

## MODELING LARVAL CONNECTIVITY OF CORAL REEF ORGANISMS IN THE KENYA-TANZANIA REGION

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# Modeling Larval Connectivity of Coral Reef Organisms in the Kenya-Tanzania Region

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9 particle tracking, ocean modeling.

## 10 Abstract

11 Most coral reef organisms have a bipartite life-cycle; they are site attached to reefs as adults but have  
12 pelagic larval stages that allow them to disperse to other reefs. Connectivity among coral reef patches  
13 is critical to the survival of local populations of reef organisms, and requires movement across gaps  
14 that are not suitable habitat for recruitment. Knowledge of population connectivity among individual  
15 reef habitats within a broader geographic region of coral reefs has been identified as key to  
16 developing efficient spatial management strategies to protect marine ecosystems. The study of larval  
17 connectivity of marine organisms is a complex multidisciplinary challenge that is difficult to address  
18 by direct observation alone. An approach that couples ocean circulation models with individual based  
19 models (IBMs) of larvae with different degrees of life-history complexity has been previously used to  
20 assess connectivity patterns in several coral reef regions (e.g., the Great Barrier Reef (GBR) and the  
21 Caribbean). We applied the IBM particle tracking approach to the Kenya-Tanzania region, which  
22 exhibits strong seasonality in the alongshore currents due to the influence of the monsoon. A 3-  
23 dimensional (3D) ocean circulation model with 2 km horizontal resolution was coupled to IBMs that  
24 track virtual larvae released from each of 661 reef habitats, associated with 15 distinct regions. Given  
25 that reefs provide homes to numerous species, each with distinctive, and in aggregate very diverse  
26 life-histories, several life-history scenarios were modeled to examine the variety of dispersal and  
27 connectivity patterns possible. We characterize virtual larvae of *Acropora* corals and *Acanthurus*  
28 surgeonfish, two coral reef inhabitants with greatly differing pelagic life-histories, to examine the

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29 effects of short (<12 days) and long (>50 days) pelagic larval durations (PLD), differences in  
30 swimming abilities (implemented as reef perception distances), and active depth keeping in reef  
31 connectivity. *Acropora* virtual larvae were modeled as 3D passive particles with a precompetency  
32 period of 4 days, a total PLD of 12 days and a perception distance of 10 m. *Acanthurus* virtual larvae  
33 were characterized by 50 days precompetency period, a total PLD of 72 days and a perception  
34 distance of 4 km. *Acanthurus* virtual larvae were modeled in two ways—as 3D passive particles and  
35 including an idealized ontogenetic vertical migration behavior. A range of distances within which  
36 larvae were able to perceive reefs and directionally swim to settle on them during the competency  
37 period were evaluated. The influence of interannual environmental variations was assessed for two  
38 years (2000, 2005) of contrasting physics. The spatial scale of connectivity is much smaller for the  
39 short PLD coral, with successful connections restricted to a 1° radius (~100 km) around source reefs.  
40 In contrast, long distance connections from the southern to the northernmost reefs (~950 km) are  
41 common for virtual *Acanthurids*. Successful settlement for virtual *Acropora* larvae was <0.3%, and  
42 within region settlement (local retention) was 0.38%, substantially greater than inter-region  
43 settlement (ca. 0.2%). Settlement of *Acanthurus* virtual larvae was >20% overall, with cross-region  
44 recruitment much increased compared to the coral larvae. Approximately 8% of *Acropora* larvae that  
45 successfully settled, recruited to their source reef (self-recruitment), an important proportion  
46 compared to only 1-2 % self-recruitment for *Acanthurus*. These rates and dispersal distances are  
47 similar to previous modelling studies of similar species in other coral reef regions and agree well  
48 with the few observational studies within the Kenya-Tanzania region.

49

### 50 1 Introduction

51 Tropical coral reef ecosystems are very important from both the ecological and economical points of  
52 view (Spalding et al., 2001). However, they are also particularly fragile, and have been declining in  
53 recent years in most regions of the world (Melbourne-Thomas et al., 2011; Hughes et al., 2003;  
54 Pandolfi et al., 2003), since they are highly susceptible to anthropogenic stressors operating at global  
55 scales (e.g., global warming and ocean acidification) and local scales (e.g., pollution/eutrophication,  
56 fishing, over-commercialization for recreation). Coral reef ecosystems are complex communities  
57 with very high species diversity. Most reef species have bipartite life histories with a planktonic  
58 larval stage and a benthos associated adult life. As adults, coral reef organisms exhibit various  
59 degrees of site attachment ranging from completely sessile, like corals and sponges, to highly mobile,  
60 like fish and crustaceans. Generally, even fish capable of swimming several kilometers in a few hours

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61 have restricted home ranges, since they are relatively territorial and are associated with specific reef  
62 habitats that are patchily distributed (Sale, 2006). Most adult reef organisms are distributed in  
63 metapopulations connected by pelagic larvae that disperse subject to the ocean currents (Bode et al.,  
64 2006; Cowen and Sponaugle, 2009).

65

66 Coral reefs extend along the coast of East Africa from the equator to approximately 14°S, being  
67 absent only at major river outflows or Pleistocene river valleys. Fringing reefs are the most common  
68 type, but complex formations occur around islands and other regions where the continental shelf  
69 extends more than a few kilometers from shore. Reefs are absent on the Somali coast north of the  
70 equator due to seasonal upwelling of cold water associated with the monsoon winds. The  
71 southernmost reef is found in Mozambique at 26°S; but scattered colonies of scleractinian corals  
72 occur as far south as 34°S, in South Africa (Day, 1974 cited in Hamilton and Brakel, 1984). Western  
73 Indian Ocean coral reef communities are characterized by high levels of species diversity and may be  
74 centers of biodiversity (Spalding et al., 2001). Coastal communities of Kenya and Tanzania depend  
75 on the reef for food. Since there is little regulation on the use of these resources through formal  
76 resource management strategies, reef areas in Kenya and Tanzania have been degraded due to  
77 overfishing, destructive fishing techniques, coastal pollution and other activities affecting the coastal  
78 environment (Hamilton and Brakel, 1984; Spalding et al., 2001). Increasing interest in coral reef  
79 tourism is simultaneously leading to increased pressure on some coral reefs while providing a  
80 powerful local incentive for conservation (Spalding et al., 2001). There are 26 Marine Protected  
81 Areas (MPAs) in Kenya and Tanzania reported in the Protected Planet Database  
82 (<http://www.protectedplanet.net/>; accessed July 2016) that encompass coral reef habitat; some of  
83 these were established as recently as 2010. Eight of the 26 MPAs are no-take areas, while 18 of them  
84 allow extraction using traditional fishing methods like handlines and traps (Muthiga et al., 2008). The  
85 benefits of MPAs for biodiversity conservation and fisheries management are well known  
86 (McClanahan and Mangi, 2000; Gell and Roberts, 2003; Roberts et al., 2005; Lester et al., 2009;  
87 Micheli et al., 2012); however, the design (spacing, size and separation distance) of effective MPA  
88 networks is not trivial (e.g. Botsford et al., 2003; McLeod et al., 2009; Edgar et al., 2014). Many  
89 studies (e.g. McCook et al., 2009; Botsford et al., 2009; Hogan et al., 2011; Rossi et al., 2014)  
90 emphasize the importance of larval connectivity on the performance of MPA spatial management for  
91 meeting conservation and fishery yield objectives.

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92

93 Larval connectivity is vital to the survival of marine metapopulations, both at ecological and  
94 evolutionary time scales (James et al., 2002; Cowen and Sponaugle, 2009; Burgess et al., 2014).  
95 Population connectivity plays a fundamental role in local and metapopulation dynamics, community  
96 dynamics and structure, genetic diversity, ecosystem responses to environmental changes, and the  
97 resiliency of populations to human exploitation (Cowen et al, 2007). Connectivity among marine  
98 metapopulations is controlled by physical transport and dispersion, temperature, and biological  
99 processes such as the timing of spawning, pelagic larval duration (PLD), larval behavior, and  
100 mortality. The net combined effect of these processes determines the spatial scales over which a  
101 population is connected (Gawarkiewicz et al., 2007). Connectivity is therefore a function of several  
102 interacting variables including species, geographical area, and ocean conditions, and is highly  
103 variable in both time and space (e.g. Cowen and Sponaugle, 2009; Christie et al., 2010b; Domingues  
104 et al., 2012). Often, little is known about the connections among different coral reef regions (Cowen  
105 et al, 2000; Mora and Sale, 2002; Sponaugle et al, 2002) and the degree to which local populations  
106 are open (dependent on recruits from external sources) (e.g. Saenz-Agudelo et al, 2011) or closed  
107 (self-replenishing) (e.g. Schultz and Cowen, 1994).

108

109 Observational approaches for studying connectivity use genetic techniques (Baums et al., 2005; Jones  
110 et al., 2005; Christie et al., 2010; Hogan et al., 2011; Harrison et al., 2012), spatially varying natural  
111 bio-markers leaving a geochemical signature in calcified structures (i.e. otoliths and statoliths)  
112 (Thorrold et al., 1998; Thorrold et al., 2007) or tagging otoliths of larvae (Jones et al., 1999; Almany  
113 et al., 2007). These techniques are limited in the spatio-temporal scales they can resolve and some of  
114 them are restricted to specific species or environments (Gawarkiewicz et al., 2007; Thorrold et al.,  
115 2007; Hedgecock et al., 2007). Challenges of applying observational techniques to larval  
116 connectivity in the Kenya-Tanzania (KT) region are that these methods are expensive, time-  
117 consuming and require highly specialized equipment and expertise (Thorrold et al., 2007). Individual  
118 based Lagrangian particle tracking models (IBM) coupled to realistic ocean circulation models are a  
119 less limiting method to study potential connectivity among East-African coral reefs. So long as the  
120 ocean circulation model reasonably depicts the time-varying flows, IBMs can resolve time varying 3-  
121 dimensional potential dispersion of planktonic larvae over large spatial scales with high spatio-  
122 temporal resolution. Results of numerical simulations can only provide estimates of potential

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123 connectivity, that need to be validated with empirical measurements (i.e. Foster et al., 2012; Soria et  
124 al., 2012) and scaled by observed reproductive input (Watson et al., 2010) and settlement (i.e.  
125 Sponaugle et al., 2012). Even in the absence of empirical confirmations, estimates of potential  
126 connectivity from modelling studies provide a comprehensive understanding of the spatial-temporal  
127 dynamics of marine populations, that inform the design of more efficient MPAs (Willis et al., 2003;  
128 Sale et al., 2005). With the exception of a few studies (McClanahan et al., 1994; McClanahan, 1994;  
129 Mangubhai, 2008; Yahya et al., 2011; Kruse et al., 2015), knowledge of reef biota ecology is lacking  
130 for much of the Western Indian Ocean region, due to the lack of infrastructure and local expertise,  
131 combined with problems of national security in some areas (Spalding et al., 2001). Few studies have  
132 examined larval supply and connectivity in coral reefs in the Western Indian Ocean (Kaunda-Arara et  
133 al., 2009; Crochelet et al., 2013; Crochelet et al., 2016). Genetic techniques have been used to study  
134 connectivity at evolutionary time scales of several reef fish (Dorenbosch et al., 2006, *Lutjanus*  
135 *fulviamma*; Visram et al., 2010, *Scarus ghobban*, and Muths et al., 2012, *Lutjanus kasmira*). High  
136 gene flow and weak genetic structure were found in these fish, even among sites as distant as 4000  
137 km (Muths et al., 2012). Recently, Van der Ven et al (2016) used genetic techniques to examine  
138 connectivity at evolutionary time scales of the branching coral *Acropora tenuis* in the Kenya-  
139 Tanzania region. They report high but variable connectivity among sample sites spanning 900 km  
140 along the coast. These studies do not address ecologically significant timescales of a few generations,  
141 and are in general concerned with large spatial scales (~1000s of km), and therefore cannot provide  
142 insights on population demography at temporal and spatial scales relevant to the implementation of  
143 management and conservation strategies at national and regional levels. Only Souter et al. (2009)  
144 used genetic techniques to examine both evolutionary and ecological connectivity of the coral  
145 *Pocillopora damicornis* in the MPAs of the KT region. They identified the Mnemba Conservation  
146 area northeast of Zanzibar Island as a potential source for the *P. damicornis* population, and Malindi  
147 Marine National Park and Reserve in north Kenya as a genetically isolated reef.

