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Title: Physical-biological interaction underlying phylogeographic pattern of coral-dependent fishes around the Arabian Peninsula

Running Head: Biophysical model of reef fishes

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Abstract

For marine taxa with freely mobile larvae, oceanographic features can act as soft barriers by disrupting the larval movements, and ultimately shaping both species and genetic diversity distributional. This study focused on three putative oceanographic barriers around the Arabian Peninsula: the Bab el-Mandeb Strait, the Strait of Hormuz and the upwelling off Oman. We aimed to assess the effects of larval fish traits and ocean circulation on the permeability of these barriers, and thus provide insights on the phylogeographic pattern of coral-dependent fish species along the peninsula. To do so, we simulated the larval dispersal through the putative barriers using an open-source program, where three-dimensional movements of particles are tracked by using ocean circulation data. We explored the range of dispersal capabilities across reef fish species by creating 72 hypothetical strategies, each representing a unique combination of five biological traits: pelagic larval duration, spawning periodicity, mortality rate, productivity and vertical migration. Our results showed that the direction and distance travelled by the virtual larvae were highly variable as a function of both the geographic position of releasing site and biannual monsoonal winds. On average, larvae released during the summer exhibited a higher potential for dispersal than larvae released in wintertime. Our biophysical models complement the few existing empirical research on population genetics, and the predictions presented here serve as testable hypotheses to future phylogeographic studies around the Arabian Peninsula.

Keywords: Biophysical modeling, connectivity, upwelling off Oman, Bab el-Mandeb Strait, Strait of Hormuz, connectivity modeling system

Introduction

The Arabian Peninsula lies on a hyper-arid region in the Southwest Asia at the junction of this continent with Africa (Fig. 1). The water-mass distribution and upper-ocean circulation surrounding the peninsula change in correspondence with biannual wind reversals, which creates seasonality in oceanographic conditions (Cutler and Swallow 1984; Shetye et al. 1994). During winter monsoon (November - March), the wind blows away from Asian continent (southwest), and the ocean surface circulation in the Arabian Sea is approximately counter-clockwise. On the opposite, during the summer monsoon (May-September) the wind reverses and blows strongly northeastward, so that the circulation in the Arabian Sea is clockwise. March-April and October are transition periods and winds are weak (see Cutler and Swallow 1984).

Large seasonal variation of such magnitude, which is generally not found elsewhere (Shetye et al. 1994), plays a critical role in fish biodiversity distribution by transporting or disrupting the movements of larvae produced by the adults (Cowen 2002). Thereby, the direction and magnitude of prevailing currents can spread out species distribution by aiding the dispersal of the propagules to future habitats. Nevertheless, currents can also act as a barrier by minimizing long-distance larval dispersal (Cowen et al. 1994, Paris and Cowen 2004) that ultimately may explain either the existence of endemic species (Cowen et al. 2000) or genetic discontinues across species range (Bowen et al. 2016). Although large expanses of ocean waters are the most notable permeable

78 barriers to larval dispersal (Bowen et al. 2016), mesoscale oceanographic processes such
79 as fronts (Galarza et al. 2009), river runoff (Rocha 2003), and upwelling (Bakun 1996;
80 Lett et al. 2007) also act as barriers to marine faunal exchange. The permeability of these
81 so-called semi-permeable barriers is taxon-specific and, therefore, affected by biological
82 traits (Ayre et al. 2009).

83 In the Arabian Peninsula, zoogeographic and population genetic studies on coral-
84 dependent fishes have shown discontinuities in both species and genetic distribution
85 along seas surrounding the peninsula (Burt et al. 2011; DiBattista et al. 2016a; Berumen
86 et al. 2017). The most remarkable of these discontinuities, distinguishes the fish fauna
87 from each side of the peninsula (DiBattista et al., 2016b). Two other discontinuities in
88 species compositions are observed, one between the Red Sea and the adjacent Gulf of
89 Aden through the Bab el-Mandeb Strait, and another between the Arabian Gulf and
90 adjacent Gulf of Oman through the Strait of Hormuz (DiBattista et al. 2016a). These
91 boundaries described by multispecies distribution records, are also logical places to
92 present-day barriers to gene flow between populations (Baums et al. 2006). Indeed,
93 population genetic studies carried out in the Northwester Indian Ocean (NIO) have
94 revealed similarities in the geographical position of barriers previously proposed
95 (DiBattista et al. 2013, 2015, 2017; Nanninga et al. 2014; Saenz-Agudelo et al. 2015;
96 Priest et al. 2016; Torquato et al. 2019).

97 Hypotheses to explain the distribution of genetic diversity in the Arabian
98 Peninsula usually rely on either parapatric speciation outcomes, which resulted from
99 either repeated vicariance events caused by lowering sea level during the last glaciation
100 or ecological speciation due to the large spatial gradients and temporal fluctuations in

101 physical conditions across the peninsula (Nanninga et al. 2014; DiBattista et al. 2016a,b).
102 An alternative hypothesis has been attributed to the seasonal upwelling in the Arabian
103 Sea off Oman, which creates unsuitable condition for coral-habitat growth (Sheppard and
104 Salm 1988) and restrict stepping-stone connectivity between both sides of the Arabian
105 Peninsula. In turn, little attention has been given to test hypotheses where the
106 combination of seascape features, ocean circulation and larval traits underling the genetic
107 patterns observed among coral-dependent fishes inhabiting the Arabian Peninsula.

108 In numerous cases, hypotheses in marine ecology are prohibitively time
109 consuming and expensive to be empirically tested, largely owing to the impossibility of
110 capturing the full range of temporal and spatial fine-scale resolution required to make
111 inferences (Cowen and Sponaugle 2009). Although a more comprehensive picture is
112 emerging in the Arabian Peninsula with respect to marine phylogeographic and
113 population genetic patterns (DiBattista et al. 2016a,b; Berumen et al. 2017), the processes
114 affecting larval dispersal across the putative barriers are not yet fully understood due to
115 the paucity of empirical studies. In addition, political realities of some countries
116 bordering the Western Indian Ocean (WIO) have limited access to scientists, hindering a
117 more complete perspective of general phylogeography in the region (Berumen et al.
118 2017). In such cases, if limited empirical data are available, reliable computational
119 models can be used to make field predictions and advance our knowledge to designing
120 future experiments for hypothesis testing (Cowen and Sponaugle 2009).

