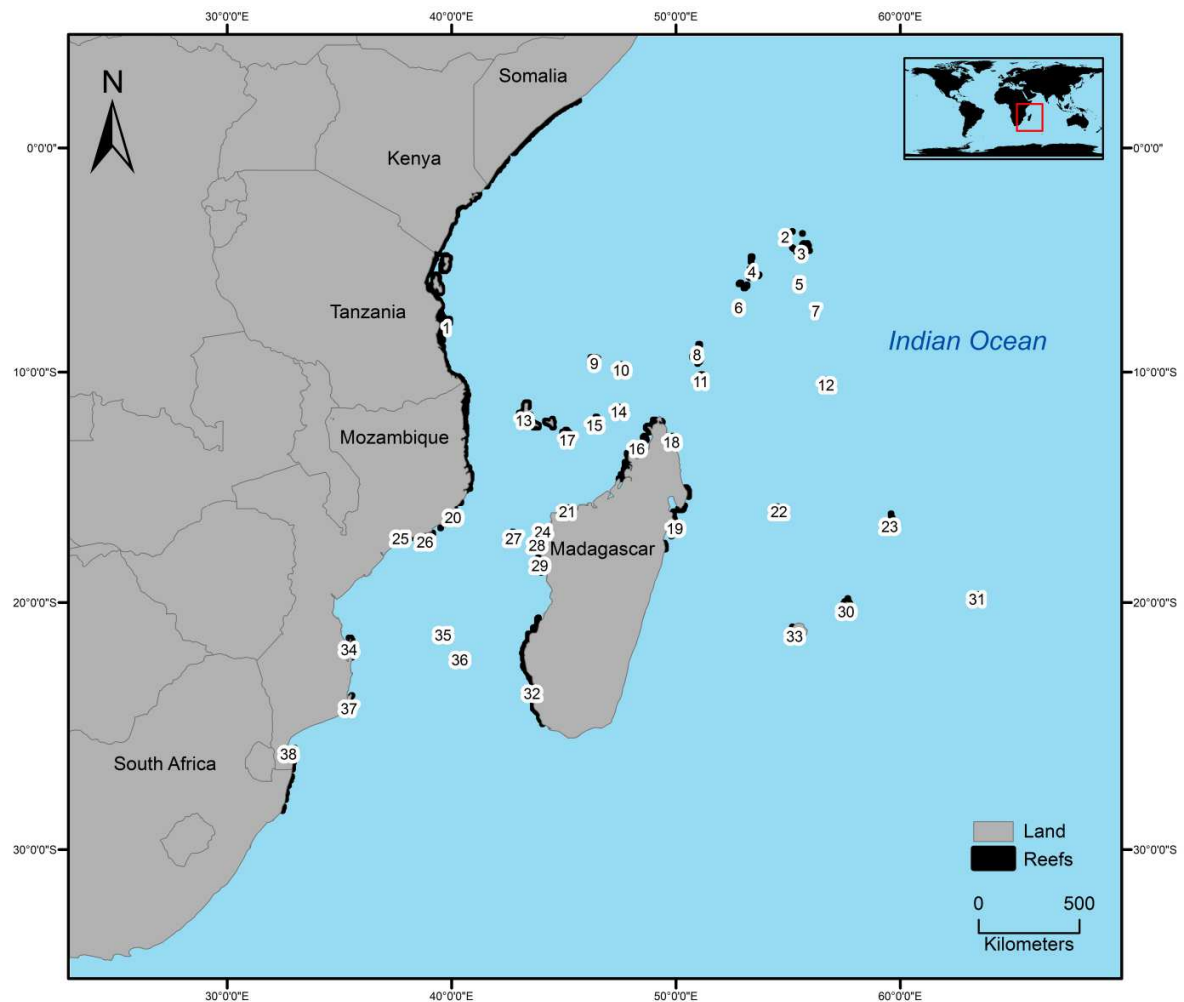

Figure 1 : Coastal and island reefs

Table 1: List of coastal and island reefs

Reef ID	Sites	Reef ID	Sites
1	Mozambique/Tanzania/ Kenya/Somalia	20	Angoche
2	Bird	21	Madagascar
3	Seychelles	22	Tromelin
4	Poivre	23	Saint Brandon
5	Platte	24	Madagascar
6	Alphonse	25	Mozambique
7	Coëtivy	26	Mozambique
8	Providence	27	Juan de Nova
9	Aldabra	28	Madagascar
10	Cosmoledo	29	Madagascar
11	Farqhar	30	Maurice
12	Agalega	31	Rodrigues
13	Comoros	32	Madagascar
14	Glorieuses	33	La Réunion
15	Geyser bank	34	Mozambique
16	Madagascar	35	Bassas da India
17	Mayotte	36	Europa
18	Madagascar	37	Mozambique
19	Madagascar	38	Mozambique/South Africa

Those reefs are over the influence of several currents (Figure 2). The *South Equatorial Current* is flowing east-to-west between 4° North and about 20° South. It splits into the *Mozambique