148 For decades the spatial connectivity of larval fish and invertebrates was thought to be a passive  
149 process governed primarily by the ocean physics and the duration of the larval period (e.g. Shanks,  
150 2009). The pelagic larval duration (PLD) of coral reef organisms varies greatly; from a few hours for  
151 some coral species to a few months for some fish and crustaceans (Shanks, 2009). Recent studies (i.e.  
152 Leis and Carson-Ewart, 2003; Paris and Cowen, 2004; Shanks, 2009; Pineda et al., 2010) have shown  
153 that larval transport of most marine organisms is not strictly passive and that there is an uncoupling  
154 between dispersal distance and PLD due to larval behavior, such as active depth selection and

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155 directional swimming. Discrepancies between the passive transport hypothesis and observed patterns  
156 of recruitment point to the importance of biological factors (i.e. behavior, predation, starvation, etc.)  
157 in the control of larval dispersal and connectivity (Cowen et al., 2006; Cowen and Sponaugle, 2009;  
158 Leis et al., 2007; Paris and Cowen, 2004; Sponaugle et al., 2012). Even excluding mortality, the  
159 degree to which biological factors influence connectivity is greater than originally hypothesized  
160 (Shanks, 2009). Recent studies have shown the importance of physiological and behavioral  
161 characteristics of larvae on influencing the connectivity and dispersal of species with a planktonic  
162 larval stage (i.e. Kingsford et al., 2002). Growth rates (e.g. Bergenius et al., 2002), ontogenetic and  
163 diel vertical migrations (Paris et al., 2007; Drake et al., 2013), swimming ability (e.g. Stobutzki and  
164 Bellwood, 1997; Wolanski et al., 1997; Leis and Carson-Ewart, 2003; Leis et al., 2007), orientation  
165 through olfaction (Atema et al., 2002; Gerlach et al., 2007; Paris et al., 2013; Atema et al., 2015) and  
166 audition (Tolimieri et al., 2000; Leis et al., 2003; Simpson et al., 2005; Heenan et al., 2009; Vermeij  
167 et al., 2010), and settlement strategies (Leis and Carson-Ewart, 1999; Lecchini et al., 2005) are  
168 important in controlling connectivity of coral reef organisms. Observational studies suggest that  
169 marked ontogenetic vertical zonation is important for larval transport (Boehlert and Mundy, 1993;  
170 Cowen and Castro, 1994). In modeling studies, vertical migration often promotes local retention and  
171 recruitment of pelagic larvae to suitable habitat. A modeling study of the California Current System  
172 (CCS) by Drake et al. (2013) showed that larvae that remained below the surface boundary layer  
173 were 500 times more likely to be retained within 5 km of the coast after 30 days than larvae that  
174 remained near the surface. Settlement in the CCS increased by an order of magnitude when larvae  
175 remained at 30 m depth. Similarly, settlement success in different regions of the Caribbean increased  
176 when a shallow ontogenetic vertical migration (OVM) behavior was added to the virtual larvae (Paris  
177 et al., 2007). Potential settlement estimates increased up to 190% in the southern Florida Keys with  
178 the OVM (Paris et al., 2007). The influence of larval physiology and behavior on connectivity and  
179 dispersal of coral reef species is now well established (Kingsford et al., 2002; Paris et al., 2007;  
180 Wolanski and Kingsford, 2014). However biological characteristics are known with certainty only for  
181 a handful of species.

182

183 The hydrodynamics of the KT coastal ocean is highly variable at seasonal and subseasonal time  
184 scales, due to the influence of the monsoons and complex tidal interactions. The coastal circulation is  
185 mainly influenced by: (1) the northward flowing East African Coastal Current (EACC) fed by (2) the

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186 regionally westward flowing North East Madagascar Current (NEMC), (3) the seasonally reversing  
187 Somali Current (SC), (4) tides and (5) local winds (see Figure 1 of Mayorga-Adame et al., 2016). SW  
188 monsoon conditions are characterized by strong continuous northward flow along the coast and  
189 relatively cool (~24°C) sea surface temperatures (SST) that prevail from May to October. During the  
190 NE monsoon, from January to March, a strong north-south SST gradient is caused by the intrusion of  
191 the shallow, southward flowing, cold and salty Somali Current that meets the slow northward  
192 flowing, warm and fresh EACC. The convergence of the two currents forms the eastward flowing  
193 South Equatorial Counter Current. The inter-monsoon seasons, in between these two periods, are  
194 characterized by strong mixing and slow currents.

195

196 The relative lack of physiological and behavioral data for larvae of coral reef species in the Kenya-  
197 Tanzania region led us to examine connectivity among coral reefs using idealized particle tracking  
198 experiments that simulate larvae with characteristics of two ubiquitous and ecologically important  
199 species groups: the *Acropora* branching corals with short PLD (ca. 12 days, (Babcock and Heyward,  
200 1986; Nishikawa et al., 2003; Nozawa and Harrison, 2008) and the *Acanthurus* surgeon fish with  
201 long PLD (72 days, (Rocha et al., 2002)) (See Mayorga-Adame, 2015 for a review of the genus life  
202 histories). Particle tracking of individual organisms using the output of ocean circulation models is a  
203 suitable, cost effective tool to examine larval connectivity among coral reefs in large areas and at  
204 finer spatio-temporal scales relevant to the population ecology of coral reef species (Werner et al.,  
205 2001; Cowen and Sponaugle, 2009). Insight developed from connectivity matrices generated from  
206 this study could aid local managers and decision makers tasked with regulating the use of marine  
207 resources in the Kenya-Tanzania region. Hindcasting the connections among reefs in the strongly  
208 dynamical Kenya-Tanzania region is challenging and the level of uncertainty is high. The results  
209 presented are a first attempt at assessing connectivity in the region and should be treated as a regional  
210 result suitable for comparison with similar studies in other coral reef regions (Great Barrier Reef;  
211 Mesoamerican Caribbean Reef). In addition, these model results should be useful for developing  
212 hypotheses and designing observational campaigns aimed at validating or improving the described  
213 connectivity patterns.

214

215 **3. Methods**



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### 216 3.1 Hydrodynamic model

217 A 2 km horizontal resolution Regional Ocean Model System (ROMS) (Haidvogel et al.,  
218 2008) that includes tides, the 2 km Kenyan-Tanzanian Coastal Model (hereafter 2KTCM), was used  
219 to generate 3-dimensional ocean velocity fields. This model is an enhanced resolution version of the  
220 4 km Kenyan-Tanzanian Coastal Model (KTCM) (Mayorga-Adame et al., 2016). The model domain  
221 is a rectangular grid extending from 38° to 47 °E and from the equator to 10 °S (Figure 1). It has 31  
222 terrain following vertical levels. The model bathymetry is from the 30 sec global GEBCO product  
223 ([www.gebco.net/data\\_and\\_products/gridded\\_bathymetry\\_data/](http://www.gebco.net/data_and_products/gridded_bathymetry_data/); accessed April 2011). The model  
224 coastline was manually edited to retain as many features as the 2 km resolution allowed. Only Pate  
225 Island in north Kenya, and Pemba, Zanzibar and Mafia Islands in Tanzania are included as dry cells  
226 in the land mask. The atmospheric forcing (wind stress, heat and freshwater fluxes) is calculated by  
227 ROMS bulk formulation using atmospheric variables from daily NCEP/NCAR reanalysis (Kalnay et  
228 al., 1996). The model is initialized and forced at the boundaries by monthly fields of T, S and  
229 velocity from the KTCM (Mayorga-Adame et al., 2016) and tides are provided by the TPXO6 global  
230 tidal model (Egbert et al., 1994; Egbert and Erofeeva, 2002). Freshwater runoff and diurnal wind  
231 variability are not included in the model. The ocean model was run continuously for 8.25 years from  
232 October 1999 to December 2007. Three-hourly averages of the velocity fields for 2000 and 2005  
233 were stored and used for the particle tracking experiments.

234

### 235 3.2 Lagrangian Particle Tracking

236 An Individual Based Model (IBM) (Batchelder, 2006) was run offline using previously stored 3-hour  
237 averages of the 3-dimensional 2KTCM velocity fields. The IBM interpolates tri-linearly in space and  
238 linearly in time the velocity and temperature fields from the ROMS simulation. Particle trajectories  
239 are computed using a 4<sup>th</sup> order Runge-Kutta algorithm. No explicit diffusion (e.g. random walk  
240 applied to the individual's position) is invoked since the 2 km horizontal resolution of the ocean  
241 circulation model is enough for significant eddy formation and horizontal mixing to occur around  
242 reefs, and the terrain following coordinates provide very high vertical resolution (<15 cm) in the  
243 shallow regions. A 3D advection-only version of the IBM was used to track forward in time the  
244 dispersal of particles (virtual larvae) originating from all reef polygons. The tracking was done using  
245 a 30 min time step. Coral larvae were tracked using the 3-dimensional passive advection scenario

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246 only. For surgeonfish, with longer PLDs and greater ability to control depth in the water column, an  
247 idealized ontogenetic vertical migration scenario was implemented.

248

### 249 3.3 Biological Assumptions

250 In the model experiments all reefs were seeded randomly with a density of 50 particles per square  
251 kilometer of reef. Reefs smaller than 1 km<sup>2</sup> were seeded with 50 particles. A total of 129 184  
252 particles were released for each modeled spawning day, using identical seeding locations for all  
253 simulations. Spawning was assumed to take place at 5:30pm local time (~sunset) during February  
254 and March, the months of peak spawning for coral reef species in the Western Indian Ocean  
255 (Mangubhai and Harrison, 2008; Mangubhai, 2008). All particles were released at 3 m depth. For the  
256 3-dimensional passive experiments (reference experiments) virtual larvae were spawned at the  
257 release locations at 3 day intervals starting on February 2<sup>nd</sup> for a total of 20 releases. PLD for  
258 Caribbean species of *Acanthurus* range from 45 to 70 days (Rocha et al., 2002). The Indo-Pacific  
259 species *A. triostegus* has a mean PLD of 54 days (range of 44-83 days) (Randall, 1961; McCormick,  
260 1999; Longenecker and Langston, 2008). *Acanthurus* virtual larva were tracked for 72 days and  
261 considered competent to settle 50 days after their release, giving them a competency period of 22  
262 days. *Acropora* virtual larvae were tracked for 12 days and considered competent after 4 days giving  
263 them a competency period of 8 days. These assumptions were made considering the results of  
264 laboratory rearing studies that reported a minimum pre-competency period of 3 to 4 days for *A.*  
265 *muricata*, *A. valida* (Nozawa et al., 2008), and *A. tenuis* (Nishikawa et al., 2003), and up to 97%  
266 settlement 10 days after spawning (Backcock and Heyward, 1986; Nishikawa et al., 2003; Nozawa et  
267 al., 2008). The ability of reef larvae to sense nearby reefs and swim towards settlement habitat is  
268 often represented in models as a sensory zone based on perception distance (Paris et al., 2007;  
269 Sponaugle et al., 2012), a buffer distance around suitable habitat that defines how far away from a  
270 reef larvae are able to successfully settle. Based on observational studies of sensing, swimming and  
271 settling ability (Atema et al., 2015; Leis and Carson-Ewart, 1999; Leis and Fisher, 2006) perception  
272 distance for competent *Acanthurus* larvae was assumed to be 4 km, which is consistent with the  
273 distance used to model other coral reef fish (Paris et al., 2007; Sponaugle et al., 2012). Perception  
274 distance for competent *Acropora* larvae was assumed to be much shorter, only 10 m, because despite  
275 their ability to perceive sounds (Vermeij et al., 2010) and chemical cues (Dixson et al., 2014)  
276 emanating from reefs they have very limited swimming ability and are unlikely to overcome water

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277 speeds (Baird et al., 2014). Virtual larvae were evaluated each night during their competency period  
278 to determine if reefs were within their perception distance. If so, they were assumed to settle on the  
279 first reef they encountered. Sensitivity analysis to evaluate whether the destination reef of settled  
280 larvae was affected by the time of evaluation during the dark hours indicated little temporal variation  
281 within a night. Therefore, settlement of virtual larvae was evaluated once per night at 11:30 PM local  
282 time. The *Acanthurus* ontogenetic vertical migration (OVM) experiment included passive dispersal  
283 for 20 days, then larvae were shifted to 50 m (or 3 m above the bottom at locations shallower than 50  
284 m). Virtual larvae at 50 m continued to be passive in their horizontal movement but were kept at  
285 fixed depth for 20 days. At day 40, the larvae migrated back to 3 m depth to find suitable reef habitat  
286 when reaching competency (50 days after spawning). After the upward migration, larvae are  
287 advected passively in three dimensions until day 72, when the trajectory was terminated. Successful  
288 settlement was assessed as described in the reference experiment. OVM experiments were run for the  
289 February to March period as the passive experiments, but with larvae released only every sixth day  
290 (for a total of 10 release dates).