121 Advances on physical circulation models enabled the investigation of population
122 connectivity by running semi-realistic simulations of virtual particles. Here we used high-
123 resolution ocean circulation model (Hybrid Coordinate Ocean Model - HYCOM) to

design a biophysical model in a Lagrangian stochastic scheme (Paris et al. 2013). The main goal of this study was to simulate multitaxon larval dispersal through the marine barriers, and thus provide insights on processes and patterns of connectivity leading to the distribution of genetic diversity of coral-dependent fishes around the Arabian Peninsula. Specifically, we shed light on three questions: (1) what biological attributes affect the larval dispersal through the Bab el-Mandeb Strait and Strait of Hormuz? (2) What is impact of the upwelling off Oman on the larval connectivity between both sides of the peninsula? (3) How does oceanographic variability, due to the seasonal monsoon, affect larval dispersal pattern (i.e. direction and magnitude travelled by the particle)? Our results provide detailed predictions that can be compared to previous and future empirical studies on the distribution of biodiversity in the Arabian Peninsula.

Material and Methods

Biophysical Model and Larval Dispersal Simulation

Idealized dispersal of fish larvae was modeled using an open-source program, Connectivity Modelling System (CMS v. 2.0, Paris et al. 2013), which is a biophysical modeling system based on stochastic Lagrangian framework and Individual-Based Model (IBM) that couple ocean current, GIS-based habitat, and biological traits. In brief, CMS uses information on currents and environmental conditions to simulate both deterministic fourth-order Runge-Kutta and/or stochastic displacements of a large number of virtual particles (hereafter called larvae), through space and time. In order to explore the range of dispersal capabilities across reef fishes species, we created 72 hypothetical strategies each of those representing a unique combination of five biological traits that may influence the

connectivity: pelagic larval duration (PLD), spawning periodicity, mortality rate, productivity and vertical migration (Table 1).

Hydrodynamic model

We used the CMS package *getdata* to download daily ocean current velocity from the three-dimensional and eddy-resolving Hybrid Coordinate Ocean Model (HYCOM, GLBa0.08) from 2014 to 2016. The model had a horizontal resolution of ca. 9 km grid (1/12˚), and was set up in a nested domain (0˚ - 30˚ N, 31˚ - 70˚ E), comprising all layers from the surface up to 100 meters depth. In studies carried out around the Arabian Peninsula, HYCOM has been used to investigate mesoscale variability in the Arabian Sea (L'Hégaret et al. 2015) as well as water circulation and exchange in the Persian Gulf (Yao and Johns 2010).

GIS-based Seascape module

The GIS served to delineate the source and recruitment habitats. Suitable releasing (source habitat) and settlement (sink habitat) locations were delineated in QGIS v.2.18 by creating a vector grid that overlaid the distribution of coral reefs data from the UNEP-WCMC (2010). A total of 181 polygons (~ 18km x 18km) representing the coral reef habitats were placed along coastal areas within our model domain.

Biological module

We assumed spatial homogenous productivity across the habitats and, therefore, all the 181 polygons released the same number of larvae every 'spawning' event.

170 However, we contrasted scenarios where productivity varies among species. In scenario
171 of high productivity, a hundred of larvae were released from each polygon, whereas in
172 low productivity conditions only ten were released. Here, three seasonal spawning
173 preferences were accounted by simulating the larval dispersal annually and accordingly
174 the two dominant seasonal oceanographic conditions around the Arabian Peninsula. After
175 being released, the larvae were let to drift over a period of 20, 30 or 40 days,
176 corresponding to the typical pelagic duration (PLD) of most coral reef fish
177 species/families (Thresher and Brothers 1985; Lindeman et al. 2005).

178 In this study the PLD was equally divided into the three ontogenetic larval stages
179 termed preflexion, flexion and postflexion. Due to the paucity of basic data regarding fish
180 larvae distribution within our study area, the model incorporated an idealized pattern of
181 ontogenetic vertical migration for the three larval stages (Fig. S1). This idealization
182 assumes the existence of a global ontogenetic trend of the fish larvae to display
183 downward ontogenetic shift in vertical distribution (Irisson et al. 2010). During the
184 postflexion stage the larvae were considered competent to settle if they are inside one of
185 the 181 reef sites. To assess the importance of vertical migration, we also modeled
186 epipelagic ichthyoplankton moving only along the sub-surface layer to then contrast with
187 models where larvae also moved vertically.

188 Little is known regarding larval mortality in the ocean. To accommodate this
189 uncertainty, our study included two levels of mortality based on the half-life, such that
190 approximately 50% of unsettled larvae would be surviving after half the maximum PLD
191 (Paris et al. 2013; Holstein et al. 2014). Thus, we determined that in high mortality

192 scenario half of the larvae died by the end of the preflexion stage, while in low mortality
193 condition half of the larvae died by the end of the postflexion stage (Table 1).
194
195 **Particle-tracking module**
196 Stochastic IBM Lagrangian model tracked offline over 157 millions larvae around
197 the Arabian Peninsula for the 72 model taxa. A total of 86,011,200 larvae were released
198 to mimic taxa spawning throughout year, whereas 35,838,000 larvae were tracked to
199 simulate taxa spawning on either winter monsoon (November 2014 – March 2015) or
200 summer monsoon (May 2015 – September 2015).
201 Preliminary sensitive analysis showed no significant difference in the settlement
202 proportion when seeding 100 larvae from the 181 polygons at every either 3 or 24 hours
203 (see Appendix S1 in Supplemental Information). Therefore, the larvae were released
204 from each reef at every 24 hours, which represents a spawning event. This uniform
205 temporal distribution of larvae allows us to assess the effects of the hydrographic
206 variability conditions on larval dispersal (e.g., extreme events, perturbation, instability).
207 Throughout the PLD, the position of each larva was updated every 6 h time-step, and the
208 trajectory information (i.e. longitude, latitude, depth) were saved to output in intervals of
209 24 hours. We accounted for diffusive turbulent motion by adding a horizontal diffusion
210 coefficient. The value of 50 m^2s^{-1} was chosen from a sensitivity test where 100 larvae
211 were released from the 181 polygons at every 24 hours (see Appendix S1 in
212 Supplemental Information).
213
214

215 **Analyses**

216 The proportion of survivor larvae that were released from each region *i* and
217 successfully settled in a downstream habitat patch (i.e., sink habitat) at region j,
218 were plotted as a connectivity matrix. Self-recruitment, i.e. larvae settling within its
219 release location, was represented by the diagonal of the matrix. In order to evaluate
220 the strength and direction of the potential connections on regional scale (e.g.,
221 between Red Sea and Gulf of Aden), all cells from each region were merged.