current* and the *East Madagascar current* when it reaches Madagascar (Tomczack & Godfrey, 1994; Chapman et al., 2003). The *Mozambique current* diverges next to Comoros. One part goes down south in the Mozambique Channel and the other part goes up north (*East African Coastal current*) and meets the *Somali current*. The *East Madagascar current* flows down along Madagascar east coast and meets the *Agulhas Current*. This latter flows down the east coast of Africa from the northern end of the Mozambique Channel to Cape Agulhas (27°S to 40°S). The sources of the Agulhas Current are with the *East Madagascar Current*, the *Mozambique Current*, and a reticulated part of the *Agulhas Current* itself.
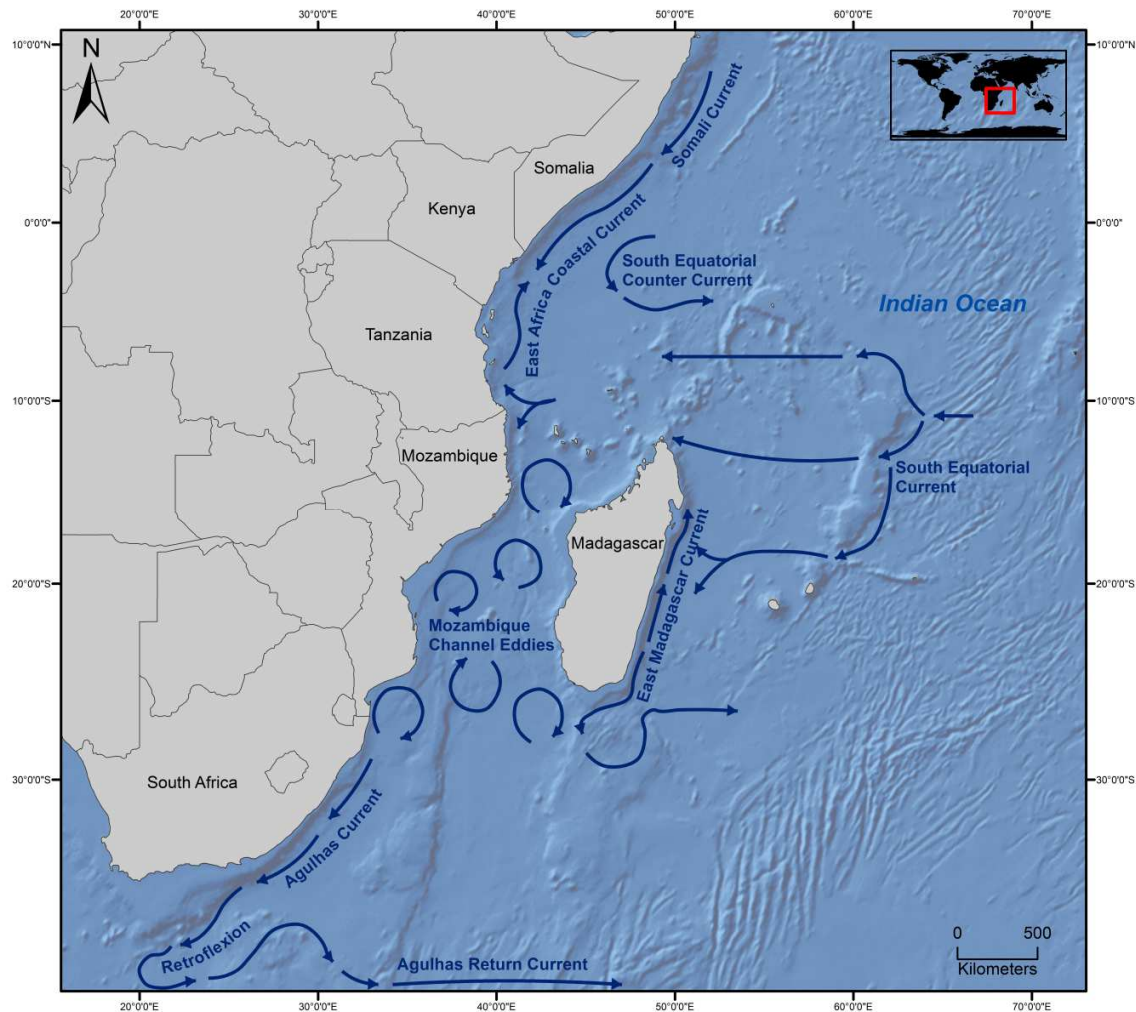
Figure 2: Some of the major currents in the western Indian Ocean (inspired from Lutjeharms & Bornman, 2010)