291

### 292 3.4 Seascape Analysis

293 Kenya and Tanzania have very narrow continental shelves, with the 200 m isobath only 12 km  
294 offshore, except at the Mafia and Zanzibar Channels. The shores of Kenya and Tanzania are bordered  
295 by a virtually continuous chain of fringing coral reefs that stretches along the coast, only breaking at  
296 river mouths and estuaries. The coral reef polygons in the model domain were extracted from the  
297 Global Distribution of Coral Reefs 2010 database available at the Ocean Data Viewer webpage  
298 (<http://data.unep-wcmc.org/>). After simplifying the polygons using ArcGIS, by merging adjacent  
299 reefs (separated by less than 20 m), and discarding individual reefs smaller than 25 m<sup>2</sup>, a total of 661  
300 individual reef polygons identified reef habitat for larval settlement (Figure 1). A connectivity matrix  
301 showing the origin locations on one axis and destination locations on the other axis is used to  
302 visualize the geographic connections among habitat patches for simple alongshore linear systems.  
303 However, the two dimensional nature of the reef systems bordering East Africa, with multiple reefs at  
304 the same latitude (e.g., mainland fringing reefs, atolls or patch reefs in the channels between the  
305 islands and mainland, fringing reefs on the west and east coast of the islands), make the reef to reef  
306 connectivity matrices organized by the latitude of the centroid of the reef polygons insufficiently  
307 informative regarding inshore-offshore connections. Due to the spatial complexity of the reef habitat,

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308 we simplified the connectivity matrices by assigning individual reefs to one of fifteen geographic  
309 subregions (Figure 1). Geographic regions considered mainland continuity of reefs, but also national  
310 borders and offshore island masses, many of which have both shoreward facing and offshore facing  
311 fringing reefs (Figure 1). This allowed a more meaningful visualization of the results. Based on the  
312 number of particles released within a region, the percentage of particles that successfully connect  
313 from region to region was calculated. Summing the percentages in the horizontal direction (all  
314 destination regions) on the connectivity matrices shows the percent of successful recruits from each  
315 region of origin.

316

317 The term local retention refers to the ratio of virtual larvae settling at their released location and the  
318 total number of virtual larvae released at that location, while self-recruitment is the ratio of virtual  
319 larvae settling at their released location and the total number of larvae settling at that location. In the  
320 results section the comparatives “weaker” and “stronger” are used to refer to the magnitude of  
321 connections between two specific sites, indicating the proportion of particles connecting from one  
322 reef or region to another. Strong connections appear as large color-coded circles in the connectivity  
323 matrices, while weak connections are small black circles. Conversely “few” and “more/lots” are  
324 used to refer to the number of sites that are connecting to a reef or region. The number of connections  
325 for a region will be represented by the number of circles on each row or column for origin and  
326 destination regions, respectively.

327

328 We use the terms “source” and “origin” interchangeably to refer to reefs or regions from which  
329 virtual larvae are released. Similarly, we use the terms “sinks” and “destinations” interchangeably to  
330 refer to reefs or regions into which virtual larvae successfully settle. We are not referring to  
331 population source/sinks according to the classical population ecology definition, since we do not  
332 consider spatially variable reproductive input nor variable mortality during the settlement phase. In  
333 this case we are referring only to source/sinks of the planktonic pool of successful virtual larvae, and  
334 therefore the terms only refer to the diversity of origins/destinations of the virtual larvae that are  
335 assumed to successfully settle.

336

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### 337 3.5 Sensitivity Analysis

338 Complementary analysis and ‘in silico’ experiments were carried out to determine the sensitivity of  
339 the resulting connectivity matrices linking origins and destinations to the perception distance  
340 assumption and to the inclusion of vertical diffusion. To investigate the sensitivity of settlement  
341 success to perception distance, the coral and surgeonfish reference runs of 2000 were re-analyzed  
342 with perception distances of 10, 500 and 4000 m. This analysis was performed for particle releases  
343 every sixth day for a total of 10 spawning days within February and March. The percent of larvae that  
344 successfully settled on reef habitat and the standard deviation among the 10 release dates was  
345 calculated.

346

347 In order to assess the effects of vertical diffusion on connectivity, and to investigate if an important  
348 proportion of reef-to-reef connections is being missed by considering advective only experiments,  
349 additional experiments similar to the advective only *Acanthurus* reference runs, but with the addition  
350 of vertical diffusion processes, were carried out for 26 selected reefs (Supplementary Figure 5). In  
351 order to perform these simulations with the same computer resources used for the advective only  
352 simulations the number of release locations had to be greatly reduced; we subsampled 10% (a total of  
353 2694 release locations) from the 26938 release locations used for the advection only scenario for  
354 these 26 reefs. For each advection-diffusion release location 100 replicate particles were released on  
355 each of 3 release dates; at the beginning, middle and end of the presumed spawning season (February  
356 2<sup>nd</sup>, March 1<sup>st</sup> and March 31<sup>st</sup>, respectively) of 2000 and 2005. Vertical diffusion was implemented as  
357 a vertical random walk scaled by the vertical viscosity coefficient of the ocean model according to  
358 the model detailed by Batchelder et al. (2002). The connectivity provided by the advection-diffusion  
359 simulations was compared to advection only results from the same 26 reefs to investigate the  
360 potential role of vertical diffusion in either enhancing or reducing connectivity and modifying the  
361 general patterns observed in the advective only experiments. Comparisons were done at the reef  
362 scale. Magnitude of the connections was calculated as the percentage of particles released per reef  
363 that settled. The number of particles released was an order of magnitude higher in the experiments  
364 with diffusion, while the number of release locations was 10 times greater in the advective only  
365 experiments (e.g., 1 particle from each of 50 different locations from a 1 km<sup>2</sup> reef in the advection  
366 only case versus 500 particles from each of only 5 release locations within the same reef in  
367 experiments including vertical diffusion). The results of all 6 release dates (three in each of 2000 and

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2005) were aggregated on a binary reef to reef connectivity matrix, which neglects the magnitude of the connections, and compared to the advective only counterpart. The subtraction of the matrices eliminates connections present in both scenarios and provides an estimate of how many connections were missed by one or the other experimental set ups. Trajectories and connectivity patterns were also visualized and compared to gain understanding of the observed differences, but are not shown.

373

### 4. Results

#### 4.1 *Acanthurus* and *Acropora* 3-D passive advective experiments

##### 4.1.1 *Settlement Success*

Larvae that find a reef within their perception distance during their competency period are assumed to successfully settle. The percentage of successful settlers differs greatly between the two modeled genera. For virtual larvae characterized as *Acanthurus* surgeonfish the mean settlement success of the 40 releases during February and March of 2000 and 2005 is  $24.4 \pm 4.7\%$  while for the *Acropora* coral virtual larvae the mean is  $0.28 \pm 0.04\%$  (Figure 2). Settlement success variability around the mean is similar between the two species groups. Changes in yearly mean settlement success are opposite for the two modeled genera (*Acanthurus* 25.5% in 2000 and 23.3% in 2005, *Acropora* 0.27% in 2000 and 0.28% in 2005).

385

##### 4.1.2. *Region to Region Connectivity Matrices*

The region to region connectivity matrices allow an easier visualization of the main connectivity patterns, synthesizing the information of reef to reef connectivity matrices (available upon request). Regional connectivity matrices with reefs grouped into 15 regions (Figure 1) show a dominant South to North connectivity pattern along the Kenya-Tanzania coast (Figure 3), as represented by the predominance of circles below the 1:1 diagonal line, which indicates sites where local retention occurred (larvae released in a region settled in the same region). This pattern is prevalent in both modeled years (2000 and 2005) for both larvae types (*Acanthurus* and *Acropora*) (Figure 3), and reflects the strong south to north flows that prevail along most of the Kenya-Tanzania region, which is influenced by the northward flowing EACC year round. Most of the small number of circles above

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396 the 1:1 line of the connectivity matrices indicate north to south connections (a few of them represent  
397 west to east connections, for example west Zanzibar (wZ) to east Zanzibar (eZ)), which are much less  
398 common but occur in the northern part of the domain due to the influence of the southward flowing  
399 Somali Current during the Northeast monsoon (December-March), or to small scale recirculation  
400 features, such as eddies, in a few other locations. The magnitude and location of north to south  
401 connections is particularly variable interannually. For the 2000 *Acanthurus* simulation (Figure 3a)  
402 small proportions of north to south connections occur in most regions, but mainly at the northern-  
403 most (Somalia [sS], Kenya regions [nK, sK]) and southern-most regions (east Mafia [eM]) and in  
404 some central regions (Dar es Salaam Peninsula [DP] and central Tanzania [cT]). In 2005 (Figure 3c)  
405 north to south connections are weak at the northern and southern limits of the domain, but somewhat  
406 stronger in the central region (Dar es Salaam Peninsula [DP], western Zanzibar [wZ] and central  
407 Tanzania [cT]).

408

409 In *Acropora* corals (Figure 3b, d) most of the connections are due to within region recruitment, and  
410 strong connections are restricted to a 1 degree (~100 km) radius around the reef of origin. The reef  
411 offshore of Dar es Salaam (oR), east Mafia (eM) and south Tanzania (sT) regions show the longest  
412 distance connections. Interannual variability in north to south connections is similar to that of  
413 *Acanthurus* virtual larvae.

414

415 Regional connectivity matrices enable differentiation among across-shore reefs at the same latitude,  
416 and yield insights about well-connected and isolated reef regions. At a regional scale, the Kenya (sK,  
417 nK) and Somali (SS) reefs receive *Acanthurus* virtual larvae from all other reef regions in both  
418 modeled years. In contrast reef regions adjacent to Pemba Island (eP, nP, wP) receive very few  
419 *Acanthurus* larvae from any other reef habitats within the model domain (Figure 3a, c). The reef  
420 offshore of the Dar es Salaam peninsula (oR at ca. 7°S), due to its oceanic location and exposure to  
421 the strong northward flowing EACC, has potential for long distance connections. Settlement of  
422 *Acanthurus* from oR was very different in the two modeled years. In 2000 it was a source for larvae  
423 settling on distant Kenyan (sK, nK) and Somali (sS) reefs only; in 2005 it exported larvae to Kenyan  
424 (sK, nK) and Somali (sS) reefs, but also to some nearer Tanzania regions (central and north Tanzania  
425 and east Zanzibar regions; cT, nT, eZ). This offshore reef (oR) is not a large sink reef for *Acanthurus*

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426 larvae, but the origin of its arriving larvae is diverse, coming from reefs to the south of it in 2000 and  
427 from all regions except east Zanzibar (eZ) in 2005. The Somalia (sS) and Kenya (sK, nK) regions are  
428 the sink regions with the greatest diversity of source reefs, followed by the north Tanzania (nT)  
429 region. Larvae from Dar es Salaam Peninsula (DP) region settling in the north Tanzania region  
430 represented the strongest connection in 2000, followed in magnitude by the connection from the east  
431 Zanzibar (eZ) region to the south Kenya (sK) region. In 2005 the strongest connection remains the  
432 same but the second strongest connection was between east Zanzibar (eZ) and the north Tanzania  
433 (nT) region. During 2005 source reefs around Zanzibar Island (eZ, wZ) and the central Tanzania (cT)  
434 region had more connections to southern destination reefs. However, local retention of *Acanthurid*  
435 surgeonfish virtual larvae at the regional scale was larger in 2000.

436

437 For *Acropora* corals (Figure 3b and d) the highest proportion of recruitment is due to local within  
438 region recruitment at the west Zanzibar (wZ) and west Pemba (wP) regions in both 2000 and 2005. In  
439 all regions except east Pemba (eP) and the offshore reef (oR), the probability of recruiting locally is  
440 higher than the probability of connecting to another reef region. Similar to *Acanthurus*, more north to  
441 south connections of *Acropora* are observed in the regions between north Tanzania (nT) and the Dar  
442 es Salaam Peninsula (DP) in 2005 than in 2000, when substantial north to south connection occurred  
443 only between Dar es Salaam (DP) and west Mafia (wM). In 2000, the offshore reef (oR) connects to  
444 all Pemba regions (eP, wP, nP) and north Kenya (nK), while in 2005 it connects to all regions north  
445 of Dar es Salam except north and west Pemba (nP, wP). This offshore reef is the only source of  
446 *Acropora* larvae for the east Pemba (eP) region. North and west Pemba get recruits from all Pemba  
447 regions in both years.

448

449 The variable number of north to south connections between the two modeled years is explained by  
450 the influence of the mesoscale circulation on the shelf circulation pattern. In 2000 the northward  
451 flowing East African Coastal Current (EACC) was weak during the spawning months ( $<0.5 \text{ m s}^{-1}$ ) as  
452 is typical during the NE monsoon season. The Somali Current (SC) that flows southward at this time  
453 of the year was strong in February ( $\sim 0.68 \text{ m s}^{-1}$ ) and its subsurface influence prevailed until April  
454 (Supplementary Figure 1). The strong influence of the southward flowing SC current in the northern  
455 part of the domain is responsible for the north to south connections in that region. In the rest of the



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456 domain the weak EACC generates slower northward velocities on the shelf during the spawning  
457 months, especially February (Supplementary Figure 2), allowing for some north to south connections  
458 at most latitudes, more evident in the reef to reef connectivity matrices (Supplementary Figure 6).