222

223 **Biological traits vs. biogeographic barriers**

224 To evaluate the effect of the biological traits highlighted in Table 1 on the
225 putative barriers, we relied on a multiple regression approach. Specifically, the
226 effects of both Bab-el-Mandeb and Hormuz strait were measured in terms of
227 permeability, which considers the proportion of surviving larvae that were released
228 from a source habitat, passed through the strait, and successfully settled on the
229 other side. In turn, the effect of the upwelling off Oman was measured in terms of
230 self-recruitment proportion along the Arabian Sea.

231 Provided that the proportions are a continuous variable that can take on
232 values restricted to the interval between 0 and 1, a beta regression model as
233 proposed by Ferrari and Cribari-Neto (2004) was used through the betareg R-
234 package (Neto and Zeilis 2010). The beta regression is essentially similar to a
235 Generalized Linear Model (GLM), where it describes the relationship between the
236 response variable Y_i (hereby, proportions) and the predictors X_i (Table 1) through a
237 linear predictor η_i. This linear predictor is then linked to the mean of the response

$E(Y_i) = \mu_i$ by means of a link function g, such that $g(\mu_i) = \eta_i$. In this way, the applied model can be summarized as:

$$Y_i \sim B(\mu_i, \phi)$$

$$\text{logit}(\mu_i) = \eta_i$$

$$\eta_i = \beta_0 + \beta_1 PLD + \beta_2 SP + \beta_3 M + \beta_4 Pr + \beta_5 VM + \varepsilon$$

Where ϕ is the precision parameter; η_i the linear predictor expressed on a logit scale; β0 the intercept; β1-5 the repressors related to each explanatory variable (PLD=Pelagic larval duration, SP = Spawning periodicity, M = Mortality, Pr = Productivity, VM = Vertical migration); and ε represents the error term. Model assumptions like residual homocedasticity, independence and normality were accessed through conventional graphical checks as mentioned in Zuur et al. (2010).

Larval dispersal pattern and oceanographic conditions

The maximum distance travelled by the larvae around the Arabian Peninsula was calculated setting up a model with the lowest mortality rate and 40-days PLD. We used the program QGIS v.2.18 to measure this distance and compare the results in both summer and winter, as well as in each of the regions within the model domain.

Results

Connectivity matrix

All the matrices representing the 72 model taxa revealed that connectivity occurred exclusively between neighbor regions, though the strength and symmetry of these connections varied either seasonally or due to larval traits (Fig. S2 – S4). The hardest barrier was observed in the south of the Arabian Peninsula, separating both sides of the peninsula, in other words, larvae that were released from the Arabian Sea, the Gulf of Oman or the Arabian Gulf, did not reach the reefs in the Gulf of Aden or the Red Sea, and vice-versa. This barrier was observed especially in simulations in which the larvae drifted for 20 days. When released during either winter or summer monsoon, 30-days PLD larvae that performed vertical migrations were also not able to cross this barrier. Importantly, the connectivity through the Strait of Hommuz was not symmetric, such that the Gulf acts as a sink habitat specially when the larvae drift for 20 days, with high mortality rate and perform vertical migration (Fig. S2).

Intra-annual variability was evident in the potential connectivity (Fig. S2 – S4), suggesting that symmetry of the connectivity was affected by the spawning periodicity of the taxa. For example, in the summer 40-PLD days larvae released from the west side of the peninsula reached the reefs located on the east side. In contrast, during the winter any of these larvae crossed the barrier in this direction.

Effects of the biological traits on the permeability of biogeographic barriers

Graphical evaluation of the model assumptions revealed that all tested models fitted well to the data, and did not violate neither the residual homocedasticity nor

independence. Table S1 summarizes the numerical output of the models, and discussed in more detail below.

Bab el-Mandeb Strait

For the larvae that were released in the Red Sea and successfully settled in the Gulf of Aden, only the larval productivity was not significant (Table S1, Fig. 2). The beta regression showed that this connectivity was significantly higher during the summer than both during the winter and throughout year. Also, the permeability through the strait was higher for those larvae that performed vertical migration and were left to drift for longer period, though no significant difference was observed between larvae that drift for 30 and 40 days.

On the other hand, larvae that moved in the opposite direction, from the Gulf of Aden to the Red Sea, showed higher success in the connection during the wintertime but larval productivity did not change the barrier's permeability (Table S1, Fig. 2). Moreover, a positive relationship was observed between the permeability and PLD, and epipelagic larvae that moved at the surface increased their permeability through the strait compared to those that performed vertical migration. Mortality rate was significant and showed the same tendency of the larvae moving from the Red Sea and to the Gulf of Aden.

Strait of Hormuz

The proportion of larvae released in the Arabian Gulf that successfully reached the reefs in the Gulf of Oman, increased when they were released throughout year or during the wintertime, performed vertical migration, had low mortality rate, and travelled

for longer period (Table S1, Fig. 3). Nevertheless, the chance to cross the strait did not depend on the larval productivity.

Likewise, among all biological attributes, only productivity was not significant for larvae that were released in the Gulf of Oman, crossed the Strait of Hormuz and successfully settled in the Arabian Gulf. The probability of this connectivity was higher in the scenarios where the larvae were release in winter, had low mortality rate, did not perform vertical migration and remained in the planktonic environment for longer period. (Table S1, Fig. 3).

Upwelling off Oman

All biological traits, except larval productivity, significantly affected the proportion of self-recruitment in the Arabian Sea (Table S1, Fig. 4). The scenario in which a taxon had higher success in self-recruitment occurred during the wintertime or throughout year, and when the 20-days PLD larvae performed ontogenetic migration under low mortality scenario. In turn, larvae produced during the summer, under upwelling conditions, had a slightly more chance to migrate.

Particles trajectories: seasonal variability of spatial scale and direction

The direction and distance travelled by the larvae were highly variable as a function of both the geographic position of releasing site and the biannual monsoonal winds (Fig. 5 and 6). On average, larvae released during the summer exhibited a higher potential for dispersal, especially in areas that are not enclosed (Fig. 5f, 6f). It was in summer that the movement of larvae southward from the Red Sea was more pronounced,

and it was also in this season that many larvae released in the Gulf of Aden reached Omani waters in the Arabian Sea. In turn, during the winter the vast majority of larvae originating in the Red Sea were retained within this area, while larvae released within the Gulf of Aden either moved eastward, though rarely reaching the Omani coast, or moved southward along the Somali coast.

