

# Seascape genetics of the spiny lobster *Panulirus homarus* in the Western Indian Ocean: understanding how oceanographic features shape the genetic structure of species with high larval dispersal potential

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## Abstract

This study examines the fine-scale population genetic structure and phylogeography of the spiny lobster *Panulirus homarus* in the Western Indian Ocean. A seascape genetics approach was used to relate the observed genetic structure based on 21 microsatellite loci to ocean circulation patterns, and to determine the influence of latitude, sea surface temperature (SST) and ocean turbidity (KD490) on population-level processes. At a geospatial level, the genetic clusters recovered corresponded to three putative subspecies, *P. h. rubellus* from the SW Indian Ocean, *P. h. megasculptus* from the NW Indian Ocean, and *P. h. homarus* from the tropical region in-between.

Virtual passive Lagrangian particles advected using satellite-derived ocean surface currents were used to simulate larval dispersal. In the SW Indian Ocean, the dispersion of particles tracked over a 4-month period provided insight into a steep genetic gradient observed at the Delagoa Bight, which separates *P. h. rubellus* and *P. h. homarus*. South of the contact zone, particles were advected south-westwards by prevailing boundary currents, or were retained in nearshore eddies close to release locations. Some particles released in southeast Madagascar dispersed across the Mozambique Channel, and reached the African shelf. Dispersal was characterized by high seasonal and inter-annual variability, and a large proportion of particles were dispersed far offshore and presumably lost. In the NW Indian Ocean, particles were retained within the Arabian Sea. Larval retention and self-recruitment in the Arabian Sea could explain the recent genetic divergence between *P. h. megasculptus* and *P. h. homarus*. Geographic distance and minimum SST were significantly associated with genetic differentiation in multivariate analysis, suggesting that larval tolerance to SST plays a role in shaping the population structure of *P. homarus*.

Keywords: Phylogeography, contact zone, ocean circulation, marine biogeography, larval retention

## **1. Introduction**

Seascape genetics – where population genetics draws on ecology, oceanography and geography to explain connectivity and spatial genetic structure, was recently reviewed by Selkoe et al. (2016). Seascape genetics provides a conceptual framework for understanding the multiple historical and contemporary processes that shape dispersal and gene flow in the sea (Selkoe et al. 2008, Riginos et al. 2011, Portnoy et al. 2014). For example, larvae that are adapted to drifting in the water column may rely on ocean currents, eddies, and fronts for dispersal, but can also use larval positioning or swimming behaviour to remain in favourable habitats or to move towards the coast (Schmalenbach and Buchholz 2010, Butler et al. 2011). Ocean circulation can actively promote genetic exchange over long distances (Chiswell et al. 2003, Groeneveld et al. 2012), or constitute a barrier to gene

flow, even when populations are geographically close to each other (Palumbi 1994, Ayre and Dufty 1994, Teske et al. 2008). Common seascape correlations of spatial genetic metrics include geography, temperature, ocean transport, habitat patch size or continuity, chlorophyll a or the presence of biogeographic breaks / ecoregions (reviewed in Selkoe et al. 2016). Environmental gradients act on dispersal processes and gene flow through influencing larval survival and post-settlement fitness – and hence recruitment success (Nanninga et al. 2013, Robitzsch et al. 2015).

The scalloped spiny lobster *Panulirus homarus* is widespread in the Indo-West Pacific, extending northwards from south-eastern Africa to the Arabian Sea, and eastwards to Japan, Indonesia and northern Australia (Holthuis et al. 1991). *Panulirus homarus* comprises several putative subspecies, and its evolutionary history and phylogeography have been popular subjects in the recent literature (Farhadi et al. 2013, 2017, Lavery et al. 2014, Reddy et al. 2014, Singh et al. 2017). Analyses of mitochondrial and nuclear sequences from several genetic markers and microsatellite loci have come to broadly similar conclusions, that at least three or four separate evolutionary lineages exist, occupying distinct geographical ranges. The genetic information largely agrees with morphological groupings (Berry 1974). *Panulirus homarus rubellus* (red megasculpta form) from the Southwest (SW) Indian Ocean is the most divergent, and possibly a separate species based on phylogenetic analyses using mitochondrial and nuclear markers (Lavery et al. 2014, Farhadi et al. 2017, Singh et al. 2017). *Panulirus homarus* “brown” is restricted to the Marquesas Islands in the Central Pacific, and *P. homarus homarus* (green microsculpta form) is widespread in intervening areas (Farhadi et al. 2017). The status of *P. homarus megasculptus* (green megasculpta form) from the Northwest (NW) Indian Ocean (mainly Arabian Sea) remains unclear. Neither Singh et al. (2017) nor Lavery et al. (2014) could find a phylogenetic basis for distinguishing it from *P. h. homarus* from the SW Indian Ocean based on mtDNA and nuclear loci, but Farhadi et al. (2013, 2017) found evidence for reduced gene flow between the NW Indian Ocean and populations in Kenya and Tanzania, further to the south.

The Western Indian Ocean extends from eastern South Africa to the Arabian Gulf, including waters around Madagascar and several small island states, such as Mauritius, Seychelles and Comoros (Figure 1). It is a tropical / subtropical region with high biodiversity and endemism, brought about by diverse habitats along the continental shelf, and around isolated islands or subsurface plateaus (van der Elst et al. 2009, Halo et al. 2017). Two western boundary currents dominate the coastal oceanography; the Agulhas Current to the south and the Somali Current to the north. The Somali Current reverses its flow direction seasonally, under the influence of the SW monsoon (flows northwards) and the northeast (NE) monsoon (flows southwards) seasons (Schott and McCreary 2001). It also receives waters from the East African Coastal Current along coastal Tanzania and Kenya. Water from the South Equatorial Current enters the northern Mozambique Channel, forming a series of eddies which propagate southwards through the channel (Otwoma and Kochzius 2016, Halo et al. 2017). These waters are augmented by eddies originating from the East Madagascar Current at the southern end of the channel (de Ruijter et al. 2004, Ridderinkhof et al. 2013) and their confluence forms the upper Agulhas Current off southern Mozambique and eastern South Africa.

Spalding et al. (2007) subdivided the Western Indian Ocean into 12 marine ecoregions, or “areas of relatively homogenous species composition, clearly distinct from adjacent systems”. Biogeographic forcing agents characteristic of ecoregions include upwelling cells (for example the Central Somali Coast), nutrient inputs from freshwater influx (Sofala Bight / Swamp Coast), the influence of ocean currents (Northern Monsoon Coastal Current), bathymetric or coastal complexity (East African Coral Coast), or differences in temperature regimes or sediments. Towards the south, the sub-tropical Natal ecoregion is characterized by high species diversity, resulting from an influx of species from the Indo-Pacific, transported by the Agulhas Current (Bustamante and Branch 1996, Spalding et al. 2007). Madagascar comprises two separate ecoregions, Southeast Madagascar with cooler water and upwelling cells, and Western and Northern Madagascar where this upwelling is negligible or absent (Spalding et al. 2007).

The concordance between marine biogeographic and phylogeographic boundaries is increasingly recognized in the literature (Bowen et al. 2016, Teske et al. 2006, 2007 and 2009). Where individual species are distributed across two or more biogeographic provinces, shifts in genotype frequencies often align with biogeographic boundaries, providing intraspecific concordance between biogeography and phylogeography. Recent examples among marine taxa include sea snails (Brante et al. 2012), clams (DeBoer et al. 2014), Indo-Pacific goatfish, *Mulloidichthys flavolineatus* (Fernandez-Silva et al. 2015), spiny lobster, *Panulirus penicillatus* (Iacchei et al. 2016), barnacles (Ewers-Saucedo et al. 2016) and seaweeds in the southeast Pacific (Guillemin et al. 2016).

We used biological information, habitats and ocean surface currents in a seascape genetics approach to explore the genetic structure observed within the *P. homarus* subspecies complex in the Western Indian Ocean. The hypothesis that isolation by distance is the main driver of differentiation among subspecies was tested. Alternatively, biogeographic breaks determined by ocean circulation patterns and environmental gradients may have constrained gene flow, resulting in genetic differentiation between the three groups. Specific aims were to: (i) evaluate potential phylogeographic boundary zones; (ii) use virtual particle tracking simulations to infer larval dispersal patterns based on surface currents; and (iii) determine the extent to which genetic structure correlates with environmental variables and simulated larval movement.

## **2. Materials and methods**

### **2.1 Microsatellite sampling**

A total of 271 *Panulirus homarus* specimens were collected from 15 sites in the Western Indian Ocean: five sites from eastern South Africa, three from Mozambique, one each in southern Madagascar, Kenya and Yemen, and four in Oman (Figure 1). All specimens were identified to subspecies level based on phenotypic and geographic information. There were 43 individuals in the

*P. h. homarus* group (22 from Kenya; 20 from Mozambique; 1 from South Africa), 53 in the *P. h. megasculptus* group (29 from Oman; 24 from Yemen) and 175 in the *P. h. rubellus* group (38 from Mozambique; 29 from Madagascar; and 108 from South Africa). DNA was extracted from pereopod tissue using the Zymo gDNA Universal DNA extraction kit (Inqaba, Zymo), as per the manufacturers protocol.

A panel of 21 microsatellite loci, consisting of eight loci (Orn4, Orn5, Orn11, Orn12, Orn16, Orn17, Orn21 and Orn32) described by Dao et al. (2013) and 13 loci (Pho G01, Pho G03, Pho G21, Pho G22, Pho G25, Pho G27, Pho G30, Pho G32, Pho G35, Pho G36, Pho G42, Pho G53 and Pho G58) described by Delghandi et al. (2015), was chosen for PCR amplification. Forward primers were labelled with a fluorescent dye on the 5' end. The microsatellite panel was partitioned into six multiplex reactions and a single reaction for Orn 17 (Table S1).

PCR's were carried out in 10 µl volume reactions, which contained 5 µl of 1X Kapa 2G Fast Multiplex Mastermix (Kapa Biosystems), 0.2 µM of each primer, and 1 µl of 10–50 ng of genomic DNA. For multiplexes A, B, C and Orn 17, cycling conditions were as follows: an initial denaturation at 95 °C for 5 minutes, followed by 28 cycles of denaturation at 95 °C for 30 seconds, annealing at 60 °C for 90 seconds, extension at 72 °C for 30 seconds, and a final extension step at 60 °C for 30 minutes. For multiplexes E, F and G, cycling conditions were: an initial denaturation step at 95 °C for 15 minutes, 32 cycles of denaturation at 94 °C for 30 seconds, annealing at 60 °C for 90 seconds, extension for 72 °C for 60 seconds and a final extension at 72 °C for 30 minutes.