459

460 In contrast, in 2005, the SC was weaker and only present during February and March since the  
461 transition to SW monsoon conditions happened very early in the year, with strong northward flow  
462 ( $>1 \text{ m s}^{-1}$ ) established in March and already re-established in the upper 300 m by April  
463 (Supplementary Figure 3). The weak SC only promotes a few north to south connections in the  
464 northern part of the domain. The strong EACC intensifies the flow reversal north of the Mafia and  
465 Zanzibar Channels, which is generated as the northward flow overshoots and turns southward into  
466 the channels when trying to follow the curved bathymetric contours past the islands (Supplementary  
467 Figure 4). This small scale circulation pattern is responsible for the north to south connections  
468 observed on regions around the north and south entrances of the Zanzibar Channel in 2000 for both  
469 *Acanthurus* and *Acropora* virtual larvae (Supplementary Figure 6).

470

### 471 **4.2 *Acanthurus* Ontogenetic Vertical migration (OVM) experiments**

#### 472 **4.2.1. *Acanthurus* OVM Settlement Success**

473 Experiments that include an idealized OVM exhibit greater variability in *Acanthurus* settlement  
474 success among release dates within a year and between the two modeled years compared to the  
475 passive larvae experiments (Figures 2a and 4). Mean settlement success is  $34.5\% \pm 14.6$  for 2000 and  
476  $17.7\% \pm 8.3$  in 2005, but due to the large variability among release dates, the year to year difference is  
477 not statistically significant. There is a marked decrease in settlement success from earlier to later  
478 spawning dates in the OVM scenario, going from 46.8% for particles released in February 2<sup>nd</sup> to  
479 7.2% for those released on March 31<sup>th</sup> in 2000 and from 34.0% to 15.9% for those same dates in  
480 2005. The decrease in settlement success occurred earlier in 2005 than during 2000, associated with  
481 the rapid transition to SW monsoon conditions in 2005 (Supplementary Figure 4). In the northern  
482 part of the model domain the core of the northward flowing EACC is subsurface (below 70 m depth)  
483 at the beginning of the spawning season (NE monsoon), but it re-establishes in the upper 300 m by  
484 May in 2000 and April in 2005 (Supplementary Figures 2 and 4). This implied that 2005 larvae

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485 migrating down to 50 m are affected longer by the strong northward flow than the 2000 larvae.  
486 Three-dimensional passive larvae tend to stay near the surface and are therefore less likely to be  
487 carried away from suitable habitat by the strong northward flowing EACC core transitioning from  
488 deep to shallow waters during the second half of the spawning season.

489

### 490 **4.2.2. *Acanthurus* OVM Region to Region Connectivity Matrices**

491 When grouped at the regional level the *Acanthurus* OVM numerical experiments showed that in 2000  
492 (Figure 5a) the strongest connection was between central Tanzania (cT) and north Tanzania (nT). The  
493 north Tanzania (nT) region received virtual larvae from all southward reefs. The south and north  
494 Kenya regions (sK, nK) and the south Somalia (sS) region receive recruitments from all other  
495 regions. Southern Tanzania (sT), east and west Mafia (eM, wM) and the Dar es Salaam Peninsula  
496 (DP) regions provide larvae to most other regions except the offshore reef (oR), but their  
497 probabilities of connecting to the Pemba regions are very low. The main sinks for larvae coming  
498 from the offshore reef (oR) in 2000 are the distant Kenya (sK, nK) and Somalia (sS) regions.  
499 Minimal north to south connections occur with larvae originating at east and west Mafia (eM, wM)  
500 and the Dar es Salam Peninsula regions (DP) in Tanzania, the south and north Kenya (sK, nK)  
501 regions and south Somalia (sS), connecting to southward regions. Across shore connections are  
502 observed mainly from west Zanzibar (wZ) to north Tanzania (nT) and from east to west Mafia (eM to  
503 wM).

504

505

506 In 2005 (Figure 5b), the offshore Dar es Salaam reef (oR) has strong connections with both Zanzibar  
507 (eZ, wZ) and north Tanzania (nT) regions as well as distant Kenya and Somalia regions. The  
508 strongest connection of 2005 occurred between the offshore reef (oR) and the south Kenya (sK)  
509 region. Most regions successfully connect to northward regions, except to the three Pemba Island reef  
510 regions, which get few recruits in both years modeled. Small proportions of the larvae spawned at the  
511 Dar es Salaam Peninsula (DP) and north Tanzania (nT) regions connect southward to the west Mafia  
512 and west Zanzibar regions, respectively. Across shore connections are weaker.

513

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514 Interannual variability in the general patterns of reef connectivity for *Acanthurus* is enhanced when  
515 the ontogenetic vertical migration behavior is included, especially regarding the magnitude of the  
516 connections. Weaker and fewer connections are observed in 2005 in comparison to 2000 (Figure 5).  
517 As in the passive scenario, a strong interannual difference is observed in the number and location of  
518 south to north connections, with stronger north to south connectivity in the southern and northern  
519 most regions in 2000, and uniformly weak north to south connections in 2005. Overall, spatial  
520 connectivity of OVM *Acanthurus* in each of 2000 and 2005 are remarkably similar to the patterns  
521 observed for 3D passive *Acanthurus*, although the overall connectivity is lower with OVM than the  
522 passive, particularly in 2005.

523

### 524 **4.3 Sensitivity Analysis**

#### 525 ***4.3.1 Sensitivity to perception distance***

526 The analysis with increased (reduced) perception distance for *Acropora* (*Acanthurus*) is presented to  
527 provide insight on one of the processes responsible for the large difference in settlement success  
528 between the modeled species groups, and to illustrate the variability that might be expected among  
529 coral reef species with different life-history strategies. The percentage of settlement success increased  
530 with greater perception distance for both the *Acanthurus* surgeonfish and the *Acropora* coral  
531 simulations (Figure 6). However, the increase in settlement success for the short PLD coral was  
532 always much higher than that of the surgeonfish for the same increase in perception distance, with the  
533 coral reaching 95% settlement success with a 4 km perception distance. The difference in settlement  
534 success between the two genera was significant for all perception distance scenarios (Figure 6),  
535 indicating that with the same perception distance short PLD virtual larvae will always be more  
536 successful. Perception distance scenarios alternative to the reference run experiments are not  
537 appropriate for the specific genera used here, but might be appropriate for other coral reef organisms  
538 with different life-history traits. *Acropora* coral larvae perceive reefs through sound (Vermeji et al.,  
539 2010) and chemical cues (Heyward and Negri, 1999; Dixson et al., 2014), but their perception  
540 capabilities are unlikely to exceed 100 m. Laboratory experiments have shown that coral larvae are  
541 able to detect reef sounds 0-1 m from the source and move towards them (Vermeji et al., 2010). If  
542 planulae are capable of detecting particle motions anticipated perception distances are on the 10-100  
543 m range (Vermeji et al., 2010). Despite their sensing abilities, the swimming ability of coral larvae is

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544 very limited and usually negligible in comparison to ocean currents (Kingsford et al., 2002; Baird et  
545 al., 2014). To the contrary, *Acanthurus* late larvae are one of the strongest swimmers among coral  
546 reef fish larvae, with reported *in situ* swimming speeds ranging from 8.7 to 65.3 cm s<sup>-1</sup> (Leis and  
547 Carson-Ewart, 1999; Leis and Fisher, 2006). They have been observed to navigate *in situ*  
548 disregarding current direction, perhaps guided by a sun compass (Leis and Carson-Ewart, 2003).  
549 Navigational capabilities exceeding 1 km are therefore expected for *Acanthurus*.

550

### 551 4.3.2 Diffusion effect

552 The inclusion of vertical diffusion greatly increased the vertical spread of the virtual larvae and  
553 distributed them throughout the water column over the shelf. This, in turn, increased the horizontal  
554 spread of virtual larvae. The main connectivity patterns of the *Acanthurus* advective only  
555 experiments were also represented in the experiments with diffusion, including the interannual  
556 differences (not shown). The strength of the connections on the *Acanthurus* diffusive scenario was,  
557 however, an order of magnitude smaller than in the advective only scenario, indicating that the  
558 vertical spread of particles released at the same location leads to the majority of them dispersing  
559 away from suitable habitat. The extent to which the inclusion of vertical diffusion generated new  
560 connections, not represented in the advective only scenario was modest (Figure 7). From the 100%  
561 represented by the total number of connections found only in one of the two scenarios, 12.4% came  
562 from the scenario that included vertical diffusion, whereas 87.6% came from the advective only  
563 scenario. Thus, it is clear that including diffusion to the advection scenario produces relatively few  
564 new connections to the matrix, and that for this particular case the inclusion of a vertical random  
565 walk component may not be essential to providing a representative connectivity matrix.

566

## 567 5. Discussion

568 The dominant pattern of connectivity for both *Acanthurus* and *Acropora* in the KT region is southern  
569 reefs providing virtual larvae to northern reefs. The spatial scale of connectivity is much smaller for  
570 the short PLD coral group; successful connections are restricted to a 1° radius (~100 km) around  
571 source reefs. 8.2% of *Acropora* larvae that successfully settle, recruited to their source reef (self-), an  
572 important proportion compared to only 1-2 % for *Acanthurus*. Some *Acropora* were capable of long

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573 distance dispersal, particularly larvae spawned at the reef offshore of Dar es Salaam peninsula. This  
574 indicates that they can take advantage of the strong offshore EACC to reach distant northern reefs,  
575 and that even for short PLD, latitudinal isolation may be minimal, especially at longer (i.e.  
576 evolutionary) timescales.

577

578 In contrast to the generally short dispersal distances of *Acropora*, long distance connections from the  
579 southern to the northern most reefs (~950 km) are common for virtual *Acanthurus*. Their longer  
580 pelagic durations lead to greater transport distances and reduced local retention. Overall settlement  
581 success was significantly greater in *Acanthurus* (24%) than in *Acropora* (<0.5%). This is due to  
582 several factors that enhance *Acanthurus* successful settlement probabilities: longer competency  
583 period, greater reef perception distance and swimming ability.

584

585 While south to north connections predominate in the connectivity matrices, some north to south  
586 connections occur, mostly in inshore regions that experience substantial eddy flows and  
587 topographically steered flow reversals. Examples of these are 1) the northern region that is seasonally  
588 influenced by the southward flowing Somali current (SC) (Figure 3), and 2) the northern entrance of  
589 the Zanzibar Channel and the region south of the Dar es Salaam peninsula where nearshore flow  
590 reversal is promoted by strong northward offshore currents (Mayorga-Adame et al., 2016). Therefore,  
591 there is strong interannual variability in the amount and location of north to south connections  
592 depending on the strength of the offshore mesoscale currents. When the Somali Current is strong  
593 (e.g., in 2000), short distance north to south connections are common at most latitudes, but are most  
594 prevalent near the northern and southern edges of the study region. When northward offshore flow is  
595 strong and the SC disappears early in the year (e.g., 2005), north to south connections are restricted  
596 to reefs in the wider shelf region between Pemba and Mafia Islands (due to enhanced small scale  
597 flow reversals) and the region north of 3°S where the Somali Current has a direct effect.

598

599 Interannual variability is also evident in the strength of the connections among reefs and the  
600 proportion of local retention. Thirteen reef regions (all but oR, eP) experience local retention in 2000,  
601 however in 2005 five regions (sT, oR, eP, nP, wP) had no or minimal local retention. In several cases

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602 the strong connections among regions are not consistent between 2000 and 2005; analysis of  
603 simulations for other years is needed to assess the persistence of connectivity patterns. Multi-year  
604 simulations (e.g. James et al. (2002), 20 years' model of reef fish connectivity in a section of the  
605 Great Barrier Reef; Dorman et al., (2015), 46 years' model of *Acropora millepora* connectivity in the  
606 South China Sea) would give further insight on the variability and robustness of the connectivity  
607 patterns and help to identify connections that are vital to maintaining regional metapopulations of  
608 different species groups.

609

610 The different connectivity patterns and scales of dispersal for the two genera characterized in these  
611 modeling experiments show that it is important to consider interspecies life-history variability when  
612 implementing conservation strategies to ecosystems as diverse as coral reefs, since ideal spatial  
613 management strategies would enhance settlement success for a wide suite of species with different  
614 perception and dispersal capabilities. Our results indicate, for example, that *Acanthurus* virtual larvae  
615 settling to coral reefs around Pemba Island come from relatively few source reefs, which highlights  
616 the need for strong local protection since the resilience, (e.g. potential recolonization of Pemba's  
617 *Acanthurus* populations from more distant reefs), is minimal, despite their relatively lengthy larval  
618 pelagic phase. Pemba Island *Acropora* coral populations are less vulnerable since they show stronger  
619 and more variable connections. This seems counter intuitive given the smaller scale of connectivity  
620 and higher local retention rates of *Acropora*, however the local oceanographic regime around Pemba  
621 Island, including a strong return flow on the western side of the island, promotes retention at short  
622 time scales, favoring *Acropora* connections, while the much longer PLD of *Acanthurus* favors  
623 transport away from Pemba's suitable habitat.