In the Arabian Sea, surface circulation exhibited a strong seasonal cycle. During the summer, larvae released along the Omani coast between 54.6˚ E and 56.1˚ E, either moved eastward alongshore toward the Gulf of Oman or sharply turned toward the open ocean. Whereas, larvae released between 57.8˚ E and 59˚ E were exclusively transported alongshore toward the Gulf of Oman (Fig. S5). In the winter, even though the larvae along the entire Omani coast moved toward offshore, on average they travelled shorter distances compared to the summer (Fig. 5f, 6f).

On the east side of the Arabian Peninsula, the temporal variability of both the direction and the distance travelled by the larvae was less evident. In the Gulf of Oman, larvae released from the eastern Omani coast tended to move southward and few larvae reached the Arabian Gulf. However, those larvae originating on the top of the Gulf of Oman were able to pass through the Strait of Hormuz, though they did not travel far away. In the Arabian Gulf the patterns of dispersal observed in both seasons were quite similar, larvae tended not to move far away and hence most of them remained in the Gulf.

Discussion

Measuring the strength of barriers has been a great challenge to understand biogeographic patterns and population genetic structure (Treml et al. 2015). In our study,

a series of individual-based simulations were performed to assess the permeability of larvae of 72 fish species through putative barriers within the Arabian Peninsula (i.e., the Bab el-Mandeb Strait, the Strait of Hormuz and the upwelling off Oman). This multitaxa comparison demonstrated how biological-physical interaction determine the success of the larvae being transported through the Bab el-Mandeb Strait and the Strait of Hormuz, as well as of those larvae being self-replenished in the Arabia Sea.

Here we took advantages of a Lagrangian three-dimensional approach to assess the effects of the hydrographic variability conditions (e.g., extreme events, perturbation, instability) on larval dispersal, and thus measuring the strength of putative barriers. Although realistic, the real number of larvae released per species per site greatly exceeds what is computationally possible for a Lagrangian approach. Alternatively, Eulerian advection-diffusion methods, that though are not spatially realistic, have a large impact on dispersal kernel and hence suitable in quantifying evolutionarily significant tails in evolutionary connectivity studies (Treml et al. 2012).

Bab el-Mandeb Strait

Our results showed that the strength of this barrier is in accordance with the seasonal water exchange pattern between the Red Sea and the Gulf of Aden, which changes from a two-layer surface flow in the winter to a three-layer flow in the summer (Smeed 2004). During the winter season warmer and fresher water from the Gulf of Aden flows into the Red Sea in the surface layer, while cooler and saltier water from the Red Sea (RSOW) flows into the Gulf of Aden in the lower layer. The summer regime at the Bab el Mandab Strait is very different, the flow in the surface layer is reversed while

intermediate water layer from the Gulf of Aden flows into the Red Sea. In turn, the RSOW forms the deepest and tiny layer (Smeed 2004).

This seasonal variation in the water exchange explains the consequences of vertical migration and spawning periodicity on the permeability of the Bab el Mandab showed in the Fig. 2. According to our biophysical model, a taxon from the Gulf of Aden that has epipelagic larvae moving horizontally and spawn during the summer has more chance to reach the reefs in the Red Sea. In contrast, a taxon moving in the same direction will decrease its probability to cross the strait if the spawning occurs in winter and the larvae perform vertical migration. Under this condition more larvae will be positioned within the RSOW at deeper layers that flows from the Red Sea to the Gulf of Aden.

To date, the strength of this barrier has been debated based on the species distribution and phylogeographic studies. For example, Kemp (1998) suggested that although the Bab el-Mandeb Strait was a site of a significant Pleistocene vicariance event, it does not act as a present-day barrier. According to the author, the paucity of information about the reef fish assemblage inhabiting the south of the Red Sea and the adjacent Gulf of Aden is the main reason to hypothesize that the strait acts as a barrier. In contrast, DiBattista et al. (2016a) recorded high endemism rates for a variety of taxonomic groups within the Red Sea, ranging from 5.5% for scleractinian coral to 16.5% for ascidians, and suggested that the Red Sea biota is isolated due to the limited water exchange between the Red Sea and the Gulf of Aden.

Strait of Hormuz

There are few evidences of the Strait of Hormuz acting as a barrier for coral-dependent fishes. Substantial differences in the structure and composition of reef fish assemblages between the Arabian Gulf and the Gulf of Oman (Burt et al. 2011), has been explained by the large spatial gradients in physical conditions (e.g. seawater temperature and salinity) along these two areas (Smith and Saleh 1987; Feary et al. 2010). Here we suggest that the spawning strategies and larval traits may also contribute to this difference.

The relatively high evaporation rate over the Arabian Gulf combined with the limited water exchange with the open ocean drives an inverse estuarine system at the Strait of Hormuz, with a shallow inflow of the Indian Ocean Surface Water (IOSW) and a deep outflow of the Persian Gulf Water (PGW, Swift and Bower 2003). The currents in the surface layers are highly variable and exhibit large amplitude variation, especially in wintertime (Johns et al. 2003). The surface inflow of IOSW occurs mainly in the northern part of the strait, and continues northward along the Iranian coast (Reynolds 1993), however in the spring the inflow is wider and fills the entire width of the strait (Chao et al. 1992). On the other hand, the deep outflow is relatively steady throughout year with little seasonal variance (Johns et al. 2003, Swift and Bower 2003).

The stability of deep-water outflow and the seasonal variability at the surface corroborates with the results obtained in our simulations (Fig. 3). It explains, for instance, the fact that the proportion of larvae leaving the Arabian Gulf did not change seasonally, and increased when the larvae performed vertical migration. From the opposite direction,

epipelagic larvae released in the Gulf of Oman had a higher chance to reach the Arabian Gulf, especially during the winter when the inflow surface is highly variable.

Upwelling off Oman

Our simulations showed that the proportion of self-recruitment in reefs along the southern Omani coast was slightly higher in the winter, during the period of no upwelling event. In this season the larvae moved away from the coast but travelled shorter distances compared to those larvae released in the summer. Under upwelling conditions, larvae released between 54.6° E and 56.1° E were transported to either open sea or eastward along the coast. This result coincides with the remote sensing images (Weaks 1983) and empirical data (Elliott and Savidge 1990) of intense upwelling in the vicinities of headlands off Dhofar and Kuria Muria Island. In this area, coral colonies are weakly developed and present a reduced number of species (Sheppard and Salm 1988; Burt et al. 2016). The lack of coral reef habitat is also seen as a potential causes faunal and genetic difference between both sides of the Peninsula (Priest et al. 2015).