Fragment analysis of amplified products was done at Central Analytical Facility at Stellenbosch University, South Africa. GeneMarker v. 2.4.0 (Soft Genetics) was used to score the genotypes. To monitor the consistency in genotype scoring, 20% of the samples were re-amplified and scored. Individuals with less than 20% missing data were considered for further analyses. Microchecker v.2.2.3 (van Oosterhout et al. 2004) was used to check for genotyping errors such as allelic dropout,

stuttering and the presence of null alleles. The Expectation Maximization Algorithm (EM) implemented in FreeNA (Chapuis and Estoup 2007) was used to estimate the null allele frequencies for each marker and population. Bootstrap resampling over loci was conducted with 100 000 replicates. The excluding null alleles (ENA) method was used to compare null allele corrected and uncorrected global and population  $F_{ST}$  values using paired t-tests.

## 2.2 Genetic diversity indices

GenAlex v.6.5 (Peakall and Smouse 2006) was used to compute the number of alleles per locus and population. Arlequin v. 3.5.2.2 (Excoffier and Lischer 2010) was used to calculate observed and expected heterozygosities and to test for departures from Hardy-Weinberg Equilibrium (HWE) and linkage equilibrium (10 000 replicates). The Bonferroni correction was applied for multiple comparisons. The allelic richness per locus was calculated using FSTAT v.2.9.3.2 (Goudet 1995). The polymorphic information content (PIC) for each locus was estimated using Cervus v.3.0.7 (Marshall et al. 1998, Slate et al. 2000, Kalinowski et al. 2007).

## 2.3 Genetic structure and gene flow

Population genetic structure between the three subspecies and between different localities was evaluated using STRUCTURE v. 2.3.4 (Pritchard et al. 2000).  $K$  was set from 1 to 12. Each  $K$  was run for 10 iterations. The admixture model was chosen, and run with and without sampling location as a prior. A total of 1 000 000 MCMC iterations were performed after a burnin period of 250 000 iterations. Structure Harvester (Earl and von Holdt 2012; <http://taylor0.biology.ucla.edu/structureHarvester/>) and Pophelper (Francis 2017; <http://pophelper.com/>) were used to identify the number of genetic clusters ( $K$ ) that fit the data best (Evanno et al. 2005). An analysis of molecular variance (AMOVA) was performed using Arlequin, to assess the magnitude of genetic differentiation between the groups identified by the STRUCTURE analysis.

The role of seascape features in population genetic structure, and potential contact zones, was inferred using the Geneland v.4.0.3 R-package (Guillot et al. 2005). This method couples multilocus microsatellite genotype data and geospatial information by using geographical sampling locality coordinates as priors, enabling the detection of subtle population structure, and also to infer the locations of genetic discontinuities or transition zones (Guillot et al. 2005). The analysis consisted of 10 independent runs of 1 000 000 MCMC iterations, sampling every 100 generations. The number of predefined genetic clusters ( $K$ ) ranged from 1 to 12. The spatial model was employed, with and without accounting for null alleles. The correlated allele frequencies model was chosen to detect subtle genetic structure (Guillot 2008).

The null hypothesis of isolation by distance was examined by testing the relationship between genetic and geographic distance using a Mantel test. The analysis was carried out using the program IBDWS (Jensen et al. 2005, <http://ibdws.sdsu.edu/~ibdws/>). The genetic distances ( $F_{ST} / (1 - F_{ST})$ ) were regressed against the geographic distances (straight-line distances on Google Earth) with 1000 randomizations between populations.

## 2.4 Environmental factors

The relationship between genetic differentiation of the *P. homarus* groups (pairwise  $F_{ST}$ ), geography and environment was tested using the multivariate multiple regression approach of a distance-based redundancy analysis (dbRDA) (Legendre and Anderson 1999). Monthly composite oceanic variable data of ocean productivity chlorophyll  $a$  (chl  $a$ ,  $\text{mg}\cdot\text{m}^{-3}$ ), sea surface temperature (mean, maximum and minimum SST,  $^{\circ}\text{C}$ ) and turbidity (diffuse attenuation coefficient  $KD490$ ;  $\text{m}^{-1}$ ), were obtained from the GMIS Marine Geodatabase ([mcc.jrc.ec.europa.eu](http://mcc.jrc.ec.europa.eu)), based on the NASA MODIS terra satellite at a 4-km spatial resolution. Data were collected for 2012 to 2015, coinciding with the genetic sampling regime. A matrix of genetic differentiation between sampling sites ( $F_{ST}$ ) was used as the response variable, and mean measurements of environmental variables (chl  $a$ , mean, max and min SST,



turbidity), and larval recruits (based on estimates from ocean modelling simulations as the number of larvae that reach settlement at each site on the coast) were used as the explanatory variables. The dbRDA analysis was carried out using the ‘capscale’ function in the Vegan package (Oksanen et al. 2015) in R. The correlation among variables was measured using Pearson’s correlation coefficient in Vegan. Where variable pairs were highly correlated (Rellstab et al. 2015) the biologically more relevant one to *P. homarus* was used. Minimum SST was considered an important correlate because it decreases along a gradient from tropical (*P. h. homarus* preference) to subtropical conditions (*P. h. rubellus* preference) (Berry 1971b, 1974b). SST is expected to affect phyllosoma larvae that disperse in the upper layers of the water column. Turbidity was selected because *P. homarus* juveniles and adults prefer turbid conditions in the shallow subtidal zone (Berry 1971b, Holthuis 1991). The Euclidean geographic distance matrix was transformed into a continuous rectangular vector by principal co-ordinates analysis (PCoA) using the ‘pcnm’ function in Vegan. The ‘ordistep’ function was used to identify the most significant variables to include in the model (Table S2). The ‘varpart’ function in Vegan was used to estimate the amount of genetic differentiation due to each predictor variable. Significance of the full model was assessed by comparing it to the null model containing only the intercept, and significance of each predictor variable was tested by comparing models which test each predictor after removing the effects of the other predictors. Significance tests were carried out using the ‘anova.cca’ function in Vegan.

## 2.5 Larval dispersal simulations

We explored the effects of ocean circulation on larval dispersal and settlement, and hence genetic differentiation, in the virtual particle tracking tool, Parcels v.0.9 (Probably A Really Computationally Efficient Lagrangian Simulator) (Lange and van Sebille 2017). Lagrangian particle trajectories were simulated using Parcels with the equation:

$$X(t + \Delta t) = X(t) + \int_t^{t+\Delta t} v(x, \tau) d\tau$$

where  $X$  is the three-dimensional position of a particle and  $v(x, \tau)$  is the three-dimensional velocity field at that location from an ocean general circulation model.

Ocean velocity data were obtained from the GlobCurrent Project (Johannessen et al. 2016; <http://www.globcurrent.org/>) which provides daily average surface ocean current estimates for the world's oceans at 25 km spatial resolution by merging data from multiple satellite altimeter missions with gravity models and combining these with Ekman currents (at surface and 15 m depth) estimated from drogued surface drifter data, Argo floats and near-surface winds.

The u- and v-component geostrophic velocities are defined by the following equations (Saraceno et al. 2008):

$$v_{geo} = -\left(\frac{g}{f}\right) \cdot \frac{\delta\eta_{y[0]} - \delta\eta_{y[1]}}{\delta y}$$

$$u_{geo} = \left(\frac{g}{f}\right) \cdot \frac{\delta\eta_{x[0]} - \delta\eta_{x[1]}}{\delta x}$$

where  $u$  represents the zonal component,  $v$  the meridional component,  $\delta\eta$  is the variation in the sea surface height,  $\delta x/\delta y$  the distance between grid points,  $g$  the gravitational acceleration and  $f$  the Coriolis force.

These products are combined with the Ekman currents estimated from Argo floats and drifter data in conjunction with wind stress estimates from the European Centre for Medium-Range Weather Forecasts (ECMWF). At depth  $z$  (0 m and 15 m), the Ekman response ( $\vec{v}_{ek}$ ) to the wind stress ( $\vec{\tau}$ ) is expressed by Rio et al. (2014):

$$\vec{v}_{ek}(z) = \beta(z) \cdot \vec{\tau} \cdot e^{i\theta(z)}$$

The combined geostrophic current components constitute the GlobCurrent ocean current data. This data provides 3-hourly, global ocean currents at the surface and at 15 m depth with a 0.25° spatial resolution, covering the period 1993–2015. A comparison of the virtual Lagrangian trajectories

advected using GlobCurrent to real trajectories from surface drifting buoys for the SW Indian Ocean indicates good agreement between the two (Hart-Davis et al. 2018). Particularly, the density distribution of the real and virtual trajectories suggests that the GlobCurrent forced Lagrangian particles are appropriate for use in studies of upper ocean dynamics.

Known life history parameters of *P. homarus* (Table 1) were taken into account in simple exploratory simulations. Some 1000 virtual particles were deployed at 12 am on 1<sup>st</sup> January and on 1<sup>st</sup> June in 2009 and 2010. These two periods were selected because adult lobsters sampled in 2013 and 2014 would presumably have been drifting larvae at the time, and because January and June are the peak breeding seasons in the SW and NW Indian Oceans, respectively. Particles were restricted to the upper (<15 m deep) layer of the water column, and dispersed passively over a period of 120 days (4 months). Trajectories and final locations of particles were plotted. The numbers of particles that reached the coast were quantified using custom python scripts. The ocean circulation model was based on work by Hart-Davis et al. (2018).

### **3. Results**

#### **3.1 Genetic diversity**

Summary statistics of 271 *P. homarus* individuals genotyped across 21 microsatellite loci are shown in Table 2 and in supplementary Tables S3 A and B. Microchecker did not detect evidence for scoring errors due to stuttering or large allelic dropout, but indicated that null alleles may be present at ten loci (Orn 11, Orn 12, Orn 16, G21, G25, G27, G30, G32, G53 and G58). All loci were included in subsequent analyses because no significant difference was found between ENA-corrected versus non-ENA corrected  $F_{ST}$  values, overall and for each population ( $p > 0.05$ ).