624

625 The level of connectivity of a reef is a component of its resilience and the extent of its ecological  
626 impact in the region. For example, strong sink reefs, those receiving settlers from many different  
627 source reefs, are more resilient to local and global stresses, since having multiple sources increases  
628 the probability of receiving recruits in any given year. The diversity of sources providing potential  
629 recruits would enhance resilience to short term local detrimental phenomena such as bleaching events  
630 and overfishing. On the other hand, important source reefs, those with potential of providing settlers  
631 to many other reefs, could have a disproportionately large ecological impact for many other reefs.

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632 Reefs that provide larvae to many other sites are important to protect from a larger ecosystem  
633 conservation perspective, since an increase of the local spawning population would likely impact  
634 recruitment to a large number of reefs elsewhere, therefore increasing the impacts of spatially limited  
635 conservation measures (e.g. MPA) beyond their boundaries (Bode et al., 2006; Figueira, 2009).  
636 “Source and sink” maps are useful for identifying ecologically important areas based on the number  
637 and type of connections present. Source and sink maps for *Acanthurus* are shown in Figures 8 and 9,  
638 and for *Acropora* virtual larvae in Figures 10 and 11. The passive and OVM scenarios (not shown)  
639 for *Acanthurus* yielded similar source and sink maps. In general reefs south of Mafia Island (8°S)  
640 provide larvae of both species groups to the greatest number of reefs. In the case of *Acanthurus*  
641 larvae (Figure 8) these reefs connect to more than 350 different reefs, and for *Acropora* (Figure 10)  
642 to more than 70 reefs. Reefs in the northern half of Tanzania are good sources of *Acropora* larvae,  
643 connecting to more than 50 reefs, while Kenyan reefs connect to approximately 30 different reefs.  
644 Local conservation efforts in these areas are likely to have an important ecological impact beyond  
645 their local ecosystem, since they can help maintain and replenish multiple other metapopulations at  
646 various destination reefs. Somali reefs to the contrary provide *Acanthurus* virtual larvae to less than  
647 50 reefs and *Acropora* virtual larvae to less than 10 different reefs. While this may be an artifact of  
648 these reefs being near the northern border outflow, the role of Somali reefs in providing recruits of  
649 reef species further north is minimal as there are few coral reefs within the immediate north region.  
650 Kenyan and Somali reefs are however the most common sink reefs, receiving larvae from many reefs  
651 to their south (Figure 11). These northern reefs may be more resilient to local threats. The source and  
652 sink patterns reflect the strong, mostly unidirectional south to north flow along the coast. For  
653 *Acropora* larvae, the source and sink maps are much more patchy (Figures 10 and 11, respectively),  
654 reflecting the effects of the smaller dispersal scale of *Acropora* larvae.

655

656 A recent genetic study of *Acropora tenuis* connectivity in the KT region, reports high but variable  
657 connectivity between sample sites, which cluster in 3 different groups: 1) Kenya and northern-  
658 Tanzania, 2) southern Tanzania, and 3) sample sites located in the Zanzibar and Pemba channels  
659 (Van der Ven, 2016). No clear genetic break on samples collected along 900 km of coral reefs was  
660 observed. Also, no genetic differentiation with increasing geographical separation was found, in  
661 contrast to similar studies in the Great Barrier Reef and Japan. They associate the genetic uniformity  
662 in the KT region with uniform oceanographic conditions promoted by the continuous south to north

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663 linear flow of the EACC. The highest differentiation observed in group 3 is associated with local  
664 oceanographic conditions causing larval retention. The connectivity patterns of our modelling study  
665 agree with their findings, despite the different time scales assessed. The north to south connectivity  
666 we report is expected to minimize genetic differences along the KT coast. Our model also  
667 corroborates the isolation they infer for their highly differentiated Pemba and Zanzibar Channel sites.  
668 Our model results indicate that west Pemba (wP) and west Zanzibar regions, receive the majority of  
669 their *Acropora* virtual larvae through within region recruitment. The circulation patterns depicted by  
670 our ROMS model included flow reversals at the northern entrance of the channels and eddy blockage  
671 in the southern entrance of the Zanzibar Channel (Mayorga-Adame et al., 2015); these might provide  
672 sufficient isolation to upstream sources to produce genetically different *Acropora* populations in the  
673 channel sites.

674

675 Genetic connectivity patterns for *Pocillopora damicornis* (a brooding coral species) based on  
676 contemporary gene flow (Souter et al., 2009) can be compared with our modeling results for the  
677 longer PLD, broadcast spawner *Acropora* corals. Souter et al., (2009) identified first generation  
678 migrants of *P. damicornis* at 29 reefs sites in the Kenya-Tanzania region, and therefore determined  
679 the degree of isolation of the different reefs sampled. They found patchiness in the degree of isolation  
680 at very small scales, with marked differences even between lagoon and fringing reefs within the  
681 Malindi Marine National Park and Reserve in south Kenya. The patchiness observed in our *Acropora*  
682 source and sink maps is consistent with their results, indicating strong small-scale spatial variability  
683 in the number of connections (degree of isolation) among nearby reefs. Souter et al. (2009) identified  
684 isolated reefs, highly dependent on local retention for population renewal, in south Kenya, west  
685 Pemba, and south Mafia. In the *Acropora* simulations these regions receive virtual larvae from less  
686 than 10 different source reefs (Figure 11). The regional *Acropora* connectivity matrices (Figure 3b,  
687 d) show that local retention is important for these regions. In our regional connectivity results,  
688 however, only west Pemba, east Mafia and south Tanzania show relative isolation, receiving  
689 *Acropora* larvae from only three and two other regions respectively; south Kenya in contrast receives  
690 settlers from many regions further south. This discrepancy between our model results and Souter et  
691 al.'s (2009) genetic study may reflect the different spatial scales considered, since our regional  
692 grouping aggregates connections for several reefs that might have different degrees of isolation.  
693 Souter et al. (2009) identify Mnemba Conservation Area (in the east Zanzibar region) as a strong



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694 source for other sampled sites. This site shows the highest genetic diversity and is similar only to one  
695 site in the Dar es Salaam Peninsula and one site in southeast Mafia Island. In the simulation  
696 *Acropora* larvae that settle in the east Zanzibar region, which includes Mnemba Island, come from  
697 few origin reefs (mainly Dar es Salaam Peninsula and east Mafia regions, Figure 3b, d). The number  
698 of regions that receive *Acropora* larvae from east Zanzibar ranges between 3 and 5 in the 2000 and  
699 2005 simulations. The source map for *Acropora* (Figure 10) shows that most reefs around Mnemba  
700 (east Zanzibar) provide larvae to approximately 30 to 60 different reefs. Our model results identify  
701 specific reefs in the west Mafia and southern Tanzania regions as the main providers of *Acropora*  
702 larvae while the genetic results of Souter et al. (2009) do not identify their south Mafia and Mtwara  
703 (south of our model domain) sites as important sources. This could be due to the high reef to reef  
704 patchiness on the level of isolation identified by both their observational and our modeling study, the  
705 uncertainty of which specific reefs were actually sampled for the genetic study, and the shorter PLD  
706 of *Pocillopora damicornis*. To the extent allowed by the comparison of this model with the genetic  
707 sampling of specific reefs results of Souter et al. (2009), the main connectivity patterns elucidated by  
708 their genetic study for an ecologically similar coral species are well represented in the connectivity  
709 results provided by the coupled biophysical model for *Acropora*. This comparison is limited to the  
710 regional level, since the exact location of the reefs sampled by Souter et al. (2009) is not reported.

711

712 Only at the beginning of the spawning season did the ontogenetic vertical migration ‘in silico’  
713 experiments of *Acanthurus* virtual larvae generate more successful settlers than the 3D passive  
714 scenario (Figures 2a and 5). This is inconsistent with prior reports in the literature for various larvae  
715 in the Caribbean (Paris et al., 2007) and the California Current System (Drake et al., 2013), where  
716 OVM consistently increased settlement success. Differences in shear and stratification of the water  
717 column of each region may be responsible for this marked difference among oceanographically  
718 distinct regions. The shelf circulation of Kenya and Tanzania is dominated by strong alongshore  
719 flows with an increased magnitude offshore, a shallow (i.e. less than 50-100 m) wind driven mixed  
720 layer is not common. Northward flow velocities dominate the coastal circulation off Kenya and  
721 Tanzania down to 300 m depth during most of the year. Therefore, a vertical migration down to 50 m  
722 depth would have little effect on transport pathways. During the SE monsoon (Dec-Mar) the Somali  
723 Current flows southward in the upper 100 m north of 3°S. During this period, which encompasses  
724 part of the spawning period, staying near the surface, instead of migrating to deeper waters, would

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725 facilitate north to south connections and retention if the duration of the pelagic phase includes the  
726 seasonal reversal to northward flow. Only during the transition between NE to SE monsoon  
727 conditions would a shallow migration result in significantly shorter horizontal displacements for  
728 *Acanthurus* larvae. Intraseasonal and interannual variability increased when the simple ontogenetic  
729 vertical migration behavior was implemented because the evolution of the vertical structure of  
730 alongshore velocities was markedly different in the two modeled years (Supplementary Figures 2 and  
731 4). The ontogenetic vertical migration pattern modeled here is based on the increased depth of the  
732 *Acanthurus* larvae during ontogeny observed by Irisson et al. (2010). The depth of the migration is  
733 not well defined and could be site dependent. For example, Irisson et al. (2010) reported post-flexion  
734 *Acanthurus* larvae in the 25-60 m depth range near reefs in French Polynesia, while Oxenford et al.  
735 (2008) found aggregations of late *Acanthurus* larvae to be more abundant at 120 m in the eastern  
736 Caribbean Sea. No observations for the East-African coast exist. Observations of vertical distribution  
737 and abundance of pelagic larvae concurrent with hydrographic conditions are needed to design more  
738 realistic vertical migration experiments, and to assess larval fish responses to temperature, light, or  
739 velocity. The implementation of vertical migration in these numerical experiments was highly  
740 idealized, shifting all particles to 50 m depth 20 days after release, ignoring their vertical position at  
741 that time. This meant that some larvae that had passively advected deeper than the 50 m fixed  
742 migration depth were actually displaced upward with this vertical migrating behavior. The number of  
743 particles that advected below 50 m depth was not an important fraction of the successful larvae since  
744 most larvae stayed in the upper 5 m when passively advected; a small proportion, however, reached  
745 depths below 100 m. Migrating only shallow particles downward would be a more realistic scenario  
746 as well as distributing the particles within a broader depth range rather than fixing them to a single  
747 specific depth. Many other, perhaps more realistic scenarios are possible next steps. However, in-situ  
748 data of larvae depth distributions would be required to properly parameterize more realistic scenarios.  
749 The aim of the simple scenario modeled here was to illustrate the potential effects on connectivity of  
750 an ontogenetic vertical migration to 50 m (with depth keeping) in a rapidly evolving water column  
751 with deep stratification and strong shear.

752

753 The numerical experiments presented here are deterministic and represent a population where all  
754 larvae develop and behave identically, without actively responding to its environment. Real larvae  
755 are complex organisms, with strong inter-specific and potentially intra-individual variability in

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756 physiology and behavior, constantly reacting to their environment. Complex models with behavior  
757 cueing on the environmental conditions experienced by the virtual larvae have been developed (e.g.  
758 Armsworth, 2001; Saaterman et al, 2012; Wolansky and Kingsford, 2014). Assuming that larvae are  
759 well adapted to the pelagic phase, larval behavior, particularly sensing, orientation and swimming  
760 abilities would enhance their probability of finding suitable settlement habitat, which might reduce  
761 interannual variability in settlement success. However, when challenged by increased environmental  
762 variability due to climate change effects, their strategies may not be guaranteed to work. The  
763 numerical experiments presented here, although idealized, serve as an initial effort to develop  
764 hypotheses that might be examined using more complex models and empirical studies. Monitoring  
765 recruitment of coral reef organisms is basic to assessing the effects of environmental variability on  
766 settlement success. Having long term time series of recruitment of coral reef dependent species in the  
767 Kenya-Tanzania region would be valuable for “tuning” models, as has been done for other coral reef  
768 regions (i.e. Sponaugle et al., 2012).

769

770 The fraction of released larvae that settle on suitable habitat is highly sensitive to the individual’s  
771 habitat perception and swimming abilities; further knowledge regarding the capabilities of coral reef  
772 larvae to perceive, navigate and settle on suitable habitat is a very important and a challenging piece  
773 of information to obtain. Both in-situ and laboratory observations of larval development and behavior  
774 are needed to further increase the realism of modeling experiments. The dependence of PLD on  
775 temperature is well established for aquatic organisms (O'Connor et al., 2007) but observations for the  
776 studied genera are insufficient to adequately parameterize the functional response between  
777 temperature and PLD. The inclusion of temperature dependent PLD in bio-physical models is  
778 essential for examining climate change effects on connectivity and settlement success of marine  
779 larvae (Lett et al., 2010; Figueiredo et al., 2014). Changes in ocean circulation will alter connectivity  
780 patterns, but physiological effects due to the increased temperature will also have an important effect  
781 (Munday et al., 2009; Lett et al., 2010; Kendall et al., 2016). Reduced pelagic larval durations are  
782 expected under faster developmental rates, which could lead to a reduction in dispersal distances and  
783 the spatial scale of connectivity (Munday et al., 2009; Lett et al., 2010). Bio-physical modeling  
784 connectivity studies including temperature dependent PLD report increased local retention (Andrello  
785 et al., 2015; Figueiredo et al., 2014) and significant changes in Marine Protected Area network  
786 interconnectivity (Andrello et al., 2015) under climate change scenarios. Well-informed idealized

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787 experiments that include temperature dependent PLD of virtual larvae are a future direction for  
788 assessing the effects of climate change scenarios on connectivity and recruitment of coral reef  
789 organisms in the East-African coast.