Hydrodynamic connectivity model

To model larval connectivity in the Western Indian Ocean, we simulated the dispersal of larvae from reefs using the modeling framework of Treml et al (2008), implemented by the Coral Reef Connectivity Simulation tool in the Marine Geospatial Ecology Tools (MGET) software (Roberts et al., 2010; Appendix A). This framework simulates the transport of larvae by dynamic ocean currents and turbulent diffusion using a two-dimensional Eulerian advection-diffusion algorithm. In this scheme, larvae are treated as a dye concentrated initially at natal reefs and spread by advection (currents) and diffusion (turbulence) as the simulation progresses. The output of the

simulation is a time series of images showing the concentration of larvae throughout the study area and a matrix that specifies, for each pair of source and destination reefs, the peak concentration of larvae released by the source reef that reached the destination reef.

To apply the framework to our study area, we prepared the required inputs: the water mask (1), the ID and location reef (2) and the reef cover (3) rasters. We first determined the geographic extent of the study area at high resolution using shoreline data from the Global Self-consistent, Hierarchical, High-resolution Shoreline database (GSHHS, ftp://ftp.soest.hawaii.edu/pwessel/gshhs/, Wessel & Smith, 1996). We extracted reef locations at a resolution of 1 km from the World Atlas of Coral Reefs assembled by the United Nations Environment Programme - World Conservation Monitoring Centre (UNEP-WCMC). We organized all data as rasters projected into the World Mercator coordinate system with the WGS84 datum and a 33 km cell size.

To drive advective transport in the simulation, we downloaded daily surface geostrophic current velocities from AVISO OPeNDAP (*Archiving, Validation and Interpretation of Satellites Oceanographic data*, http://www.aviso.oceanobs.com/).We used the 1/3° resolution "Global DT-Upd Merged MADT" products from 2008 thorough 2010. Current values missing (because of AVISO products resolution) are estimated by the Laplace interpolation method available in the toolbox.

Finally, we parameterized and executed the MGET tool. Simulations are run for a set of five groups of species, depending on their pelagic larval duration (i.e. PLD) which are set to 10, 20, 30, 40 and 50 days. The larval release time (t0) is back-calculated for each new moon and corresponds to "new moon date – PLD" (Appendix B). The tool also required us to specify the initial density of larvae (N0) spawned from natal reefs. We accepted the default value, 10000 larvae per km^2, as our goal was to model whether a connection was made between the reefs by looking at the quantity of larvae transported between them relative to the amount spawned. Other parameters such as the time step of the simulation are calculated depending on the current number which has to be less or equal to 0.25. The diffusivity coefficient is set by default ($25m^2.s^{-1}$).

Deliverables

This connectivity study between Western Indian Ocean reefs runs over 2008 to 2010. It produces one larval transport movie per year for each PLD and GIS layers on dispersal patterns parameters (max dispersal and larvae emission/reception origin).

Larval transport simulations
Those simulations are available on the device at the following path: "X:\Animations\".

Please find in the table below the name of transport simulation movies.