Genetic variability was high at most loci, but low at Orn 21 (PIC = 0.072) and G27 (PIC = 0.185). The  $N_A$  per locus ranged from 2 (locus G42) to 14 (locus Orn 12). The expected heterozygosity was higher

than observed at Orn 4, Orn 11, Orn 12, Orn 16, G01, G21, G25, G27, G30, G32, G53 and G58. Following Bonferroni correction, Orn 5, Orn 12, Orn 16, Orn 17, Orn 32, G03, G21, G22, G27, G32, G36, G42 and G53 deviated significantly from HWE. However, out of the 12 populations, Orn 5 deviated significantly from HWE in 5 populations, Orn 12 in 6, Orn 16 in 3, Orn 17 in 5, Orn 32 in 1, G21 in 5, G22 in 2, G32 in 6, G36 in 2, G42 in 9 and G53 in 1 population. The analyses were also conducted after removing loci that deviated from HWE, which resulted in a smaller dataset with 8 loci from 257 individuals. The results from analyses of the smaller dataset did not contradict those obtained from using the full dataset, and hence all loci were retained (see supplementary results). At the population level,  $N_A$  and  $A_R$  were highest in Oman ( $N_A = 7.19$ ,  $A_R = 6.07$ ) and lowest in Zavora ( $N_A = 4.95$ ,  $A_R = 4.8$ ). At the subspecies level,  $N_A$  and  $A_R$  were highest in *P. h. rubellus* ( $N_A = 8.6$ ,  $A_R = 8.6$ ).

### 3.2 Genetic structure

Genetic differentiation between the subspecies could clearly be distinguished using the clustering analyses implemented in STRUCTURE and Geneland. STRUCTURE analysis indicated that  $K = 3$  was optimal for the *P. homarus* subspecies dataset (Figure 2 A and B). The AMOVA indicated that there was 4.5% difference between each of the groups identified by the STRUCTURE analysis (Table 3). Individuals collected from the Arabian Sea (Oman and Yemen) clustered as a single population which corresponded to *P. h. megasculptus*. Similarly, individuals collected from Kenya and the northernmost Mozambique site, Zavora, clustered together as *P. h. homarus*. The majority of specimens collected at Chidenguele and Xai Xai in Mozambique, Madagascar and South Africa clustered as *P. h. rubellus*, although some evidence of admixture was observed.

When comparing the genetic clusters with specimens assigned to each of the three subspecies based on their morphology (morphotypes), some evidence of admixture was observed, especially when the locprior model was not used. With locprior, all *P. h. megasculptus* morphotypes matched their corresponding genetic clusters when using locprior, but 8% showed admixture when locprior was

not used. In Kenya, *P. h. homarus* morphotypes all matched the corresponding genetic clusters, irrespective of the model used. All *P. h. homarus* morphotypes collected from Zavora, Chidenguele and Xai Xai in Mozambique, and Mdumbi in South Africa also matched their respective genetic clusters, irrespective of the model used.

In Madagascar, 20% of *P. h. rubellus* morphotypes showed some evidence of admixture with *P. h. megasculptus* without locprior, but all clustered with *P. h. rubellus* when locprior was used. Of the *P. h. rubellus* morphotypes in the South African populations, 12% showed evidence of admixture with other subspecies without locprior, but when the locprior model was used, one individual from Port St Johns (5%) and another from Mdumbi (5%) corresponded to the *P. h. homarus* cluster. Out of 6 individuals from Zavora that were morphologically identified as *P. h. rubellus*, 4 (67%) showed a high degree of admixture with *P. h. homarus*, even when using the locprior model – thus suggesting that interbreeding and high genetic variability occurs predominantly at this location.

The spatially explicit Bayesian clustering model implemented in Geneland also resulted in three clear genetic clusters, corresponding to samples from Oman and Yemen (*P. h. megasculptus*; Figure 3A), Mozambique, Madagascar and South Africa (*P. h. rubellus*; Figure 3B), and Kenya with some Mozambique samples (*P. h. homarus*; Figure 3C). Steep contour lines indicated a genetic transition zone between *P. h. homarus* and *P. h. rubellus* in southern Mozambique, where they are sympatric. Genetic and geographical distance were weakly correlated ( $R^2 = 0.23$ ,  $p = 0.04$ ) suggesting that geographic distance plays a minor role in genetic differentiation (Figure 3D).

### 3.3 Environmental factors

The 'ordistep' function identified geography, minimum SST and larval recruits of 2009 as the most significant variables affecting the response matrix of genetic variation (Table S2). This model was significant when compared to the null model ( $F = 6.20$ ,  $p = 0.001$ ). The first axis accounted for 55% of the fitted variation and 35% of the total variation, and the second axis explained 42% of the fitted

variation and 27% of the total variation (Figure 4). Variance partitioning indicated that minimum SST explained 18% of the total variation ( $F = 6.98$ ,  $p = 0.004$ ), and that larval recruits of June 2009 could explain 8% of the variation, but was not significant ( $F = 1.82$ ,  $p = 0.15$ ). Geography explained 13% of the total variation ( $F = 4.67$ ,  $p = 0.019$ ) and was significant (Figure 4).

### 3.4 Virtual particle dispersal simulations

#### a) NW Indian Ocean and Kenya

At the NW Indian Ocean sites (Oman, Yemen) and Kenya, the peak breeding season of *P. homarus* is in June. Particle density plots are shown for June (Figure 5) and January (Figure S1) along with dispersal trajectories for January and June (Figures S2 and S3). Particles released in June at sites in Oman became trapped in eddies close to their release location in 2009, but dispersed wider in 2010. The proportion of released particles reaching the coast after 120 days was 30% in 2009 and 20% in 2010. Particles released in January at sites in Oman dispersed widely in offshore eddies in the Arabian Sea, and fewer of them reached the coast after 120 days, 14% in 2009 and 15% in 2010. Notably, all trajectories remained south of the Sea of Oman, where *P. homarus* adults are rarely encountered.

Particles released in Yemen in June were retained in the Gulf of Aden, with a high rate of reaching the coast ( $> 95\%$  in 2009 and  $33\%$  in 2010). Those released in January were advected offshore into the NW Indian Ocean, with  $< 2\%$  of the particles reaching the coast in either year.

Particles released in June in Kenya were retained near their release site in both years ( $> 50\%$  in 2010), with some dispersal northwards into Somalia in 2009. Those released in January were swept eastwards, potentially entrained in the South Equatorial Return Current. Few particles returned to the coast after 120 days ( $6.8\%$  in 2009 and  $9.7\%$  in 2010), but a small proportion entered the northern Mozambique Channel in 2009. Overall, trajectories reflect dispersal within eddies and

gyres, high seasonal and inter-annual variability, and retention in eddies near release locations at several sites in June.

#### b) SW Indian Ocean

Particle density plots for SW Indian Ocean sites (Mozambique, Madagascar and South Africa) for the peak breeding season in January are shown in Figure 6. Density plots are also shown for June (Figure S4) along with particle trajectories for January (Figure S5) and June (Figure S6). Particles released in southern Mozambique in January were mostly swept up in the Agulhas Current, shown as southwestwards trajectories along the shelfbreak, either retroflecting eastwards into the SW Indian Ocean or leaking into the SE Atlantic basin. After 120 days, 14.9% of particles released at sites in Mozambique reached the coast in 2009 and 13% in 2010, mostly south of Zavora in Mozambique, and the majority of them in eastern South Africa. No particles reached the coast to the north of Zavora. Particles released in June showed high settlement on the coast in 2009 (62%), particularly at Chidenguele, where they were likely retained in the Delagoa Bight by a seasonal eddy. Some 12% of particles released in June 2010 reached the coast.

Particles released in southeast Madagascar in both years and seasons tracked across the Mozambique Channel towards the mainland coast of southern Mozambique and eastern South Africa, and most became entrained in eddies, remaining in the channel or south of it after 120 days. Although some particles released in January reached the mainland coast after 120 days (1.6% in 2009 and 1.7% in 2010), many were close to it, just off the shelf. Some 2% of particles released in January were returned to southern Madagascar, and of those released in June, 1.2% were returned.

Particles released in January at all sites in eastern South Africa were advected southwestwards by the Agulhas Current, and either reached the coast, retroflected into the SW Indian Ocean, or leaked into the SE Atlantic after 120 days. Some 13.4% of particles released at Blood Reef reached the coast after 120 days in 2009 and 10.2% in 2010, mostly to the south of their release locations. Particles

released from the southernmost sites rarely reached the coast after 120 days, suggesting that populations occurring here receive larvae from sites further to the north. Particles released in June (outside the main breeding season) were dispersed further offshore than those released in January at nearly all sites. On average, particles released in January at South African sites reached the coast in 10% (2009) and 5% (2010) of cases after 120 days, compared to < 1% (2009) and 6% (2010) of particles released in June. High seasonal and interannual variability in dispersal patterns were also observed in the SW Indian Ocean region, with evidence that particles can become trapped and retained in eddies near, or downstream of their release locations, despite the narrow shelf and proximity of the Agulhas Current along the shelf-edge.

#### **4. Discussion**

##### **4.1. Genetic structure and boundary zones**

We examined the fine-scale population genetic structure and phylogeography of *P. homarus* in the Western Indian Ocean, based on fast-evolving nuclear microsatellite markers. We also used a seascape genetics approach to relate the observed genetic structure to oceanographic influences. Three clear genetic clusters corresponded with samples from the Arabian Sea (NW Indian Ocean; *P. h. megasculptus*), SW Indian Ocean (*P. h. rubellus*) and the more tropical region in-between (*P. h. homarus*). A contact zone between *P. h. homarus* and *P. h. rubellus* near Zavora (in the Delagoa Bight, Mozambique) was inferred from the high degree of admixed individuals originating from Zavora in the STRUCTURE analysis, and from the genetic transition zone in the Geneland analysis.

The microsatellite analysis suggests that *P. h. homarus* (Kenya) and *P. h. megasculptus* (Oman and Yemen) are evolutionarily distinct ( $F_{ST} > 0.07$ , Table S4). Farhadi et al. (2013, 2017) also found evidence of genetic divergence between Arabian Sea and more equatorial *P. homarus* populations, based on hypervariable control region sequences and microsatellites. The two groups are morphologically distinguishable (microsculpta versus macrosculpta forms), and inhabit distinct



geographic ranges, with some overlap in Oman (pers obs. J. Groeneveld). Nevertheless, more conserved mitochondrial and nuclear DNA markers could not differentiate the two groups (Lavery et al. 2014, Singh et al. 2017), thus suggesting a recent divergence.