Although the effects of offshore transport on coral reef organisms are rarely investigated (but see Roughan et al. 2011), the effect of offshore Ekman transport on the larval recruitment has been well documented for small pelagic fishes. These studies have described that offshore drift does not favor retention in costal areas and act as a hindrance to larval connectivity (Parrish et al. 1981). The Benguela upwelling system, for example, acts as a barrier to some species of phytoplankton, copepods and pelagic fishes between North and South (Lett et al. 2007).

440 The effect of Ekman transport on the larval dispersal is stronger at the surface
441 (Lett et al. 2007). Therefore, larvae that performed vertical migration during the summer
442 presented a higher change to find suitable habitats in coastal areas along the Omani coast,
443 supporting the hypothesis that vertical migration is a viable retention mechanism for coral
444 reef fish larvae (Paris and Cowen, 2007). Simulations carried out in the Benguela
445 upwelling system, also showed that anchovy larvae at the surface travelled longer
446 distances (Lett et al. 2007). Another biological attribute that was significant to the self-
447 recruitment under upwelling conditions off Oman was the PLD. Shorter periods in the
448 planktonic environment enhanced the self-recruitment along the southern Omani coast.
449 This result reflects the assumption of our biophysical models in which lower PLD also
450 means early competence period and vertical migration.

451 The connectivity matrices showed in the southern Arabian Peninsula a hard west-
452 east barrier for several combinations of biological traits. The position and strength of this
453 barrier corroborates to all previous results obtained of phylogeography and fauna
454 composition studies carrier out in the Arabian Peninsula (Kemp 2000; DiBattista et al.
455 2016a). Specifically, matrices visualization indicates that symmetry and strength of
456 connectivity largely varied as a function of biological traits (Fig. 4). For example, our
457 simulations showed that higher connectivity could be achieved with longer duration of
458 the larval stage, but empirically the importance of PLD to explain biogeographical
459 patterns and population genetic structure is debatable (Weersing and Toonen 2009;
460 Selkoe and Toonen 2011). Because the simple notion that the longer a larva spends in the
461 water column, the higher its potential for dispersal by ocean currents, PLD is a common
462 proxy for dispersal potential in coral reef fish. This expectation is based on the

assumption that larvae are largely passive particles, however, fish larvae exhibit strong behavioral preferences including swimming capabilities during their late ontogenetic stages. In addition, variation in PLD can occur among and within marine taxa, especially due to larval responses to environmental stochasticity (Woodson and McManus 2007).

Moreover, spawning periodicity was largely affected by oceanographic variability due to the seasonal monsoon. During the winter counter-clockwise ocean circulation in the Arabian Sea restricted eastward dispersal, and hence larvae released in the Gulf of Aden only reached the Omani coast during the summer monsoon. During the summer, in turn, the ocean circulation in the Arabian Sea restricted the westward dispersal. Nevertheless, empirical data that support the hypothesis relating symmetry in connectivity (e.g., genetic studies) along the Arabian Peninsula are lacking.

Conclusion

Our biophysical models complement the existing research on comparative fish population genetic by providing a snapshot of the present-day seascape permeability around the Arabian Peninsula. The comparative and cross-taxon models could identify key biological traits and biophysical interactions that limit the transport of ichthyoplankton in our study area. Therefore, we could show that the strength of putative barriers depending on species spawning strategies. The predictions presented here serve as testable hypotheses for future studies on population genetics and fish larval distributions around the Arabian Peninsula.

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TABLES

Table 1. Range in biological parameter values to characterize the 72 hypothetical model taxa.

PLD (days)	Spawning periodicity	Larval mortality	Vertical migration	Productivity
20	Annual	High	Yes	High
30	Summer)	Low	No	Low
40	Winter)			

FIGURES

Legends

Fig. 1. Study region. Northwestern Indian Ocean with previously described barriers depicted shown as shaded line. (a) Bab-el-Mandeb Strait, (b) Upwelling off Oman and (c) Strait of Hormuz.

Fig. 2. Results on the beta regression models showing the effects of the biological traits on the permeability of the Bab-el-Mandeb Strait. The red triangles represent the mean value. Different letters indicate signicant differences ($p < 0{\cdot}05$).

Fig. 3. Results on the beta regression models showing the effects of the biological traits on the permeability of the Strait of Hormuz. The red triangles represent the mean value. Different letters indicate signicant differences ($p < 0{\cdot}05$).

Fig. 4. Results on the beta regression models showing the effects of the biological traits on the self-recruitment along Omani coast. The red triangles represent the mean value. Different letters indicate significant differences ($p < 0{\cdot}05$).

Fig. 5. Modeled dispersal paths of epipelagic virtual larvae with larval duration of 40 days released in the wintertime from (a) the Red Sea, (b) Gulf of Aden, (c) Arabian Sea, (d) Gulf of Oman and (e) Arabian Gulf. One larva was released from each habitat cell (total of 181) per day in 2015. The distances travelled by the larvae are represented in (f).

Fig. 6. Modeled dispersal paths of epipelagic virtual larvae with larval duration of 40 days released in the summertime from (a) the Red Sea, (b) Gulf of Aden, (c) Arabian Sea, (d) Gulf of Oman and (e) Arabian Gulf. One larva was released from each habitat cell (total of 181) per day in 2015. The distances travelled by the larvae are represented in (f).

Fig. 1.

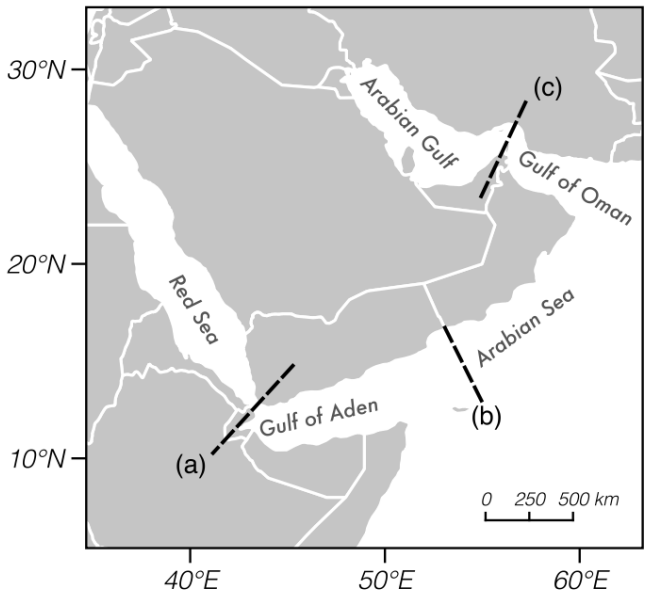

30°N
20°N
10°N
40°E
50°E
60°E
Arabian Gulf
Gulf of Oman
Red Sea
Arabian Sea
Gulf of Aden
(a)
(b)
(c)
0 250 500 km

Fig. 2.