Table 2: Name of the larval transport simulation movies

PLD \ Year	2008	2009	2010
10	*2008d10.avi*	*2009d10.avi*	*2010d10.avi*
20	*2008d20.avi*	*2009d20.avi*	*2010d20.avi*
30	*2008d30.avi*	*2009d30.avi*	*2009d30.avi*
40	*2008d40.avi*	*2009d40.avi*	*2009d40.avi*
50	*2008d50.avi*	*2009d50.avi*	*2009d50.avi*

Each movie presents successively the larval transport for each "new moon – PLD" period of the year (i.e 12 for 2009 and 2010, or 13 times for 2008 respectively to the number of new moon during the year). For example, the *2008d10.avi* movie shows 13 simulations of the transport of 10 days PLD larvae from January to December during 2008.

The simulation color scale ("blue-to-red") is set from 10 to 800 larvae per km². It has been determined to obtain a good color stretch for the movie visualization.

Graph theoretic illustrations

Those graph theoretic illustrations are available on the device at the following path: "X:\Edges\". GIS data are delivered in projected (World Mercator, datum WGS 84) and unprojected (Lat/Long, datum WGS 84) format ("projected" and "unprojected" folders). You can open each shape individually or access all of them together from : "X:\Edges\Projected\graph.mxd" ArcMap project (ArcMap 10.0).

Please find in the table below the name of graph theoretic illustrations.

Table 3: Name of the graph theoretic illustrations

PLD \ Year	2008	2009	2010
10	*edges2008d10.shp*	*edges2009d10.shp*	*edges2010d10.shp*
20	*edges2008d20.shp*	*edges2009d20.shp*	*edges2010d20.shp*
30	*edges2008d30.shp*	*edges2009d30.shp*	*edges2009d30.shp*
40	*edges2008d40.shp*	*edges2009d40.shp*	*edges2009d40.shp*
50	*edges2008d50.shp*	*edges2009d50.shp*	*edges2009d50.shp*

Edges are derived from connectivity matrices, produced for each simulation (i.e for each new moon and PLD). Indeed the Coral Reef Connectivity Simulation tool provides a "Max Dispersal" parameter which reflects the connectivity between reefs. For each year, we averaged all simulations matrices out. We thus obtained a connectivity matrix for one precise PLD over the

year. For example, the *edges2008d10.shp* refers to the mean connectivity between reefs over 2008 for 10 days PLD larvae.

Results

For the analysis, we average "Max Dispersal" parameter for each PLD and over the three years of the simulation. We thus obtain 5 matrices (one per PLD and over 2008 to 2010). Edges are then derived from those matrices. They are presented in Figure 3, which shows the averaged connectivity (over 2008 to 2010) between reefs according to the "Max Dispersal" and the PLD.