The simulated particle trajectories strongly support the retention of *P. h. megasculptus* larvae within the NW Indian Ocean. Final locations after 120 days suggest that a proportion of larvae will reach, and presumably recruit back to populations in the Gulf of Aden and in the Arabian Sea. Mesoscale eddies in the Gulf of Aden are likely to retain larvae released in June within the Gulf, but the eddies weaken seasonally (Bower and Furey 2012), giving rise to eastward dispersal of particles released in January, into the Arabian Sea. *Panulirus homarus megasculptus* in Oman has a prolonged breeding season with multiple broods (Al-Marzouqi et al. 2007, 2008), and drifting larvae are expected to be present in the Arabian Sea throughout the year. Ocean circulation is influenced by the seasonally reversing Somali Current and eddies which develop along the coasts of Oman, Yemen and Somalia (Schott and McCreary 2001). These eddies likely retain larvae in the NW Indian Ocean, thereby facilitating the incipient genetic structure observed between *P. h. megasculptus* and *P. h. homarus* (our results and see also Farhadi et al. 2013). The oceanographic boundary is not restricted to dispersal of lobster larvae, and also prevents northwards dispersal of starfish *Acanthaster planci* larvae from east Africa into the northern Arabian Sea (Vogler et al. 2012).

For the SW Indian Ocean populations, spatially explicit clustering provided empirical support for a barrier to gene flow between *P. h. homarus* and *P. h. rubellus* near the Delagoa Bight, where they are sympatric. Isolation by distance did not play a crucial role in influencing population genetic structure among the subspecies. For example, *P. h. homarus* at Zavora (northern edge of Delagoa Bight) were more closely related to those in Kenya, thousands of kilometres away ( $F_{ST} = 0.016$ , Table S4), and Xai Xai which is 169 km to the south ( $F_{ST} = 0.015$ ), than to those in Chidenguele (122 km

south of Zavora,  $F_{ST} = 0.066$ ). This provides strong evidence for the presence of a phylogeographic barrier between subspecies in the Delagoa Bight.

#### 4.2 Environmental drivers of genetic discontinuities

The multivariate analysis dbRDA was used to investigate the correlation between genetic variation, environmental and spatial factors across the seascape. Minimum SST was correlated with genetic variability (Figure 4), suggesting that ambient temperature may affect the success of larval dispersal. Coastal waters become progressively cooler towards the south (i.e. southern Mozambique and eastern South Africa), potentially playing a selective role by reducing the fitness of *P. h. homarus* larvae originating from more tropical waters to the north of Zavora in Mozambique. Nevertheless, low densities of *P. h. homarus* do occur in eastern South Africa – potentially originating from Zavora or further north, and they must have survived the temperature gradient associated with southwards dispersal into cooler coastal waters. The absence of definitive evidence for hybrids between the two forms supports a hypothesis of specific mating and spawning preferences that may be spatially and/or temporally distinct, and potentially maintained through adaptation and behavioural reproductive isolation (Farhadi et al. 2017). Van der Meeren et al. (2008) demonstrated similar behavioural mechanisms among clawed lobsters *Homarus gammarus* and introduced *H. americanus* in the NE Atlantic.

#### 4.3 A biogeographic perspective

From a biogeographic perspective, *P. h. homarus* and *P. h. megasculptus* inhabit the Western Indo-Pacific region, whereas *P. h. rubellus* is restricted to the southwestern edge of the region, spilling over into the temperate Southern African region. At a finer resolution, *P. h. rubellus* extends southwards from the Delagoa Bight ecoregion in Mozambique, to the Natal and Agulhas Bank ecoregions in South Africa, and the Southeast Madagascar ecoregion (Spalding et al. 2007). We propose the Delagoa Bight ecoregion as a contact zone between *P. h. homarus* and *P. h. rubellus*.

The Bight is a coastal indentation at the southern end of the Mozambique Channel, and both its location and unique oceanographic features may have contributed to the genetic discontinuity seen here. The Bight is affected by eddies moving gradually southwards through the Mozambique Channel, and also by cross-channel eddies originating from the East Madagascar Current, on its path around the southern tip of Madagascar (Lutjeharms 2006, Cossa et al. 2016). Additionally, the Bight is located near the upper reaches of the Agulhas Current (Lutjeharms 2006), and particles released here were frequently advected southwestwards.

A quasi-stationary and topographically-induced Delagoa Bight Eddy (Saetre and da Silva 1984, Lutjeharms and da Silva 1988, Lamont et al. 2010, Cossa et al. 2016, Halo et al. 2017) creates strong upwelling and a cool Delagoa Bight cell, with near-surface temperatures of  $< 16^{\circ}\text{C}$  at 150 m depth. The cell can potentially form a boundary that restricts gene flow between the two subspecies, but it is intermittent and therefore unlikely to be impermeable. A mixture of equatorial and sub-tropical waters in this area may also contribute to the contact zone, facilitating settlement of post-larvae of *P. h. homarus* originating from further north, and of *P. h. rubellus* originating in the Bight or from southeast Madagascar.

Teske et al. (2009) identified a tropical / subtropical phylogeographic break near Cape St Lucia (some 200 km south of the Delagoa Bight) based on data from estuarine prawns. These authors proposed a selection gradient resulting from the diminishing effects of the Agulhas Current on nearshore waters to the south of St Lucia, where the Natal Bight deflects the current away from the coast, resulting in lower SSTs and potential changes in circulation patterns, such as the formation of eddies and nearshore return currents (Teske et al. 2011). Our study suggests a similar genetic break, acting on spiny lobster larvae, but further to the north, at the Delagoa Bight.

#### 4.4 Influence of ocean currents on gene flow and connectivity

A large, seasonal anticyclonic cell prevails at the northern entrance to the Mozambique Channel (Donguy and Piton 1991), followed by a succession of mesoscale cyclonic and anticyclonic eddies propagating southwards through the channel (Collins et al. 2014, 2016, Halo et al. 2017). These eddies create strong dynamic gradients which act on larval dispersal. Silva et al. (2010) speculated that the anti-cyclonic circulation pattern in the channel randomizes larval dispersal in the mangrove crab *Perisesarma guttatum*, resulting in panmictic populations to the north of the channel. Similarly, Madeira et al. (2012) suggested that the upper Agulhas Current transports *Cerithidea decolata* larvae southwards, thus homogenizing populations in southeast Africa.

The genetic structure in *P. homarus* in the SW Indian Ocean is similarly attributed to the prevailing current systems in the Mozambique Channel. Evidence that populations to the north of the channel are differentiated from those at the south has been documented for shallow-water prawns *Fenneropenaeus indicus* and *Metapenaeus monoceros* (Mkare et al. 2017), green turtle *Chelonia mydas* (Bourjea et al. 2007), blotcheye soldierfish *Myripristis berndti* (Muths et al. 2011), honeycomb grouper *Epinephelus merra* (Muths et al. 2015), and coral species *Acropora austera* and *Platygyra daedalea* (Montoya-Maya et al. 2016).

Particles released at Mozambican sites in the peak January breeding season of *P. h. rubellus* were often entrained in the Agulhas Current or its inshore filaments, and dispersed southwestwards. Some particles retroflected eastwards into the SW Indian Ocean (presumably lost), or leaked into the SE Atlantic basin through ring shedding, eddies and filaments (Gordon, 2003). A proportion of particles released at Mozambican sites reached the coast, mostly near their release locations in southern Mozambique or in eastern South Africa, suggesting that many *P. h. rubellus* postlarvae that settle off eastern South Africa may originate from Mozambique. Overall, the high seasonal and inter-annual variability in dispersal patterns is expected to result in genetic panmixia of *P. h. rubellus* (see

Madeira et al. 2012). From a fisheries management perspective, genetic panmixia implies *that P. h. rubellus* in eastern South Africa and southern Mozambique may be considered a shared resource.

Particles released in southeast Madagascar could not fully explain the connectivity between Madagascar and African shelf populations, potentially because particles are assumed to be passive drifters in the Lagrangian model. In reality, spiny lobster phyllosomas are able to swim and position themselves in the water column to benefit from water movements at different depths (Chiswell and Booth 1999, 2005, 2008, Bradford et al. 2005). Vertical migrations to deeper habitats during the day would reduce predation, with phyllosomas rising to the surface at night to feed (Bradford et al. 2005, Butler et al. 2011). Directional swimming is also not included in the particle model. Jeffs et al. (2005) demonstrated that late stage larvae receive sensory cues directing them towards the shore; cues may include acoustic reef sounds (Hinojosa et al. 2016), chemical (Hadfield and Paul 2001), celestial, magnetic field or electrosense signals (Jeffs et al. 2005). The post-larval puerulus stage is also a strong swimmer, able to cross the shelf using stored energy reserves (Phillips and Olsen 1975, Wilkin and Jeffs 2011). It is therefore clear that behaviour will affect the dispersal of larvae (Butler et al. 2011). Particles released in southeast Madagascar were propagated across the Mozambique Channel on several occasions, reaching the African shelf. Directed swimming by larvae dispersed to here may have assisted them in reaching coastal settlement habitats in Mozambique or eastern South Africa.

Migrations and spawning behaviour of adult spiny lobsters may mitigate the influence of the Agulhas Current on the downstream dispersal of larvae (Groeneveld and Branch 2002, Santos et al. 2014), through determining the location and timing of larval release. Vertical migration of larvae in the water column has been shown to favour larval retention close to local shores (Phelps et al. 2015, Rivera et al. 2013). Teske et al. (2015, 2016) showed that larvae can remain close to the shore and be dispersed by inshore counter-currents. We suggest that *P. homarus* larvae can position

themselves to avoid being caught up in the main Agulhas Current, and are instead dispersed by inshore counter-currents. This observation is supported by a considerable proportion of particles reaching the coast near, or a moderate distance to the southwest of their release locations, after 120 days at large. Had they all been caught up in the Agulhas Current, we suggest that none, or very few of them would have been returned to the coast.