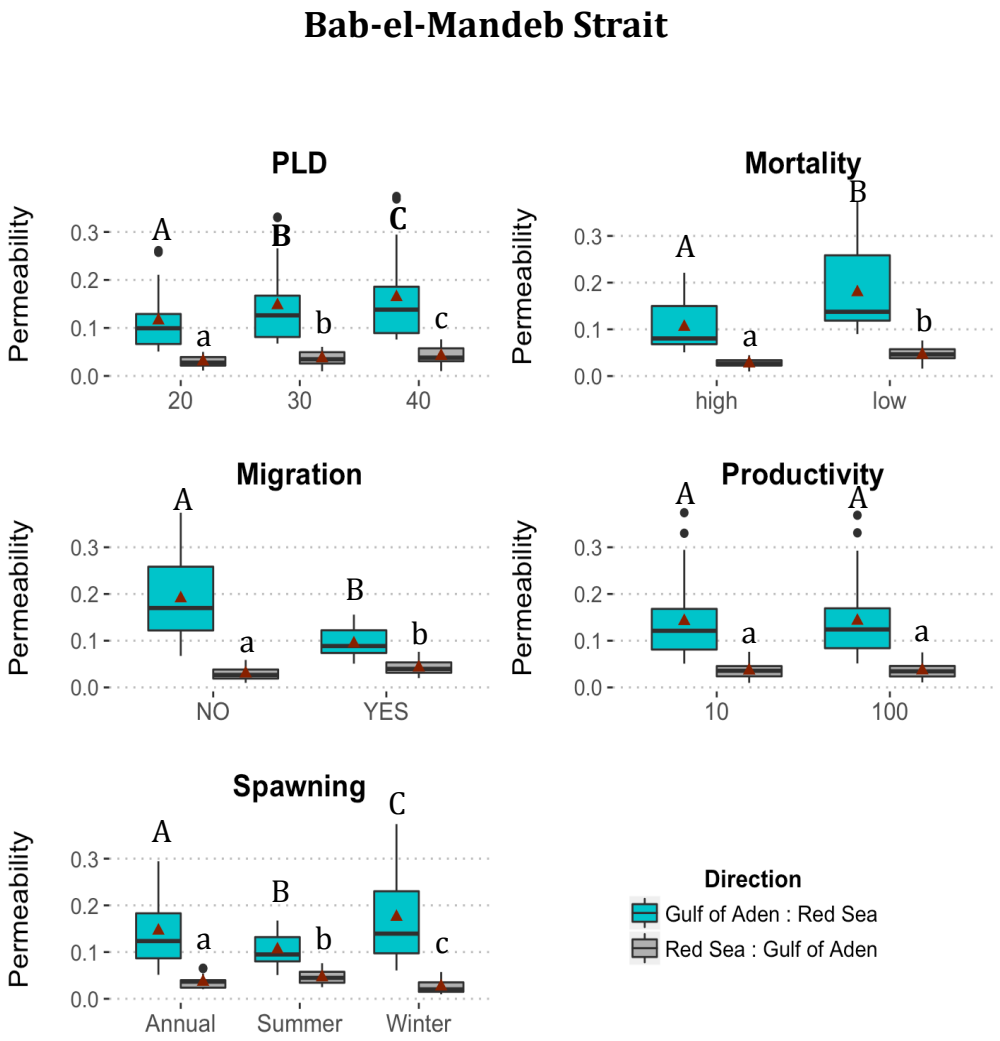

Bab-el-Mandeb Strait
PLD
Mortality
Migration
Productivity
Spawning
Permeability
0.0
0.1
0.2
0.3
20
30
40
high
low
NO
YES
10
100
Annual
Summer
Winter
A
a
B
b
C
c
Direction
Gulf of Aden : Red Sea
Red Sea : Gulf of Aden

Fig. 3.