790

791 Larvae in the ocean are subject to mixing at scales smaller than those represented in the ocean  
792 circulation model. In particle tracking models these unresolved motions are often implemented as a  
793 random walk scaled by the model diffusivity. Simulations that implement a random walk to mimic  
794 diffusion are considered more realistic but computationally expensive. We conducted a few  
795 sensitivity experiments that included 3-dimensionally variable vertical diffusion. Simulations that  
796 included vertical diffusion (not shown) reproduced the main connectivity patterns produced by the  
797 3D advective only experiments, but with smaller connectivities—mostly due to greater vertical  
798 dispersion that subjected larvae to greater horizontal flow variation. These results are probably more  
799 realistic for early or weakly swimming larvae (e.g., coral species) that are unable to maintain their  
800 vertical position in the water column in the presence of vigorous vertical mixing.

801

802 While reef-to-reef connectivity is important in metapopulation ecology, regional connectivity is  
803 expected to be more robust to the uncertainty introduced by the oceanographic and biological  
804 assumptions made in these models. Region to region connectivity matrices synthesize the  
805 information of reef to reef connectivity matrices, making it more manageable and easier to interpret.  
806 The regional summary could assist managers, policy makers and the general public to understand the  
807 interconnections among coral reef regions due to pelagic larval dispersion of their local populations.  
808 Previous bio-physical connectivity studies highlight the importance of considering larval connectivity  
809 at regional levels when trying to prioritize the implementation of management strategies for both  
810 conservation and fisheries enhancement goals. One of the insights of examining connectivity at a  
811 regional scale is that the importance of international connections becomes obvious, as has been  
812 shown by Kough et al. (2013) for the Mesoamerican reefs and by Rossi et al., (2014) for the  
813 Mediterranean Sea. In all numerical experiments Tanzanian reefs were an important source of settlers  
814 to Kenyan reefs; this provides insight and guidance on the spatial scale at which management  
815 strategies are required and points to the need for regional international collaborations in order to  
816 provide enduring conservation measures and protection to the east African coral reef ecosystem.

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817

818 This modeling study is a first approach to understanding the connectivity among coral reef  
819 populations in a data poor region. The information provided, even though preliminary, presents a  
820 general pattern of the potential regional connectivity and identifies particularly resilient and  
821 vulnerable areas as well as the hydrodynamic features driving the connections. Spatial scales of  
822 connectivity and settlement success rates are within the ranges reported by other bio-physical  
823 modeling studies for similar genera in other coral reef regions (Paris et al., 2007; Dorman et al.,  
824 2015). However, the robustness of the connectivity patterns presented needs to be further evaluated  
825 by performing experiments for more years and longer spawning seasons, and carrying out more  
826 extensive sensitivity analysis to the model assumptions. After gaining more confidence in the  
827 modeled connectivity patterns, the information provided by this modeling study could be carefully  
828 and critically evaluated, in order to be applied to optimize the effectiveness of marine protected area  
829 management and other marine protection efforts. Further modeling experiments similar to those  
830 presented here, but better informed by empirical data, and including the capability of larvae to  
831 respond to the ocean conditions will provide greater detail on the complex biophysical interactions  
832 that occur in the sea, and will provide a more realistic, and less uncertain, representation of  
833 connectivity patterns. These results will aid in understanding how a range of species specific  
834 individual responses influence the distribution and connectivity patterns and should enable more  
835 specific guidelines for spatial management that provide better resource resiliency and protection  
836 throughout the Kenya-Tanzania coastal region.

837

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843

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- 1305
- 1306 **8. Figures**
- 1307 **8.1 Figure legends**
- 1308 Figure 1: Study area with coral reefs grouped by color into 15 regions: sS = south Somalia, nK =  
1309 north Kenya, sK = south Kenya, wP = west Pemba, eP = east Pemba, nP = north Pemba, nT = north  
1310 Tanzania, wZ = west Zanzibar, eZ = east Zanzibar, cT = central Tanzania, DP = Dar es Salaam  
1311 Peninsula, oR = offshore Reef, wM = west Mafia, eM = east Mafia, and sT = south Tanzania.
- 1312
- 1313 Figure 2: Percentage of settlement success per each simulated release date during 2000 and 2005 for  
1314 the a) *Acanthurus* and b) *Acropora* genera.
- 1315
- 1316 Figure 3: Region to region connectivity matrices with reefs grouped into 15 regions marked with  
1317 different colors in Figure 1 and identified as sS=south Somalia, nK = north Kenya, sK = south  
1318 Kenya, wP = west Pemba, nP = north Pemba, eP = east Pemba, nT = north Tanzania, wZ = west  
1319 Zanzibar, eZ = east Zanzibar, cT = central Tanzania, DP = Dar es Salaam Peninsula, oR = offshore  
1320 Reef, wM = west Mafia, eM = east Mafia, and sT = south Tanzania. Color and size of the circles are  
1321 proportional to the percentage of successful connections from source to sink reefs according to the  
1322 colorbar.
- 1323
- 1324 Figure 4: Percentage of settlement success per each simulated release date during 2000 and 2005 for  
1325 *Acanthurus* virtual larvae with an idealized Ontogenetic Vertical Migration (OVM).
- 1326

## Larval Connectivity of Coral Reef Organisms in the Kenya-Tanzania Region

1327 Figure 5: Region to region connectivity matrices for *Acanthurus* virtual larvae with OVM. Reefs  
1328 were grouped into 15 regions identified by two letters in Figure 1. Color and size of the circles are  
1329 proportional to the percentage of successful connections from source to sink reefs according to the  
1330 colorbar.

1331

1332 Figure 6: Settlement success for *Acropora* (magenta circles) and *Acanthurus* (green triangles) larvae  
1333 with different perception distances (10, 500 and 4000 m). The mean of 10 release dates during 2000  
1334 ( $\pm 1$  standard error) is shown.

1335

1336 Figure 7: *Acanthurus* connectivity matrix for the 26 origin reefs selected for the experiments  
1337 including vertical diffusion (Supplementary Figure 5), showing only the unique connections present  
1338 in either the advective only experiments (blue) or the advection-diffusion experiments (red). The  
1339 figure is the cumulative result of 3 release dates in each modeled year (2000 and 2005). The size of  
1340 the bubbles is proportional to the percentage of particles exchanged with the biggest bubble  
1341 representing 11%)

1342

1343 Figure 8: Reefs color coded by the number of different destination reefs reached by *Acanthurus*  
1344 virtual larvae originated from them, in both simulated years to identify the best source reefs.

1345

1346 Figure 9: Reefs color coded by the number of different source reefs it received *Acanthurus* virtual  
1347 larvae from, in both simulated years to identify the best sink reefs.

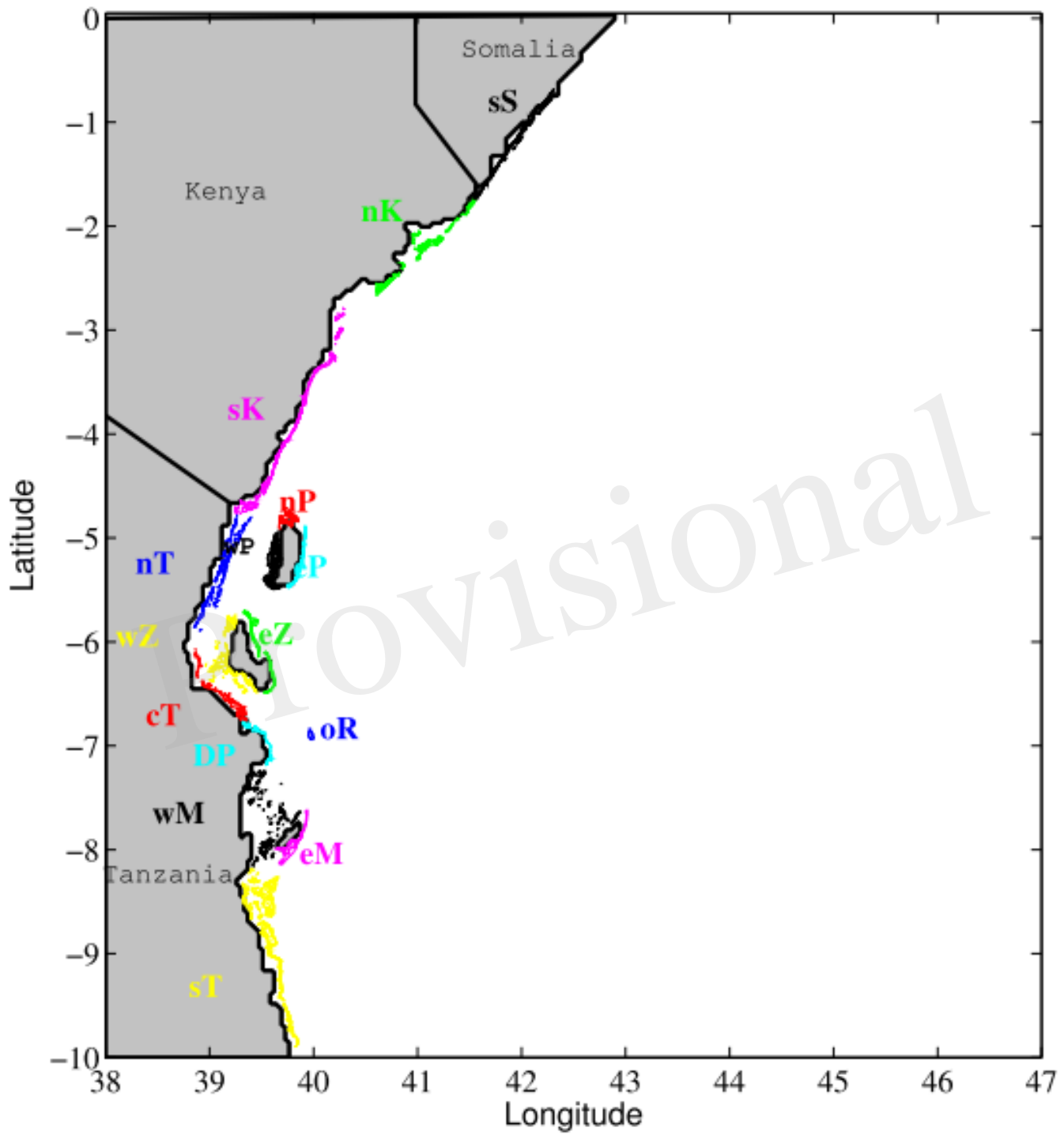
1348

1349 Figure 10: Reefs color coded by the number of different destination reefs reached by *Acropora*  
1350 virtual larvae originated from them in both simulated years to identify the best source reefs.

1351

1352 Figure 11: Reefs color coded by the number of different source reefs it received *Acropora* virtual  
1353 larvae from, in both simulated years to identify the best sink reefs.