The particle model used here may overstate the magnitude of larval dispersal. The spatial resolution of the GlobCurrent model is 25 km, and coastal sub-mesoscale processes are therefore not resolved. Fine-scale hydrographic processes that may 'push' or 'pull' particles towards or away from the coast are most likely crucial in determining larval settlement patterns, but could not be resolved with the model used. While global operational ocean models (e.g. <http://hycom.org/> or <http://marine.copernicus.eu/>) are approaching spatio-temporal resolutions to resolve sub-mesoscale processes, they are unable to represent the correct levels of variability, particularly in the highly dynamic Agulhas Current (Meyer et al. 2017).

Particle tracking simulations were constrained to January and June to provide seasonal contrast to dispersal patterns. The simulations included the peak breeding seasons of *P. h. rubellus* in the SW Indian Ocean (January) and of *P. h. megasculptus* and *P. h. homarus* in the NW Indian Ocean and Kenya (June). Simulations were further restricted to 2009 and 2010, and showed considerable inter-annual variability – a factor that has been implicated in recruitment patterns of species with drifting larvae (Chelton et al. 1982, Botsford 2001, Griffin et al. 2001). *Panulirus homarus* females can carry up to four batches of eggs per year, releasing them during different months (Al-Marzouqi et al. 2008), when oceanographic conditions would differ from those in the models. The present particle model can therefore only provide a broad indication of larval dispersal patterns. Nevertheless, the close correlation between its outputs and the observed genetic structure provides new insights into the scale of larval dispersal and settlement of *P. homarus* in the Western Indian Ocean.

In conclusion, a seascape genetics approach illustrated that complex physical oceanography and biogeographical boundaries could explain genetic diversity among *P. homarus* subspecies, along with isolation by distance. Eddies in the Arabian Sea potentially retain larvae in that region, thus contributing to the differentiation between *P. h. megasculptus* and *P. h. homarus*. A steep genetic gradient between *P. h. homarus* and *P. h. rubellus* was demonstrated in the Delagoa Bight ecoregion in Mozambique. Virtual particles released south of the Bight were advected southwestwards by boundary currents, or reached the coast near or downstream of their release locations. Minimum SST was correlated with genetic variability, suggesting ambient temperature and larval tolerance as selective factors in dispersal success. Ocean currents and SST may play key roles in maintaining the cooler subtropical and warmer tropical distribution ranges of *P. h. rubellus* and *P. h. homarus* in the SW Indian Ocean.

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## References

- Al-Marzouqi, A., A. Al-Nahdi, N. Jayabalan, and J. Groeneveld. 2007. An assessment of the spiny lobster *Panulirus homarus* fishery in Oman—Another decline in the Western Indian Ocean? *Western Indian Ocean Journal of Marine Science* **6**: 159-174.
- Al-Marzouqi, A., J. C. Groeneveld, A. Al-Nahdi, and A. Al-Hosni. 2008. Reproductive season of the scalloped spiny lobster *Panulirus homarus* along the coast of Oman: management implications. *Agricultural and Marine Sciences, Sultan Qaboos University* **13**: 33-42.
- Amaral, A. R., L. B. Beheregaray, K. Bilgmann, D. Boutov, L. Freitas, K. M. Robertson, M. Sequeira, K. A. Stockin, M. M. Coelho, and L. M. Möller. 2012. Seascape genetics of a globally distributed, highly mobile marine mammal: The short-beaked common dolphin (genus *Delphinus*). *PLoS ONE* **7**. DOI: 10.1371/journal.pone.0031482.
- Ayre, D. J., and S. Dufty. 1994. Evidence for restricted gene flow in the viviparous coral *Seriatopora hystrix* on Australia's Great Barrier Reef. *Evolution* **48**: 1183-1201.
- Beerli, P., and M. Palczewski. 2010. Unified framework to evaluate panmixia and migration direction among multiple sampling locations. *Genetics* **185**: 313-326.
- Benzie, J. A. H., E. Ballment, A. T. Forbes, N. T. Demetriades, K. Sugama, S. Haryanti, and S. Moria. 2002. Mitochondrial DNA variation in Indo-Pacific populations of the giant tiger prawn, *Penaeus monodon*. *Molecular Ecology* **11**: 2553-2569.
- Berry, P. F. 1971a. The biology of the spiny lobster *Panulirus homarus* (Linnaeus) off the east coast of southern Africa. *South African Association for Marine Biological Research, Investigational Report* **28**: 3-75.
- Berry, P. F. 1971b. The spiny lobsters (Palinuridae) of the coast of southern Africa: distribution and ecological notes. *South African Association for Marine Biological Research, Investigational Report* **27**: 4-23.
- Berry, P. F. 1974a. Palinurid and scyllarid lobster larvae of the Natal coast, South Africa. *South African Association for Marine Biological Research, Investigational Report* **34**: 3-44.
- Berry, P. F. 1974b. A revision of the *Panulirus homarus*-group of spiny lobsters (Decapoda, Palinuridae). *Crustaceana* **27**: 31-42.
- Booth, J. D. 2002. Early life history, recruitment processes and settlement of spiny lobsters. *Fisheries Science* **68**: 384-389.
- Botsford, L. 2001. Physical influences on recruitment to California Current invertebrate populations on multiple scales. *ICES Journal of Marine Science* **58**: 1081-1091.
- Bourjea, J., S. Lapegue, L. Gagnevin, D. Broderick, J. A. Mortimer, S. Ciccione, D. Roos, C. Taquet, and H. Grizel. 2007. Phylogeography of the green turtle, *Chelonia mydas*, in the Southwest Indian Ocean. *Molecular Ecology* **16**: 175-186.



Bowen, B. W., M. R. Gaither, J. D. Di Battista, M. Iacchei, K. R. Andrews, W. S. Grant, R. J. Toonen and J. C. Briggs. 2016. Comparative phylogeography of the ocean planet. *PNAS* **113**: 7962-7969.

Bower, A.S. and H.H. Furey. 2012. Mesoscale eddies in the Gulf of Aden and their impact on the spreading of Red Sea Outflow Water. *Progress in Oceanography* **96**: 14-39.

Bradford, R. W., B. D. Bruce, S. M. Chiswell, J. D. Booth, A. Jeffs, and S. Wotherspoon. 2005. Vertical distribution and diurnal migration patterns of *Jasus edwardsii* phyllosomas off the east coast of the North Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **39**: 593-604.

Brante, A., M. Fernández, and F. Viard. 2012. Phylogeography and biogeography concordance in the marine gastropod *Crepidatella dilatata* (Calyptraeidae) along the southeastern Pacific Coast. *Journal of Heredity* **103**: 630-637.

Butler, M. J., C. B. Paris, J. S. Goldstein, H. Matsuda, and R. K. Cowen. 2011. Behavior constrains the dispersal of long-lived spiny lobster larvae. *Marine Ecology Progress Series* **422**: 223-237.

Caputi, N., W. Fletcher, A. Pearce, and C. Chubb. 1996. Effect of the Leeuwin Current on the recruitment of fish and invertebrates along the Western Australian Coast. *Marine and Freshwater Research* **47**: 147-155.

Carr, M. H., J. E. Neigel, J. A. Estes, S. Andelman, R. R. Warner, and J. L. Largier. 2003. Comparing marine and terrestrial ecosystems: implications for the design of coastal marine reserves. *Ecological Applications* **13**: 90-107.

Chapuis, M.-P., and A. Estoup. 2007. Microsatellite null alleles and estimation of population differentiation. *Molecular Biology and Evolution* **24**: 621-631.

Chelton, D., P. Bernal, and J. McGowan. 1982. Large-scale interannual physical and biological interaction in the California Current. *Journal of Marine Research* **40**: 1095-1125.

Chiswell, S. M., and J. D. Booth. 1999. Rock lobster *Jasus edwardsii* larval retention by the Wairarapa Eddy off New Zealand. *Marine Ecology Progress Series* **183**: 227-240.

Chiswell, S. M., J. Wilkin, J. D. Booth, and B. Stanton. 2003. Trans-Tasman Sea larval transport: Is Australia a source for New Zealand rock lobsters? *Marine Ecology Progress Series* **247**: 173-182.

Chiswell, S. M., and J. D. Booth. 2005. Distribution of mid- and late-stage *Jasus edwardsii* phyllosomas: Implications for larval recruitment processes. *New Zealand Journal of Marine and Freshwater Research* **39**: 1157-1170.

Chiswell, S. M., and J. D. Booth. 2008. Sources and sinks of larval settlement in *Jasus edwardsii* around New Zealand: Where do larvae come from and where do they go? *Marine Ecology Progress Series* **354**: 201-217.

Collins, C., J. C. Hermes and C. J. C. Reason. 2014. Mesoscale activity in the Comoros basin from satellite altimetry and a high-resolution ocean circulation model. *Journal of Geophysical Research Oceans* **119**: 4745-4760.

- Collins, C., J. C. Hermes, R. E. Roman and C. J. C. Reason. 2016. First dedicated hydrographic survey of the Comoros Basin. *Journal of Geophysical Research Oceans* **121**: 1291-1305.
- Cossa, O., S. Pous, P. Penven, X. Capet, and C. J. C. Reason. 2016. Modelling cyclonic eddies in the Delagoa Bight region. *Continental Shelf Research* **119**: 14-29.
- Dao, H. T., E. V. Todd, and D. R. Jerry. 2013. Characterization of polymorphic microsatellite loci for the spiny lobster *Panulirus* spp. and their utility to be applied to other *Panulirus* lobsters. *Conservation Genetics Resources* **5**: 43-46.
- Dao, H. T., C. Smith-Keune, E. Wolanski, C. M. Jones, D. R. Jerry, and N. Suzuki. 2015. Oceanographic currents and local ecological knowledge indicate, and genetics does not refute, a contemporary pattern of larval dispersal for the ornate spiny lobster, *Panulirus ornatus* in the South-East Asian Archipelago. *PLoS ONE* **10**. DOI: 10.1371/journal.pone.0124568.
- DeBoer, T. M., M. R. A., Naguit, M. V. Erdmann, M. C. A. Ablan-Lagman, Ambariyanto, K. E. Carpenter, A. H. A. Toha, and P. H. Barber. 2014. Concordance between phylogeographic and biogeographic boundaries in the Coral Triangle: conservation implications based on comparative analyses of multiple giant clam species. *Bulletin of Marine Science* **90**: 277 – 300.
- Delghandi, M., S. Goddard, D. R. Jerry, H. T. Dao, H. S. Afzal, and S. Al-Jardani. 2015. Isolation, characterization, and multiplexing of novel microsatellite markers for the tropical scalloped spiny lobster (*Panulirus homarus*). *Genetics and Molecular Research* **14**: 19066-19070.
- de Ruijter, W. P. M., H. M. van Aken, E. J. Beier, J. R. E. Lutjeharms, R. P. Matano, and M. W. Schouten. 2004. Eddies and dipoles around South Madagascar: Formation, pathways and large-scale impact. *Deep Sea Research Part I: Oceanographic Research Papers* **51**: 383-400.
- Donguy, J.-R., and B. Piton. 1991. The Mozambique Channel revisited. *Oceanologica Acta* **14**: 549-558.
- Dubois, S., T. Comtet, C. Retiere, and E. Thiebaut. 2007. Distribution and retention of *Sabellaria alveolata* larvae (Polychaeta: Sabellariidae) in the Bay of Mont-Saint-Michel, France. *Marine Ecology Progress Series* **346**: 243-254.
- Duda, T. F., and S. R. Palumbi. 1999. Population structure of the black tiger prawn, *Penaeus monodon*, among western Indian Ocean and western Pacific populations. *Marine Biology* **134**: 705-710.
- Earl, D. A., and B. M. von Holdt. 2012. STRUCTURE HARVESTER: A website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conservation Genetics Resources* **4**: 359-361.
- Evanno, G., S. Regnaut, and J. Goudet. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: A simulation study. *Molecular Ecology* **14**: 2611-2620.