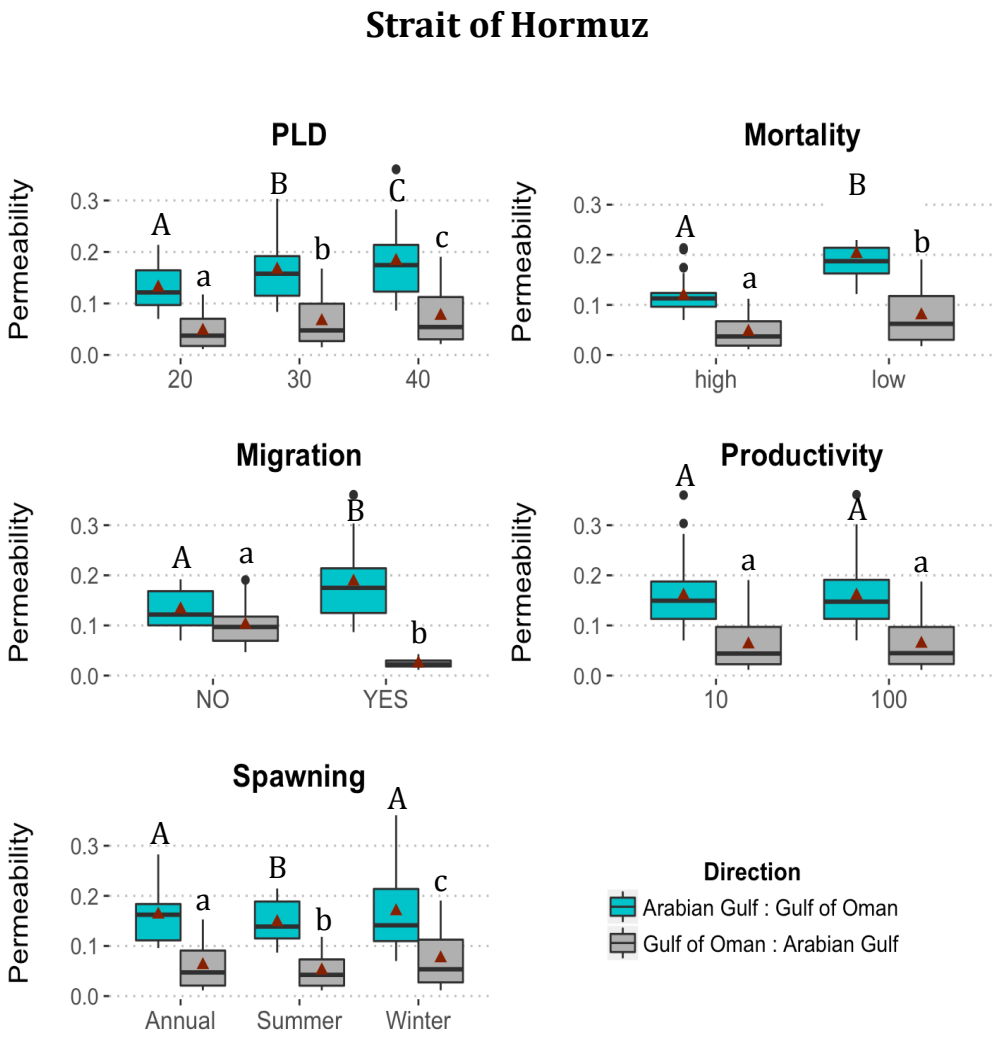

Strait of Hormuz
PLD
Mortality
Migration
Productivity
Spawning
Permeability
0.0
0.1
0.2
0.3
20
30
40
high
low
NO
YES
10
100
Annual
Summer
Winter
A
a
B
b
C
c
Direction
Arabian Gulf : Gulf of Oman
Gulf of Oman : Arabian Gulf

Fig. 4.

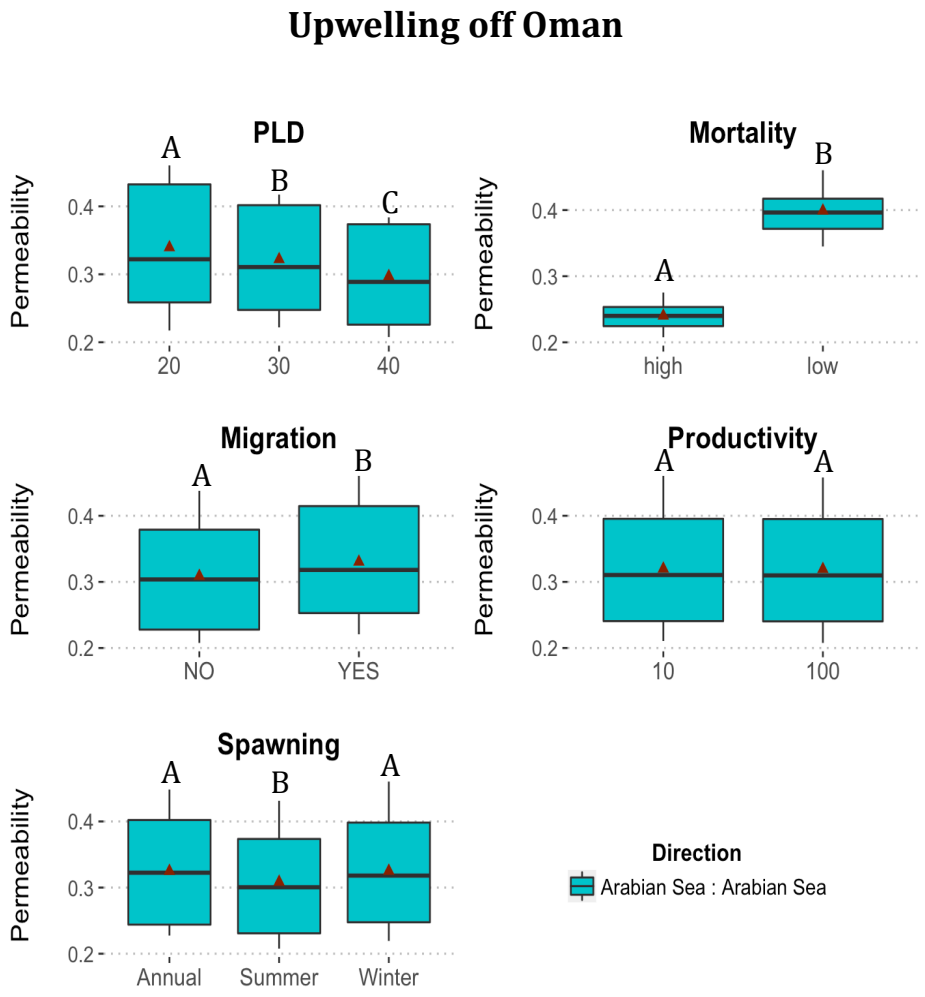

Upwelling off Oman
PLD
Mortality
Migration
Productivity
Spawning
Permeability
0.4
0.3
0.2
A
B
C
20
30
40
high
low
NO
YES
10
100
Annual
Summer
Winter
Direction
Arabian Sea : Arabian Sea

Fig. 5.