MaxDispersal values are classified in 5 classes (from high threshold to low threshold) which have been determined according to the "Jenks natural breaks" classification method : (a) > 58.0e-4, (b) > 31.0e-4, (c) > 14.0e-4, (d) > 4.0e-4, (e) > 0. They illustrate high to low connectivity. A high threshold emphasizes strong connections whereas a low threshold emphasizes all possible connections between reefs. Thus Figure 3 exhibits the increase of connectivity in relation to the increase of PLD and the decrease of "Max Dispersal" threshold. Connections are made between a pair of reefs.
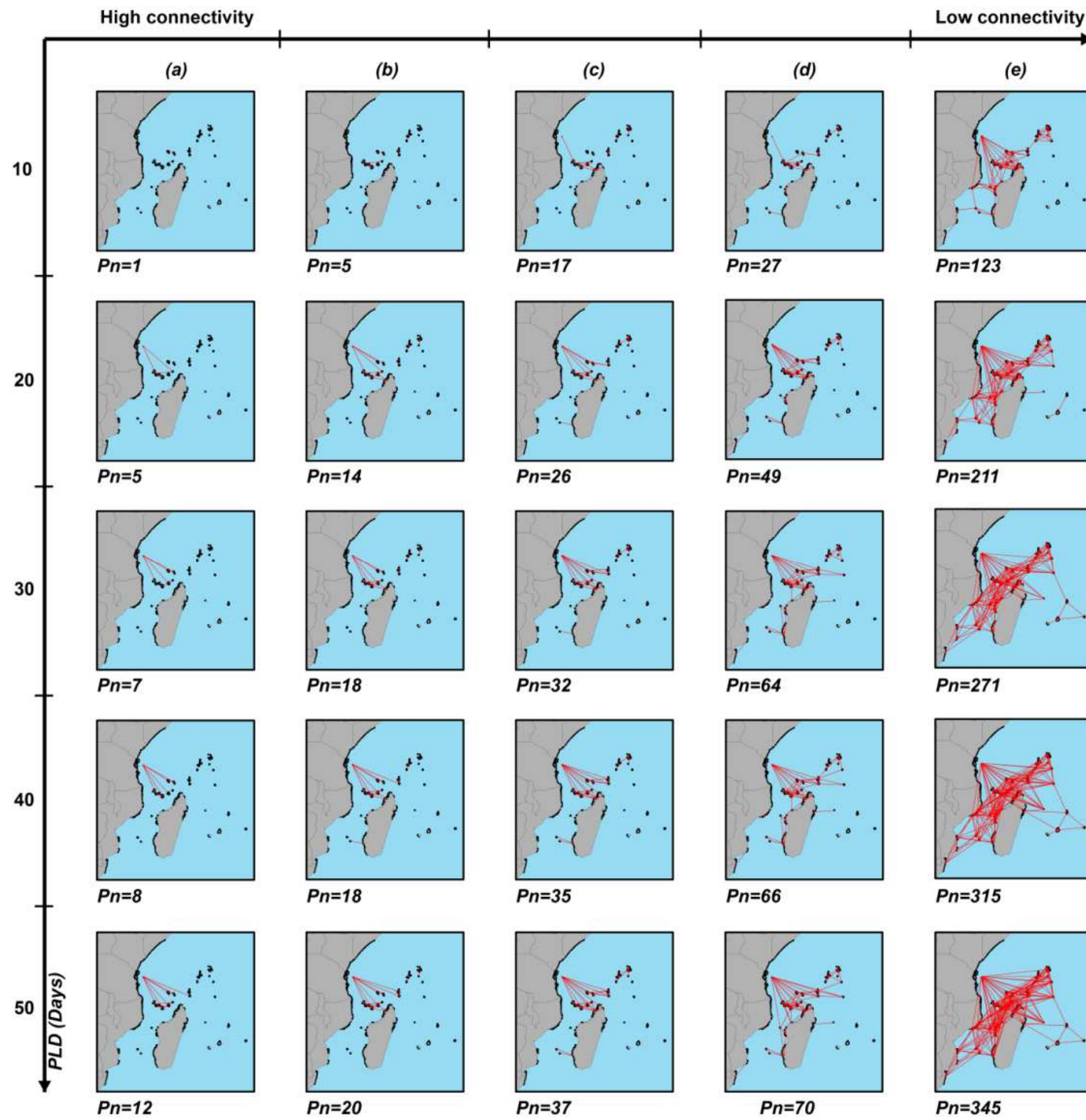
Figure 3: Averaged connectivity from 2008 to 2010, for a 10 to 50 days PLD.
(Max Dispersal threshold: (a) > 58.0e-4, (b) > 31.0e-4, (c) > 14.0e-4, (d) > 4.0e-4, (e) > 0; *Pn*: Pair number).

Discussion

The hydrodynamic circulation model presented here suggests that the reefs in the Western Indian Ocean are connected by larval dispersal. We will develop now the results of this connectivity study and present the limits and improvements of the model used here (Roberts, 2010). Finally we will see how these results have profound implication from both ecological and management perspectives.

Connectivity and clustering

Results show that connectivity depends on "Max Dispersal" parameter. Indeed when the "Max Dispersal" threshold is high, it highlights strong connectivity between reefs. On the opposite when the threshold is low, results show all possible connectivity between reefs.

On the other hand, connectivity also depends on PLD. Indeed, connectivity increases with the increase of PLD. Reefs are a lot more connected when PLD is equal to 50 days than when it is equal to 10 days.

Connections between two reefs can be one-way or two-way. In this last case, the "Max dispersal" parameter is not equal (from i to j, and from j to i) and the connection is often more important in one way than in the other. It is important to know the way of the connectivity to define larval sources and sinks. Please refer to figure 3 at high resolution on the device at the following path: "X:\Edges\map.tiff" to see the way of connections between reefs.