Ewers-Saucedo, C., J. M. Pringle, H. H. Sepúlveda, J. E. Byers, S. A. Navarrete and J. P. Wares. 2016. The oceanic concordance of phylogeography and biogeography: a case study in *Notochthamalus*. *Ecology and Evolution* **6**: 4403–4420.

Excoffier, L., and H. E. L. Lischer. 2010. Arlequin suite v. 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resources* **10**: 564-567.

Farhadi, A., H. Farahmand, M. A. Nematollahi, A. G. Jeffs, and S. D. Lavery. 2013. Mitochondrial DNA population structure of the scalloped lobster *Panulirus homarus* (Linnaeus 1758) from the West Indian Ocean. *ICES Journal of Marine Science* **70**: 1491-1498.

Farhadi, A., A. G. Jeffs, H. Farahmand, T. S. Rejiniemon, G. Smith, and S. D. Lavery. 2017. Mechanisms of peripheral phylogeographic divergence in the indo-Pacific: lessons from the spiny lobster *Panulirus homarus*. *BMC Evolutionary Biology* **17**: 195.

Fernandez-Silva, I., J. E. Randall, R. R. Coleman, J. D. Di Battista, L. A. Rocha, J. D. Reimer, C. G. Meyer and B. W. Bowen. 2015. Yellow tails in the Red Sea: phylogeography of the Indo-Pacific goatfish *Mulloidichthys flavolineatus* reveals isolation in peripheral provinces and cryptic evolutionary lineages. *Journal of Biogeography* **42**: 2402-2413.

Forbes, A. T., N. T. Demetriades, J. A. H. Benzie, and E. Ballment. 1999. Allozyme frequencies indicate little geographic variation among stocks of giant tiger prawn *Penaeus monodon* in the south-west Indian Ocean. *South African Journal of Marine Science* **21**: 271-277.

Foster, N. L., C. B. Paris, J. T. Kool, I. B. Baums, J. R. Stevens, J. A. Sanchez, C. Bastidas, C. Agudelo, P. Bush, O. Day, R. Ferrari, P. Gonzalez, S. Gore, R. Guppy, M. A. McCartney, C. McCoy, J. Mendes, A. Srinivasan, S. Steiner, M. J. A. Vermeij, E. Weil, and P. J. Mumby. 2012. Connectivity of Caribbean coral populations: Complementary insights from empirical and modelled gene flow. *Molecular Ecology* **21**: 1143-1157.

Francis, R. M. 2017. Pophelper : an R package and web app to analyse and visualize population structure. *Molecular Ecology Resources* **17**: 27-32.

Fratini, S., and M. Vannini. 2002. Genetic differentiation in the mud crab *Scylla serrata* (Decapoda: Portunidae) within the Indian Ocean. *Journal of Experimental Marine Biology and Ecology* **272**: 103-116.

George, R. W. 2005. Evolution of life cycles, including migration, in spiny lobsters (Palinuridae). *New Zealand Journal of Marine and Freshwater Research* **39**: 503-514.

Gordon, A. L. 2003. The brawniest retroflexion. *Nature* **421**: 904–905.

Goudet, J. 1995. FSTAT (Version 1.2): A Computer Program to Calculate F-Statistics. *Journal of Heredity* **86**: 485-486.

- Griffin, D. A., J. L. Wilkin, C. F. Chubb, A. F. Pearce, and N. Caputi. 2001. Ocean currents and the larval phase of Australian western rock lobster, *Panulirus cygnus*. *Marine and Freshwater Research* **52**: 1187-1199.
- Groeneveld, J.C., and G.M. Branch. 2002. Long-distance migration of South African deep-water rock lobster *Palinurus gilchristi*. *Marine Ecology Progress Series* **232**: 225-238.
- Groeneveld J. C., S. von der Heyden, and C. A. Matthee. 2012. High connectivity and lack of mtDNA differentiation among two previously recognised spiny lobster species in the southern Atlantic and Indian Oceans. *Marine Biology Research* **8**: 764-770.
- Guillemin, M., M. Valero, F. Tellier, E. C. Macaya, C. Destombe, and S. Faugeron. 2016. Phylogeography of seaweeds in the South East Pacific: Complex evolutionary processes along a latitudinal gradient. In: *Seaweed Phylogeography*. Z. M. Hu and C. Fraser (Eds). Springer, Dordrecht. Pages 251-277.
- Guillot, G. 2008. Inference of structure in subdivided populations at low levels of genetic differentiation—the correlated allele frequencies model revisited. *Bioinformatics* **24**: 2222-2228.
- Guillot, G., F. Mortier, and A. Estoup. 2005. GENELAND: A computer package for landscape genetics. *Molecular Ecology Notes* **5**: 712-715.
- Hadfield, M., and V. Paul. 2001. Natural chemical cues for settlement and metamorphosis of marine-invertebrate larvae. In: *Marine Chemical Ecology*. CRC Press. Pages 431-461.
- Halo, I., B. Malauene, and M. Ostrowski. 2017. Physical oceanography. In: *The RV Dr Fridtjof Nansen in the Western Indian Ocean: Voyages of marine research and capacity development*. J.C. Groeneveld and K. A. Koranteng (Eds). FAO, Rome, Italy. Pages 37-50.
- Hart-Davis, M. G., B. C. Backeberg, I. Halo, E. van Seville, J. A. Johannessen. 2018. Assessing the accuracy of satellite derived ocean currents by comparing observed and virtual buoys in the Greater Agulhas Region. *Remote Sensing of Environment*. DOI: <https://doi.org/10.1016/j.rse.2018.03.040>.
- Hinojosa, I. A., B. S. Green, C. Gardner, J. Hesse, J. A. Stanley, and A. G. Jeffs. 2016. Reef sound as an orientation cue for shoreward migration by pueruli of the rock lobster, *Jasus edwardsii*. *PLoS ONE* **11**. DOI: 10.1371/journal.pone.0157862.
- Hoareau, T. B., E. Boissin, G. Paulay, and J. H. Bruggemann. 2013. The Southwestern Indian Ocean as a potential marine evolutionary hotspot: perspectives from comparative phylogeography of reef brittle-stars. *Journal of Biogeography* **40**: 2167-2179.
- Holthuis, L. B. 1991. FAO Species Catalogue. Marine lobsters of the world. An annotated and illustrated catalogue of species of interest to fisheries known to date. *FAO Fisheries Synopsis* No. 125. Rome, Food and Agricultural Organization of the United Nations. Page 292.

- Iacchei, M., M. R. Gaither, B. W. Bowen and R. J. Toonen. 2016. Testing dispersal limits in the sea: range-wide phylogeography of the pronghorn spiny lobster *Panulirus penicillatus*. *Journal of Biogeography* **43**: 1032-1044.
- Jeffs, A. G., J. C. Montgomery, and C. T. Tindle. 2005. How do spiny lobster post-larvae find the coast? *New Zealand Journal of Marine and Freshwater Research* **39**: 605-617.
- Jensen, J. L., A. J. Bohonak, and S. T. Kelley. 2005. Isolation by distance, web service. *BMC Genetics* **6**: 1-6.
- Johannessen, J. A., B. Chapron, F. Collard, M.-H. Rio, J.-F. Piollé, L. Gaultier, G. Quartly, J. Shutler, R. Escola, R. P. Raj, C. Donlon, R. Danielson, A. Korosov, F. Nencioli, V. Kudryavtsev, M. Roca, J. Tournadre, G. Larnicol, G. Guitton, P. Miller, M. Warren and M. W. Hansen. 2016. GlobCurrent: Multisensor synergy for surface current estimation. *Proceedings of Living Planet Symposium 2016*, SP-740.
- Kalinowski, S. T., M. L. Taper, and T. C. Marshall. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology* **16**: 1099-1106.
- Khvorov, S., S. Piontkovski and E. Popova. 2012. Spatio-temporal distribution of the palinurid and scyllarid phyllosoma larvae in Oman coastal waters. *Journal of Agricultural and Marine Sciences*, 17(1).
- Lamont, T., M. J. Roberts, R. G. Barlow, T. Morris, and M. A. van den Berg. 2010. Circulation patterns in the Delagoa Bight, Mozambique, and the influence of deep ocean eddies. *African Journal of Marine Science* **32**: 553-562.
- Lange, M., and E. van Sebille. 2017. Parcels v0.9: prototyping a Lagrangian Ocean Analysis framework for the petascale age. *Geoscientific Model Development Discussions*: 1-20.
- Lavery, S. D., A. Farhadi, H. Farahmand, T. Y. Chan, A. Azhdehakoshpour, V. Thakur, and A. G. Jeffs. 2014. Evolutionary divergence of geographic subspecies within the scalloped spiny lobster *Panulirus homarus* (Linnaeus 1758). *PLoS ONE* **9**. DOI: 10.1371/journal.pone.0097247.
- Legendre, P., and M. J. Anderson. 1999. Distance-Based Redundancy Analysis: testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs* **69**: 1-24.
- Liggins, L., E. A. Treml, and C. Riginos. 2013. Taking the plunge: an introduction to undertaking seascape genetic studies and using biophysical models. *Geography Compass* **7**: 173-196.
- Liggins, L., E. A. Treml, H. P. Possingham, and C. Riginos. 2016. Seascape features, rather than dispersal traits, predict spatial genetic patterns in co-distributed reef fishes. *Journal of Biogeography* **43**: 256-267.
- Lobel, P. S. 1989. Ocean current variability and the spawning season of Hawaiian reef fishes. *Environmental Biology of Fishes* **24**: 161-171.