Figure 01.TIF



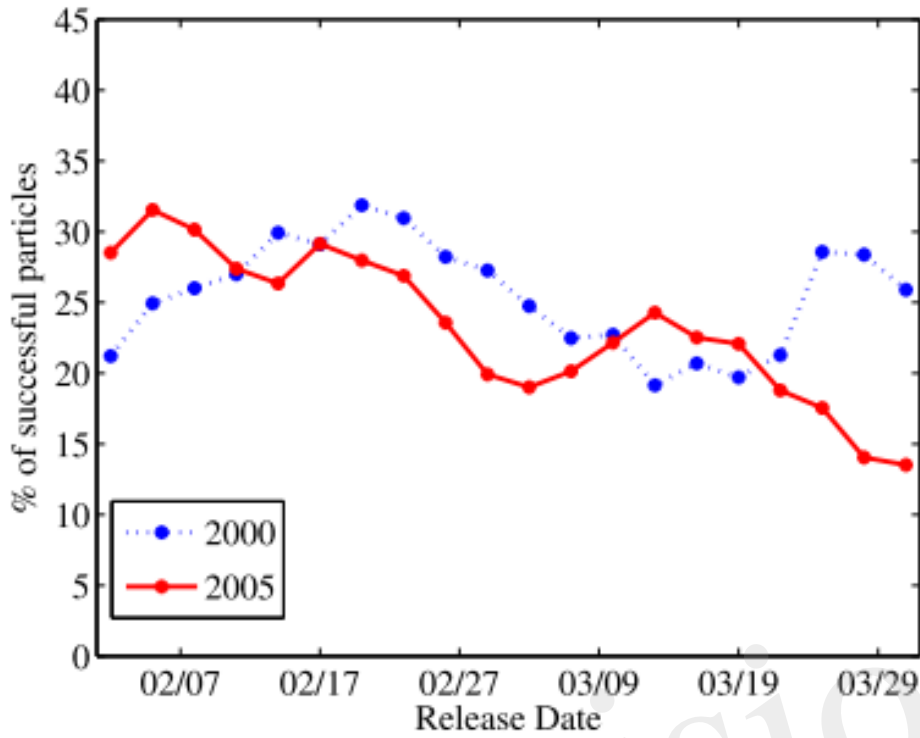
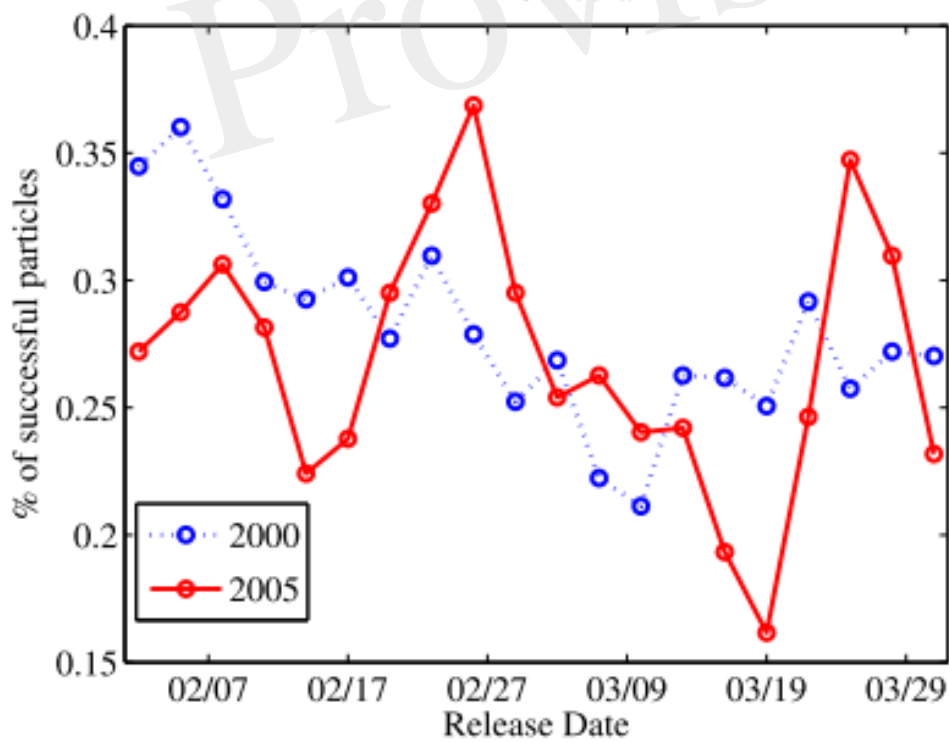
a) *Acanthurus*b) *Acropora*