Based on connectivity simulation outputs, groups of reefs were identified. We used *APCluster, an R package for affinity propagation clustering* (Bodenhofer et al., 2011; Frey and Dueck, 2007). The algorithm input is the connectivity matrix defined for each PLD over 2008 to 2010. Reefs with no connections to any other one were discarded from the analysis (table 4).

Table 4: Reefs clustering

PLD (days)	10	20	30	40	50
Number of clusters	12	12	10	9	10
Clusters	Cluster 1: 1, 21	Cluster 1: 1, 13, 14	Cluster 1: 1, 9, 10, 13, 14, 15, 16, 17, 18	Cluster 1: 1, 9, 10, 13, 14, 15, 16, 17, 18, 21	Cluster 1: 1, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 21
	Cluster 2: 2, 3, 5, 7	Cluster 2: 2, 3, 5, 7	Cluster 2: 2, 3, 5, 7	Cluster 2: 2, 3, 4, 5, 6, 7	Cluster 2: 2, 3, 5, 7
	Cluster 3: 4, 6	Cluster 3: 4, 6	Cluster 3: 4, 6	Cluster 3: 8, 11, 12	Cluster 3: 4, 6
	Cluster 4: 8, 11	Cluster 4: 9, 10	Cluster 4: 8, 11, 12	Cluster 4: 19, 22	Cluster 4: 19, 22
	Cluster 5: 9, 10	Cluster 5: 8, 11, 12	Cluster 5: 19, 22	Cluster 5: 20, 26	Cluster 5: 23, 31
	Cluster 6: 15, 16, 18	Cluster 6: 15, 16, 17, 18, 21	Cluster 6: 20, 26	Cluster 6: 24, 28	Cluster 6: 20, 26
	Cluster 7: 13, 14, 17	Cluster 7: 19, 22	Cluster 7: 21, 24, 27, 28, 29	Cluster 7: 23, 30, 31, 33	Cluster 7: 24, 28
	Cluster 8: 20, 26, 35	Cluster 8: 20, 26	Cluster 8: 23, 30, 31, 33	Cluster 8: 27, 29, 32, 35, 36	Cluster 8: 30, 33
	Cluster 9: 24, 27, 28, 29	Cluster 9: 24, 27, 28, 29	Cluster 9: 32, 35, 36	Cluster 9: 34, 37, 38	Cluster 9: 27, 29, 32, 35, 36
	Cluster 10: 32, 36	Cluster 10: 23, 30, 33	Cluster 10: 34, 37, 38		Cluster 10: 34, 37, 38
	Cluster 11: 34, 37	Cluster 11: 32, 35, 36			
	Cluster 12: 38	Cluster 12: 34, 37, 38			
Discarded reefs	12,19, 22, 23, 25, 30, 31, 33	25, 31	25	25	25

The number of clusters differs according to the PLD from 9 to 12 clusters. There are different zones where reefs inside each zone are strongly connected (= intra-connectivity). Those zones are also connected to each other (= inter-connectivity).

The connectivity is essentially driven by currents (see larval transport simulations) AND reefs geographic location. Indeed, two reefs geographically close are more likely to be connected.

All those regions are inter-connected with each other during the study period (2008 to 2010). However it has to be noticed that the "Mascarene archipelago and Saint Brandon region" (situated on the East side of Madagascar) is few connected to other ones.

Dispersal model improvements

The larval transport simulation discussed above demonstrated the potential connectivity between Western Indian Ocean reefs. Nonetheless, the model could be improved by accounting for additional oceanographic and biological factors. Here we discuss some of those improvements.

The model used was based on AVISO geostrophic currents data derived from satellite altimetry observations. Such data are available globally and for a relatively long period of time (1992 to the present day). However these products are not reliable in the direct vicinity of islands due to the proximity of land and are impacted by strong cloud cover (AVISO, personal communication). For a regional analysis, as performed in this study, the resolution of those products is sufficient (1/3°). In addition this is a two-dimensional model which does not account for the vertical stratification of current in the water column which can affect the way larvae are transported.