- Lutjeharms, J. R. E., and J. da Silva. 1988. The Delagoa Bight eddy. *Deep Sea Research II* **35**: 619-634.
- Lutjeharms, J. R. E. 2006. The Agulhas Current. Springer-Verlag Berlin Heidelberg. 329 pages.
- MacDonald, N.J., M. H. Davies, A. K. Zundel, J. D. Howlett, Z. Demirbilek, J. Z. Gailani, T. C. Lackey, and J. Smith. 2006. *PTM: Particle Tracking Model*. US Army Corps of Engineers: Washington DC.
- Mace, A. J., and S. G. Morgan. 2006. Larval accumulation in the lee of a small headland: Implications for the design of marine reserves. *Marine Ecology Progress Series* **318**: 19-29.
- Madeira, C., M. Judite Alves, N. Mesquita, S. E. Silva, and J. Paula. 2012. Tracing geographical patterns of population differentiation in a widespread mangrove gastropod: genetic and geometric morphometrics surveys along the eastern African coast. *Biological Journal of the Linnean Society* **107**: 647-663.
- Mann, K. and J. R. N. Lazier. 2006. Dynamics of marine ecosystems: biological-physical interactions in the oceans. Blackwell Publishing. 512 pages.
- Marshall, T. C., J. Slate, L. E. B. Kruuk, and J. M. Pemberton. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. *Molecular Ecology* **7**: 639-655.
- Masterson, C. F., B. S. Danilowicz, and P. F. Sale. 1997. Yearly and inter-island variation in the recruitment dynamics of the bluehead wrasse (*Thalassoma bifasciatum*, Bloch). *Journal of Experimental Marine Biology and Ecology* **214**: 149-166.
- McGaughran, A., K. Morgan, and R. J. Sommer. 2014. Environmental variables explain genetic structure in a beetle-associated nematode. *PLoS ONE* **9**. DOI: 10.1371/journal.pone.0087317.
- Mendez, M., H. C. Rosenbaum, A. Subramaniam, C. Yackulic, and P. Bordino. 2010. Isolation by environmental distance in mobile marine species: Molecular ecology of Franciscana dolphins at their southern range. *Molecular Ecology* **19**: 2212-2228.
- Meyer, I., L. Braby, M. Krug, and B. C. Backeberg. 2017. *Mapping the Ocean Current Strength and Persistence in the Agulhas to Inform Marine Energy Development*. In: *Marine Renewable Energy*. Z. Yang and A. Copping (Eds). Springer International Publishing AG. Pages 179-215.
- Mkare, T. K., J. C. Groeneveld, P. R. Teske, and C. A. Matthee. 2017. Comparative genetic structure in two high-dispersal prawn species from the Southwestern Indian Ocean. *African Journal of Marine Science* **39**: 467-474.
- Montoya-Maya, P. H., M. H. Schleyer, and A. H. H. Macdonald. 2016. Limited ecologically relevant genetic connectivity in the south-east African coral populations calls for reef-level management. *Marine Biology* **163**: 1-16.
- Morgan, S. G., J. L. Fisher, and J. L. Largier. 2011. Larval retention, entrainment, and accumulation in the lee of a small headland: Recruitment hotspots along windy coasts. *Limnology and Oceanography* **56**: 161-178.

- Muths, D., P. Grewe, C. Jean, and J. Bourjea. 2009. Genetic population structure of the swordfish (*Xiphias gladius*) in the southwest Indian Ocean: Sex-biased differentiation, congruency between markers and its incidence in a way of stock assessment. *Fisheries Research* **97**: 263-269.
- Muths, D., E. Tessier, and J. Bourjea. 2015. Genetic structure of the reef grouper *Epinephelus merra* in the West Indian Ocean appears congruent with biogeographic and oceanographic boundaries. *Marine Ecology* **36**: 447-461.
- Muths, D., E. Tessier, G. Gouws, M. Craig, M. Mwale, J. Mwaluma, A. Mwandya, and J. Bourjea. 2011. Restricted dispersal of the reef fish *Myripristis berndti* at the scale of the SW Indian Ocean. *Marine Ecology Progress Series* **443**: 167-180.
- Nanninga, G. B., P. Saenz-Agudelo, A. Manica, and M. L. Berumen. 2013. Environmental gradients predict the genetic structure of a coral reef fish in the Red Sea. *Molecular Ecology*: 23. DOI10.1111/mec.12623.
- Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O' Hara, G. L. Simpson, P. Solymos, M. H. Stevens, and H. Wagner. 2015. Vegan: Community Ecology Package. Available at: <http://CRAN.R-project.org/package=vegan>.
- Otwoma, L. M., and M. Kochzius. 2016. Genetic population structure of the Coral Reef Sea Star *Linckia laevigata* in the Western Indian Ocean and Indo-West Pacific. *PLoS ONE* **11**. DOI: 10.1371/journal.pone.0165552.
- Palumbi, S. R. 1994. Genetic divergence, reproductive isolation, and marine speciation. *Annual Review of Ecology and Systematics* **25**: 547-572.
- Paris, C. B., and R. K. Cowen. 2004. Direct evidence of a biophysical retention mechanism for coral reef fish larvae. *Limnology and Oceanography* **49**: 1964-1979.
- Paris, C. B., L. M. Chérubin, and R. K. Cowen. 2007. Surfing, spinning, or diving from reef to reef: Effects on population connectivity. *Marine Ecology Progress Series* **347**: 285-300.
- Peakall, R., and P. E. Smouse. 2006. GENALEX 6: Genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes* **6**: 288-295.
- Phelps, J. J. C., J. A. Polton, A. J. Souza, and L. A. Robinson. 2015. Behaviour influences larval dispersal in shelf sea gyres: *Nephrops norvegicus* in the Irish Sea. *Marine Ecology Progress Series* **518**: 177-191.
- Phillips, B., and L. Olsen. 1975. Swimming behaviour of the puerulus larvae of the western rock lobster. *Marine and Freshwater Research* **26**: 415-417.
- Phillips, B. F. 2013. Lobsters : Biology, Management, Aquaculture and Fisheries. Wiley-Blackwell.
- Pollock, D. E. 1993. Speciation in spiny lobsters - clues to climatically-induced changes in ocean circulation patterns. *Bulletin of Marine Science* **53**: 937-944.

- Portnoy, D. S., C. M. Hollenbeck, C. N. Belcher, W. B. Driggers III, B. S. Frazier, J. Gelsleichter, R. D. Grubbs, and J. R. Gold. Contemporary population structure and post-glacial genetic demography in a migratory marine species, the blacknose shark, *Carcharhinus acronotus*. *Molecular Ecology* **23**: 5480–5495.
- Postaire, B., J. H. Bruggemann, H. Magalon, B. Faure, and T. Backeljau. 2014. Evolutionary dynamics in the Southwest Indian Ocean marine biodiversity hotspot: A perspective from the rocky shore gastropod genus *Nerita*. *PLoS ONE* **9**. DOI: 10.1371/journal.pone.0095040.
- Pritchard, J. K., M. Stephens, and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. *Genetics* **155**: 945-59.
- Rellstab, C., F. Gugerli, A. J. Eckert, A. M. Hancock, and R. Holderegger. 2015. A practical guide to environmental association analysis in landscape genomics. *Molecular Ecology* **24**: 4348-4370.
- Riccioni, G., M. Stagioni, M. Landi, G. Ferrara, G. Barbuiani, and F. Tinti. 2013. Genetic structure of Bluefin Tuna in the Mediterranean Sea correlates with environmental variables. *PLoS ONE* **8**. DOI: 10.1371/journal.pone.0080105.
- Ridderinkhof, W., D. Le Bars, A. S. von der Heydt, and W. P. M. de Ruijter. 2013. Dipoles of the South East Madagascar Current. *Geophysical Research Letters* **40**: 558-562.
- Ridgway, T., and E. M. Sampayo. 2007. Population genetic status of the Western Indian Ocean: What do we know? *Western Indian Ocean Journal of Marine Science* **4**: 1-10.
- Riginos, C., K. E. Douglas, Y. Jin, D. F., Shanahan, and E. A. Trembl. 2011. Effects of geography and life history traits on genetic differentiation in benthic marine fishes. *Ecography* **34**: 566-575.
- Riginos, C., and L. Liggins. 2013. Seascape genetics: populations, individuals, and genes marooned and adrift. *Geography Compass* **7**: 197-216.
- Rivera, A., N. Weidberg, A. F. Pardiñas, R. González-Gil, L. García-Flórez, and J. L. Acuña. 2013. Role of upwelling on larval dispersal and productivity of Gooseneck Barnacle populations in the Cantabrian Sea: management implications. *PLoS ONE* **8**. <https://doi.org/10.1371/journal.pone.0078482>.
- Robins, P. E., S. P. Neill, L. Giménez, S. R. Jenkins, and S. K. Malham. 2013. Physical and biological controls on larval dispersal and connectivity in a highly energetic shelf sea. *Limnology and Oceanography* **58**: 505-524.
- Robitzsch, V., E. Banguera-Hinestroza, Y. Sawall, A. Al-Sofyani, and C. R. Voolstra. 2015. Absence of genetic differentiation in the coral *Pocillopora verrucosa* along environmental gradients of the Saudi Arabian Red Sea. *Frontiers in Marine Science* **2**: <https://doi.org/10.3389/fmars.2015.00005>.
- Saetre, R., and da Silva, A. J. 1984. The circulation of the Mozambique Channel. *Deep-Sea Research* **31**: 485-508.