Figure 04.TIF

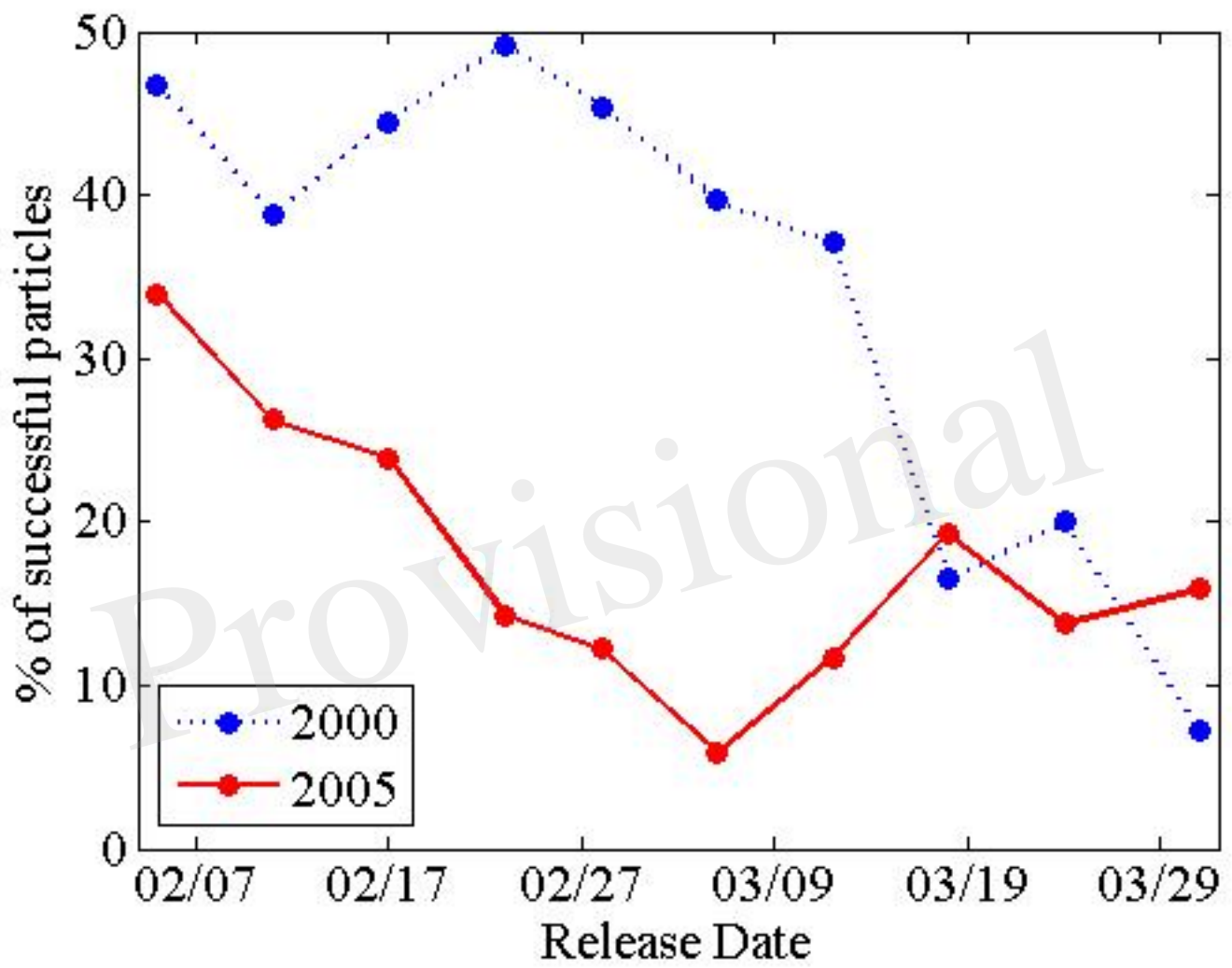






Figure 06.JPEG

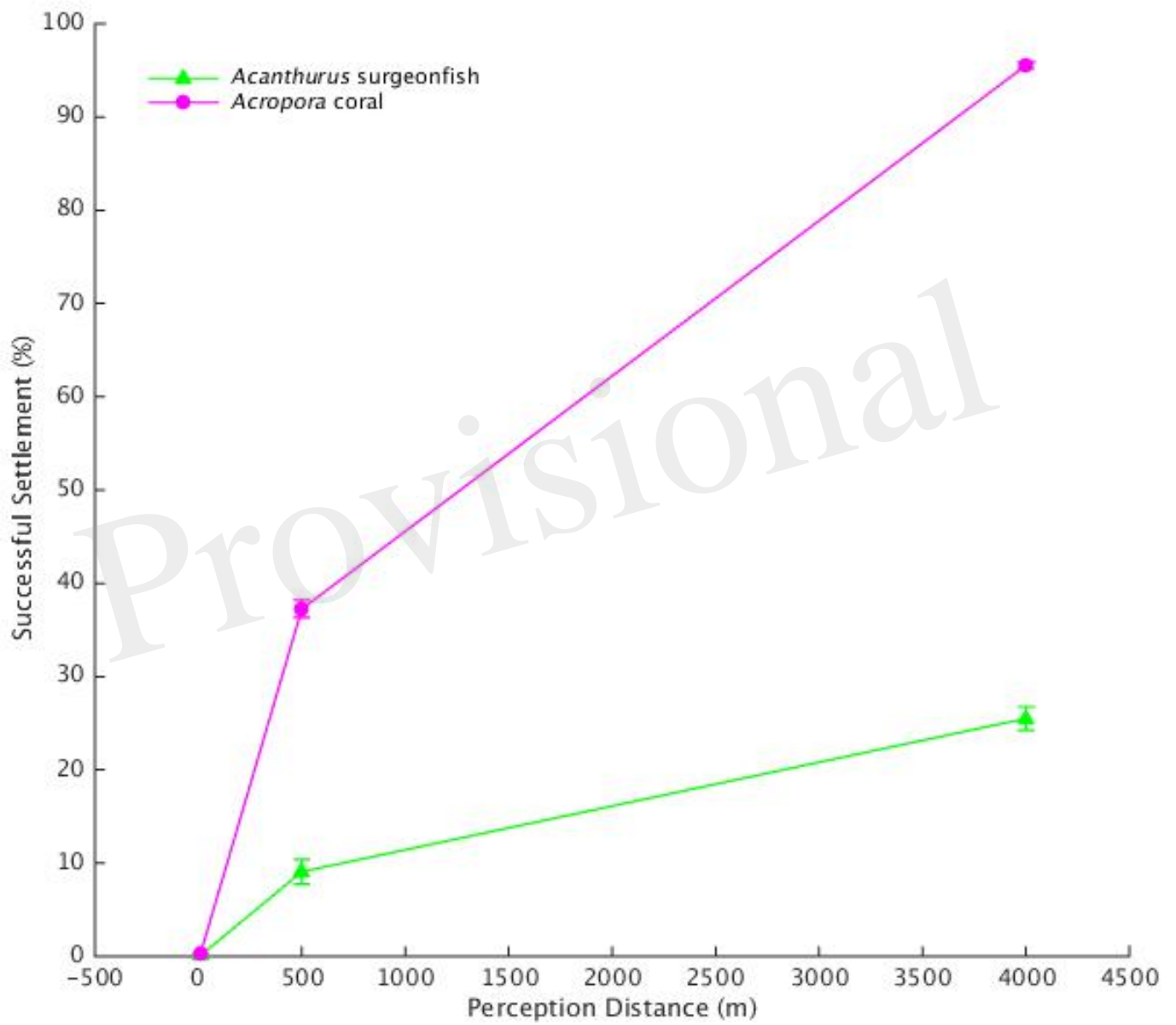


Figure 07.TIF

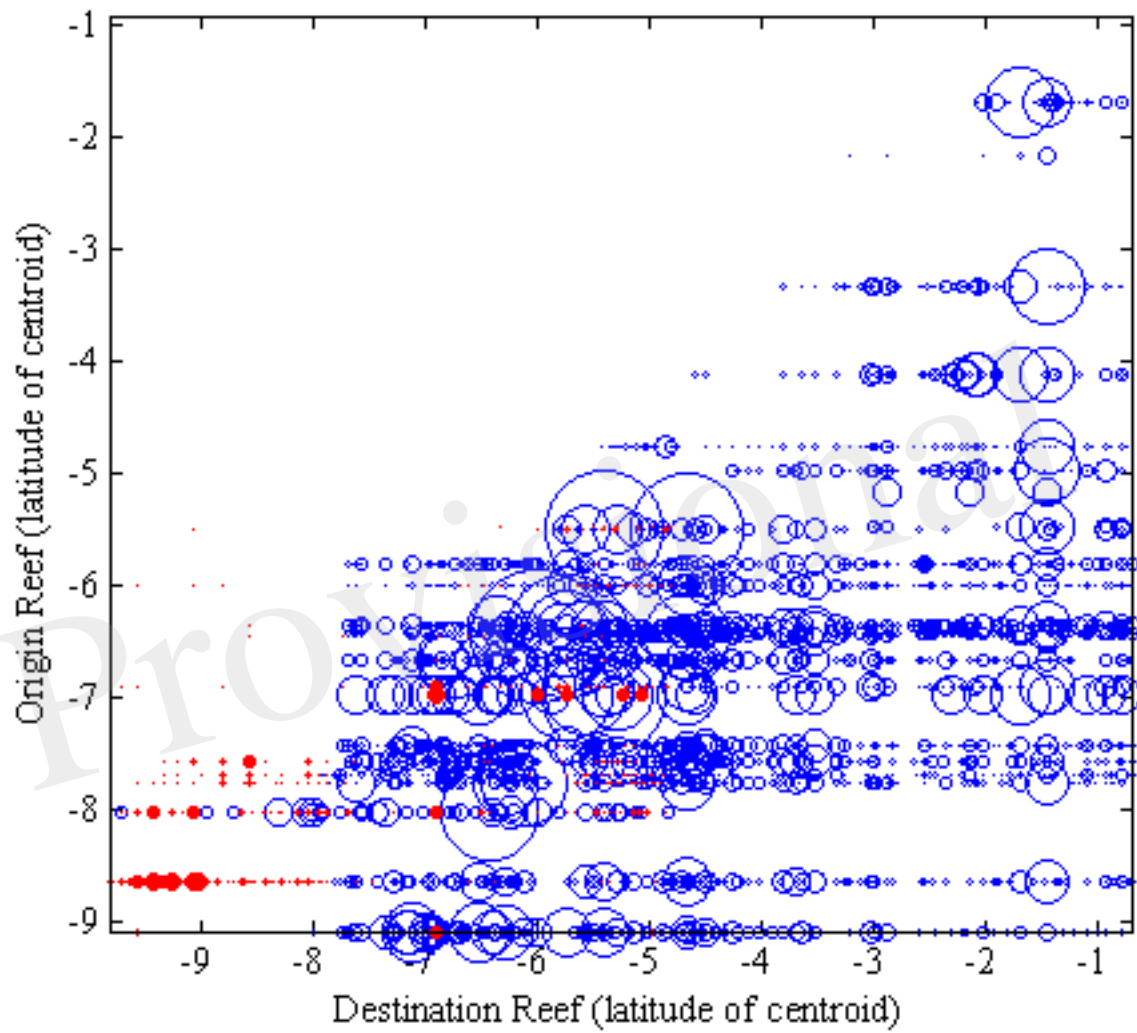


Figure 08.TIF

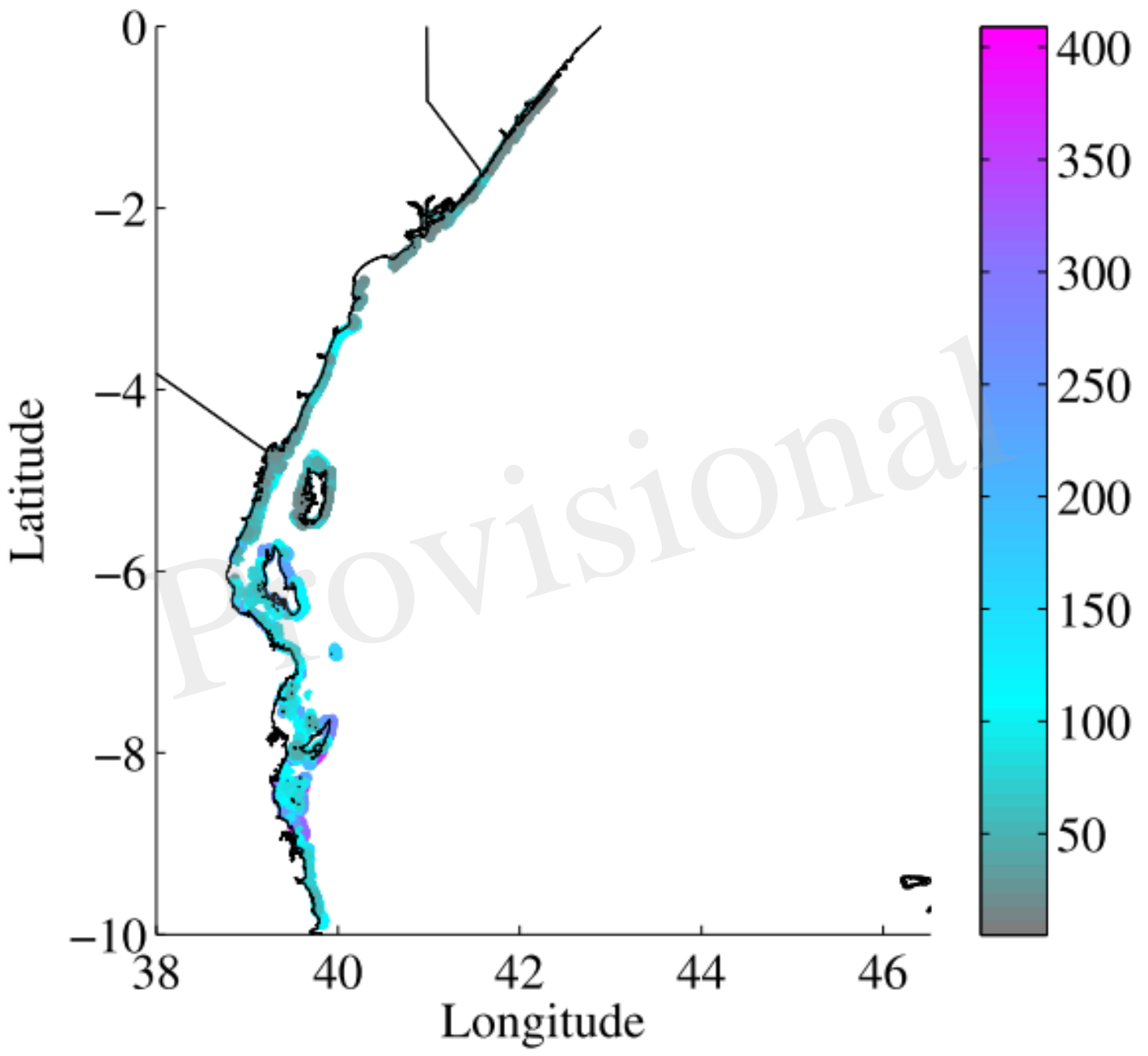


Figure 09.TIF

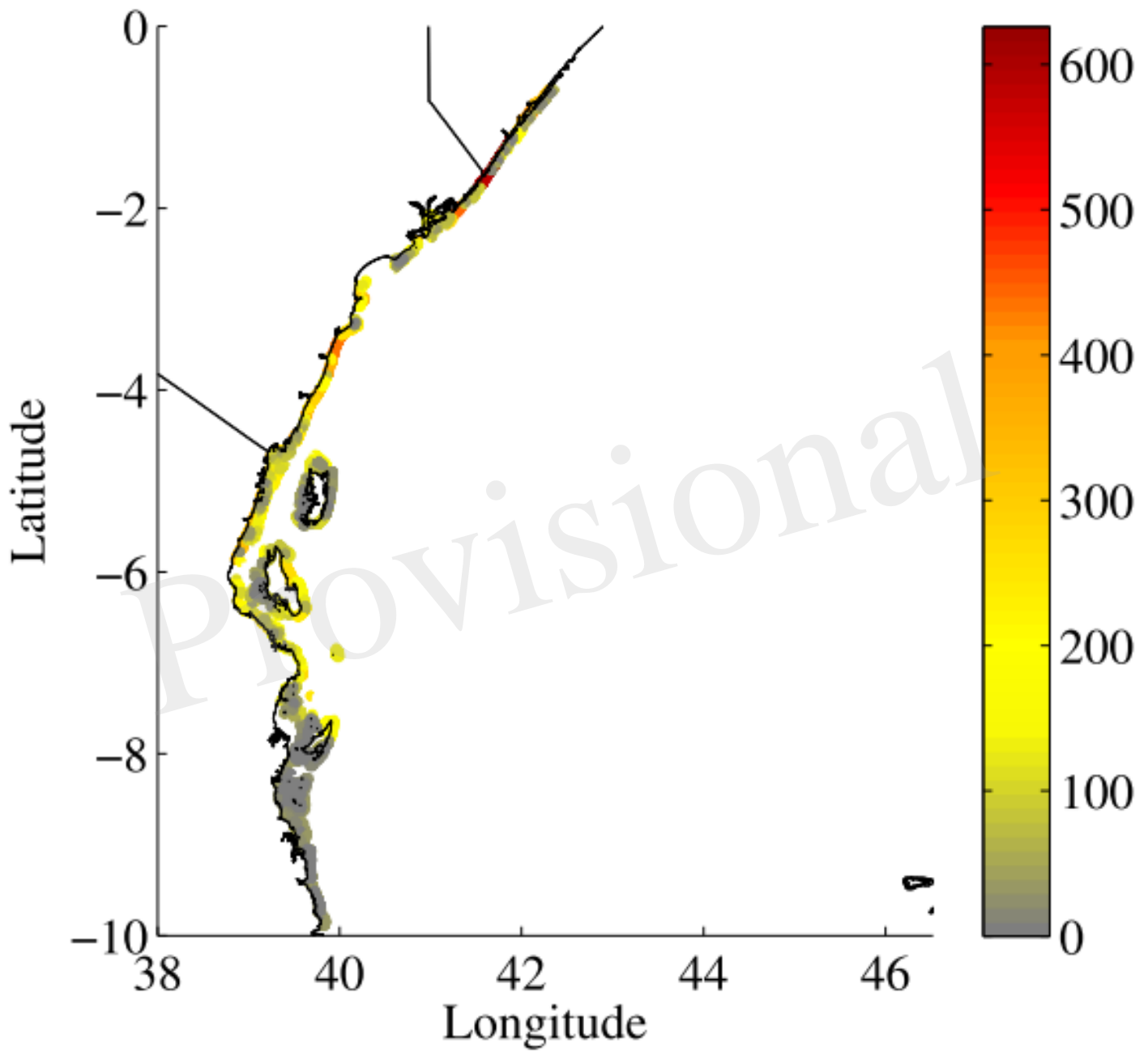


Figure 10.TIF

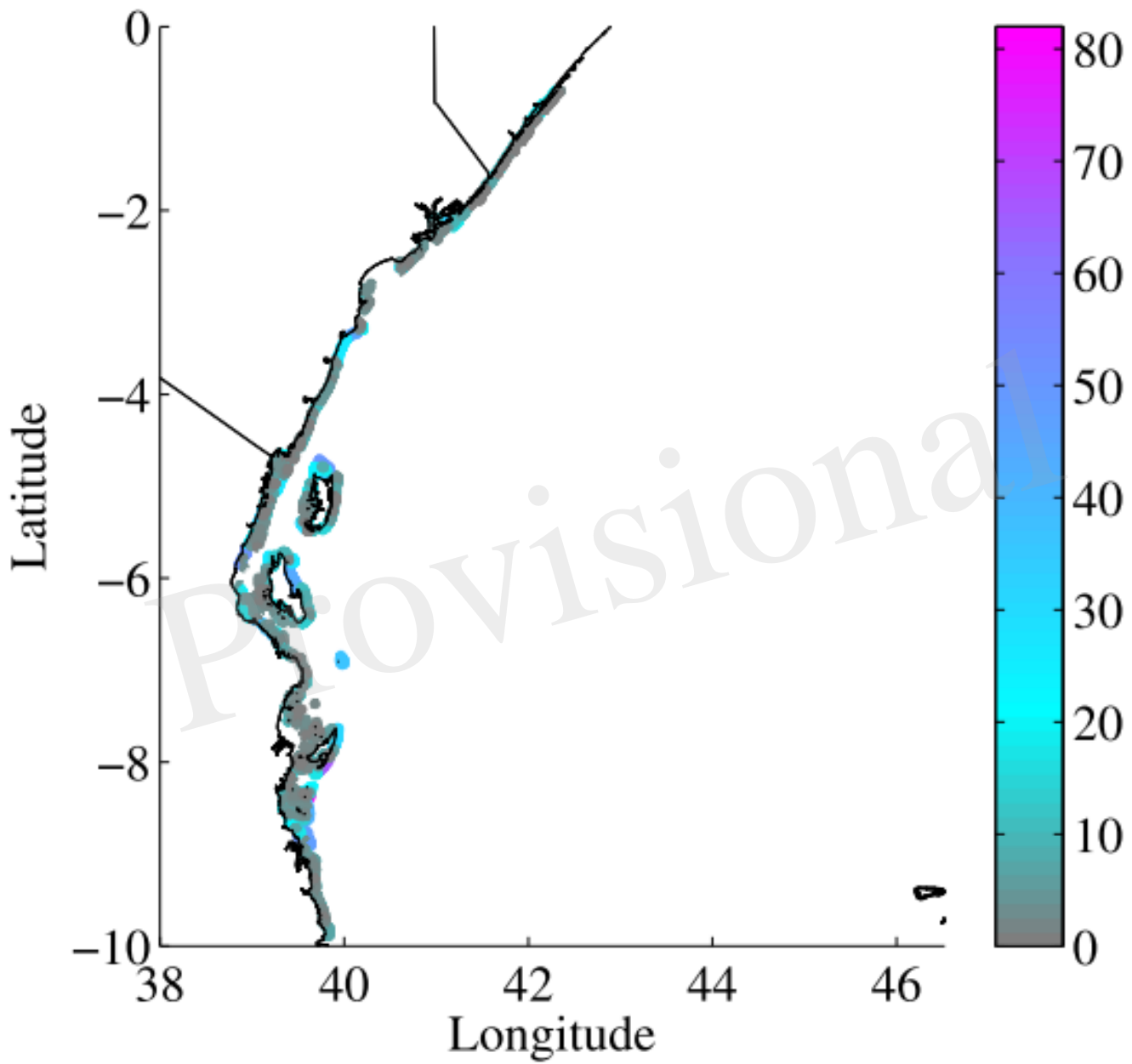


Figure 11.TIF