Larvae are considered passive particles by this model and others (Black et al., 1990, 1991). However reef fish larvae have great swimming abilities (Stobutzki & Bellwood, 1997; Leis et al., 1996; Leis & McCormick, 2002) and can position themselves in the water column. Larvae begin their pelagic phase as plankton (weak, ineffective swimmers, with little or no control over trajectory, except perhaps vertically) but end it as nekton (strong, effective swimmers, with great control over trajectory) (Leis & McCormick, 2002). At this stage they are capable of sustained speeds higher than ambient currents and of swimming nonstop for tens of kilometers over tens of hours (Jager, 1999; Bay, 2000; Ochavillo et al., 2000; Leis & McCormick, 2002; Leis, 2006).

Larvae also have a complex sensory system (Kingsford & Choat, 1989) which allows them to detect and orient to reefs using sound (Leis et al., 1996; Leis & Carson-Ewart, 2002; Tolimieri et al., 2000), chemical signals (Sweatman, 1988; Kingsford et al., 2002) and temperature gradients (Doherty et al., 1996). They can exhibit a pattern of daily vertical migration (Irisson, 2010), staying hidden at depth during daytime and going up to feed at night when obscurity keeps them safe from predators (Lampert, 1989). Their vertical distribution was found to correlate with many environmental factors, including temperature (Annis, 2005), light intensity (Munk et

al. 1989; Job & Bellwood 2000; Guizien et al. 2006) and the depth of clines (Munk et al. 1989; Boehlert et al. 1992; Annis 2005; Lampert et al. 2003). These phenomena also affect how larvae are advected by currents. A shear is often present between fast surface velocities and moderate flow at depth, because of wind stress at the surface or bottom friction at depth (Irisson, 2010). Cowen (2002) suggested that larvae may use their swimming and behavioral abilities to reduce their dispersion and enhance self-recruitment.

We suggest that future larval dispersion models take in consideration biological parameters related to the larval abilities listed above and physical data such as current vertical stratifications. Furthermore, environmental conditions can affect PLD and consequently constrain potential larval dispersal. For example, a greater access to food and an increase in water temperature were both found to speed up development, leading to shorter PLDs (Houde, 1989; Leis & McCormick, 2002). Finally, physical processes such as fronts and eddies (Wolanski & Hamner, 1988) and the presence of oceanic islands (Doty & Oguri, 1956; Gilmartin & Relevante, 1974) can promote the introduction of nutrients into surface waters through upwelling and terrestrial runoff (Rougerie & Wauthy, 1986). These nutrients can quickly be converted in potential prey (primary and secondary production) and thereby favor larval survival. As a result it is important to consider those processes in future models as well.

Implications for marine spatial planning

An increasing number of regional MPA networks are being designed and implemented to promote the persistence of marine ecosystems and populations for both conservation and fishery management (Planes et al., 2009). Their geographic distribution should consider local and global connectivity patterns (Shulman, 1998), important for species life cycles and long-term evolution of biota. Connectivity promotes recovery from local extinctions and increases ecosystem resilience (Almany et al., 2007), particularly in a context of climate change and increasing pressures on marine ecosystems (Game et al., 2008). Nevertheless, the spatial scale over which marine populations are connected by larval dispersal remains poorly understood in terms of empirical evidence (Planes et al., 2009).

On the other hand, recent numerical dispersion models provide some insight (see, for example, Mora et al., 2011) and models and data are becoming easily accessible to non-experts, allowing virtually anyone to model larvae dispersal. As accurate information on larvae dispersal is critical to design spatially-relevant management strategies for conserved and exploited marine species, the validation of numerical dispersal models is crucial.

In the Western Indian Ocean, the fact that all reefs/regions seem to be connected has strong and immediate implications for conservation and fishery management. First, it means that coastal fish population connectivity operates at a broader scale than the individual islands and local MPAs, and that those populations not replenished exclusively by self-recruitment. Second, population and ecosystem management at the regional scale are intrinsically linked: for

instance, pressures on marine ecosystems, i.e. overfishing and pollution, in "North Seychelles islands" could affect fish population in "South Seychelles islands". Third, the degree of this interaction remains unknown and should be further investigated using improved numerical dispersal models and compared to other evidence including population genetics and otolith analyses.

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