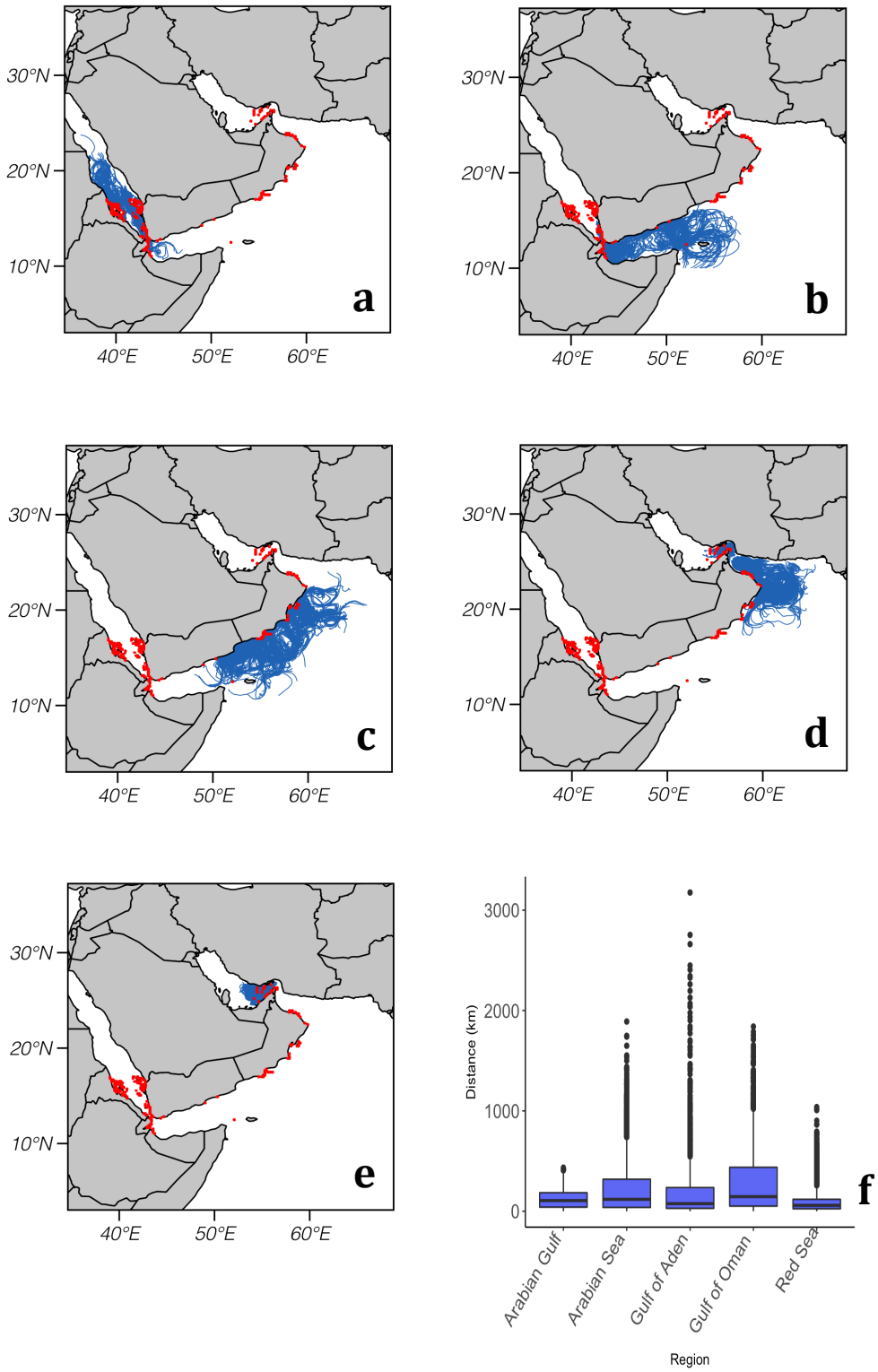
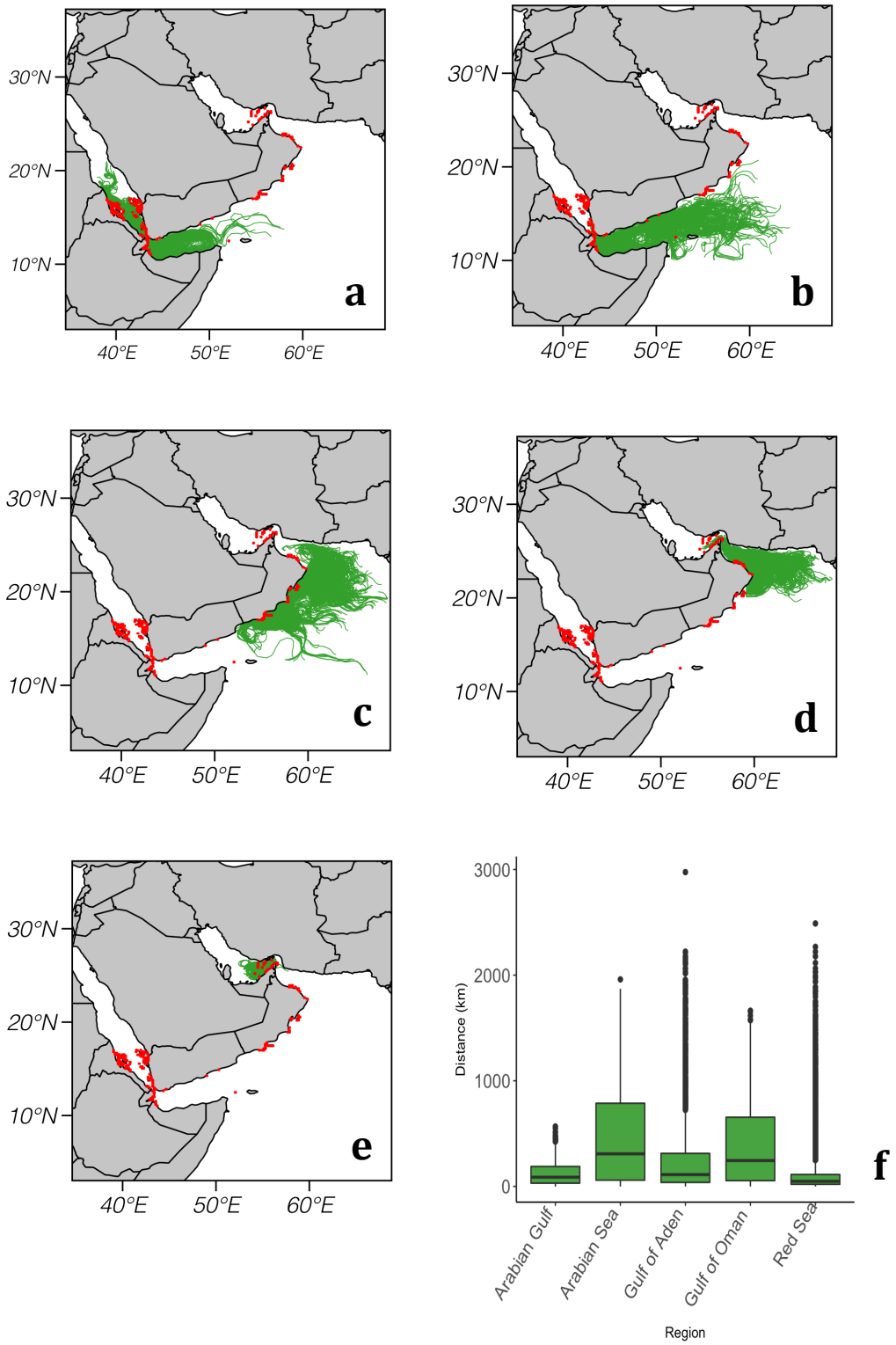

30°N
20°N
10°N
40°E
50°E
60°E
a
b
c
d
e
f
Distance (km)
3000
2000
1000
0
Arabian Gulf
Arabian Sea
Gulf of Aden
Gulf of Oman
Red Sea
Region

Fig. 6.


30°N
20°N
10°N
40°E
50°E
60°E
a
b
c
d
e
f
3000
2000
1000
0
Distance (km)
Arabian Gulf
Arabian Sea
Gulf of Aden
Gulf of Oman
Red Sea
Region