- Santos, J., D. Rouillard, and J.C. Groeneveld. 2014. Advection-diffusion models of spiny lobster *Palinurus gilchristi* migrations for use in spatial fisheries management. *Marine Ecology Progress Series* **498**: 227-241.
- Saraceno, M., P. T. Strub, and P. M. Kosro. 2008. Estimates of sea surface height and near-surface alongshore coastal currents from combinations of altimeters and tide gauges. *Journal of Geophysical Research: Oceans (1978–2012)* **113**: C11013.
- Schott, F. A., and J. P. McCreary. 2001. The monsoon circulation of the Indian Ocean. *Progress in Oceanography* **51**: 1-123.
- Schouten, M. W., W. P. M. de Ruijter, P. J. van Leeuwen, and H. Ridderinkhof. 2003. Eddies and variability in the Mozambique Channel. *Deep-Sea Research Part II: Topical Studies in Oceanography* **50**: 1987-2003.
- Selkoe, K. E., C. M. Henzler, and S. D. Gaines. 2008. Seascape genetics and the spatial ecology of marine populations. *Fish and Fisheries* **9**: 363–377.
- Selkoe, K., K. T. Scribner, and H. M. Galindo. 2016. Waterscape genetics - applications of landscape genetics to rivers, lakes, and seas. In: *Landscape Genetics: Concepts, Methods, Applications*. N. Balkenhol, S. Cushman, A. Storfer, and L. Waits (Eds). First Edition. John Wiley & Sons. Pages 220-244.
- Selkoe, K. A, C. D'Aloia, E. Crandall, M. Iacchei, L. Liggins, J. Puritz, S. von der Heyden, and R. Toonen. 2016. A decade of seascape genetics: Contributions to basic and applied marine connectivity. *Marine Ecology Progress Series* **554**: 1-19.
- Silva, I. C., N. Mesquita, J. Paula. 2010. Genetic and morphological differentiation of the mangrove crab *Perisesarma guttatum* (Brachyura: Sesamidae) along an East African latitudinal gradient. *Biological Journal of the Linnean Society* **99**: 28-46.
- Singh, S. P., J. C. Groeneveld, A. Al-Marzouqi, and S. Willows-Munro. 2017. A molecular phylogeny of the spiny lobster *Panulirus homarus* highlights a separately evolving lineage from the Southwest Indian Ocean. *Peer J* **5**:e3356. DOI 10.7717/peerj.3356.
- Slate, J., T. Marshall, and J. Pemberton. 2000. A retrospective assessment of the accuracy of the paternity inference program Cervus. *Molecular Ecology* **9**: 801-808.
- Soria, G., A. Munguía-Vega, S. G. Marinone, M. Moreno-Báez, I. Martínez-Tovar, and R. Cudney-Bueno. 2012. Linking bio-oceanography and population genetics to assess larval connectivity. *Marine Ecology Progress Series* **463**: 159-175.
- Spalding, M. D., H. E. Fox, G. R. Allen, N. Davidson, Z. A. Ferdaña, M. Finlayson, B. S. Halpern, M. A. Jorge, A. Lombana, S. A. Lourie, K. D. Martin, E. McManus, J. Molnar, C. A. Recchia, and J. Robertson. 2007. Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *BioScience* **57**: 573-583.

- Steyn, E., and M. Schleyer. 2011. Movement patterns of the East Coast rock lobster *Panulirus homarus rubellus* on the coast of KwaZulu-Natal, South Africa. *New Zealand Journal of Marine and Freshwater Research* **45**: 85-101.
- Storfer, A., M. A. Murphy, S. F. Spear, R. Holderegger, and L. P. Waits. 2010. Landscape genetics: Where are we now? *Molecular Ecology* **19**: 3496-3514.
- Swart, N. C., J. R. E. Lutjeharms, H. Ridderinkhof, and W. P. M. de Ruijter. 2010. Observed characteristics of Mozambique Channel eddies. *Journal of Geophysical Research: Oceans* **115**.
- Teske, P. R., C. D. McQuaid, W. P. Froneman, and N. P. Barker. 2006. Impacts of marine biogeographic boundaries on phylogeographic patterns of three South African estuarine crustaceans. *Marine Ecology Progress Series* **314**: 283-293.
- Teske, P. R., P. W. Froneman, N. P. Barker, and C. D. McQuaid. 2007. Phylogeographic structure of the caridean shrimp *Palaemon peringueyi* in South Africa: further evidence for intraspecific genetic units associated with marine biogeographic provinces. *African Journal of Marine Science* **29**: 253-258.
- Teske, P. R., I. Papadopoulos, B. K. Newman, P. C. Dworschak, C. D. McQuaid, and N. P. Barker. 2008. Oceanic dispersal barriers, adaptation and larval retention: an interdisciplinary assessment of potential factors maintaining a phylogeographic break between sister lineages of an African prawn. *BMC Evolutionary Biology* **8**: 341.
- Teske, P. R., H. Winker, C. D. McQuaid, and N. P. Barker. 2009. A tropical/subtropical biogeographic disjunction in southeastern Africa separates two evolutionarily significant units of an estuarine prawn. *Marine Biology* **156**: 1265-1275.
- Teske, P. R., I. Papadopoulos, K. L. Mmonwa, T. G. Matumba, C. D. McQuaid, N. P. Barker, and L. B. Beheregaray. 2011. Climate-driven genetic divergence of limpets with different life histories across a southeast African marine biogeographic disjunction: Different processes, same outcome. *Molecular Ecology* **20**: 5025-5041.
- Teske, P. R., J. Sandoval-Castillo, E. van Sebille, J. Waters, and L. B. Beheregaray. 2015. On-shelf larval retention limits population connectivity in a coastal broadcast spawner. *Marine Ecology Progress Series* **532**: 1-12.
- Teske, P. R., J. Sandoval-Castillo, E. van Sebille, J. Waters, and L. B. Beheregaray. 2016. Oceanography promotes self-recruitment in a planktonic larval disperser. *Scientific Reports* **6**: 34205.
- Thomas, L. and J. J. Bell. 2013. Testing the consistency of connectivity patterns for a widely dispersing marine species. *Heredity* **111**: 345-354.
- Truelove, N. K., A. S. Kough, D. C. Behringer, C. B. Paris, S. J. Box, R. F. Preziosi, and M. J. Butler. 2017. Biophysical connectivity explains population genetic structure in a highly dispersive marine species. *Coral Reefs* **36**: 233-244.

- van der Meeren, G. I., A. Chandrapavan, and T. Breithaupt. 2008. Sexual and aggressive interactions in a mixed species group of lobsters *Homarus gammarus* and *H. americanus*. *Aquatic Biology* **2**: 191-200.
- van Oosterhout, C., W. F. Hutchinson, D. P. M. Wills, and P. Shipley. 2004. MICRO-CHECKER: Software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes* **4**: 535-538.
- Vijayakumaran, M., A. Maharajan, S. Rajalakshmi, P. Jayagopal, and M. C. Remani. 2014. Early larval stages of the spiny lobsters, *Panulirus homarus*, *Panulirus versicolor* and *Panulirus ornatus* cultured under laboratory conditions. *International Journal of Development Research* **4**: 377-383.
- Vogler, C., J. Benzie, P. H. Barber, M. V. Erdmann, M. Ambariyanto, C. Sheppard, K. Tenggardjaja, K. Gérard, and G. Wörheide. 2012. Phylogeography of the crown-of-thorns starfish in the Indian Ocean. *PLoS ONE* **7**. DOI: 10.1371/journal.pone.0043499.
- Werner, F. E., R. C. Cowen, and C. B. Paris. 2007. Coupled biological and physical models: present capabilities and necessary developments for future studies of population connectivity. *Oceanography* **20**: 54-69.
- Wilkin, J. L., and A. G. Jeffs. 2011. Energetics of swimming to shore in the puerulus stage of a spiny lobster: Can a postlarval lobster afford the cost of crossing the continental shelf? *Limnology and Oceanography: Fluids and Environments* **1**: 163-175.
- Williams, D. M., E. Wolanski, and J. C. Andrews. 1984. Transport mechanisms and the potential movement of planktonic larvae in the central region of the Great Barrier Reef. *Coral Reefs* **3**: 229-236.

#### **Data accessibility**

Genotype data files, input files for analyses, R-scripts and raw particle dispersal data will be deposited onto Dryad.

#### **Author contributions**

S.P.S., J.C.G. and S.W-M. conceived the sampling design; S.P.S conducted laboratory work; S.P.S and M.G.H-D conducted analyses and wrote the manuscript; J.C.G, S.W-M., and B.C.B contributed to versions of the manuscript.

## Tables

Table 1. Known life-history parameters of *P. homarus* incorporated.

Geographical area	Egg-bearing	Larval behavior	Settlement of pueruli	Reference
Laboratory (India)	Eggs developed in 22-30d at 25-30 °C	Larvae released at night or early morning  Phyllosomas grew to stage V in 46-61d  Cumulative intermount period: I=7-10d; II=13-20d; IIIa=21-25d; IIIb=26-30d; IIIc=32-38d		Vijayakumaran et al. 2014
NW Indian Ocean (Oman)	Protracted breeding season from May/Jun to Jan/Feb	Maximum abundance of stage I in Apr-May.  Larvae present in water column during productive SE monsoon season		Al-Marzouqi et al. 2008 Khvorov et al. 2012
SW Indian Ocean (South Africa)	Egg-bearing peaks in Nov-Feb, sharp decline in Mar-Aug  Repetitive breeding (up to 4 broods/y) depending on female size  Rapid embryonic development takes 29-59 days, depending on water temperature	Larval release starts in Aug and peaks in March, and occurs mainly at night  4-6 mo dispersal duration  9 stages defined from field samples  Remain within 65 km of the shore (max = 117 km)	Pueruli observed mainly in Apr-Jul  Settle near the coast (shark nets) and on shallow inshore reefs	Berry 1971 a, b Berry 1974a

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Speculation that larvae are retained in reversing current systems inshore of the Agulhas current

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Table 2. *Panulirus homarus* summary statistics for microsatellite data by population. N = total number of individuals, N<sub>A</sub> = mean number of alleles, H<sub>O</sub> = observed heterozygosity, H<sub>E</sub> = expected heterozygosity, A<sub>R</sub> = allelic richness, PHH = *P. h. homarus*, PHM = *P. h. megasculptus*, PHR = *P. h. rubellus*.

Population	N	N <sub>A</sub>	H <sub>O</sub>	H <sub>E</sub>	A <sub>R</sub>
All	271	5.849	0.604	0.590	5.86
OM	29	7.190	0.644	0.615	6.070
YEM	24	6.333	0.605	0.610	5.690
KEN	22	5.238	0.603	0.564	4.780
ZV	17	4.952	0.573	0.555	4.800
CH	19	5.524	0.584	0.589	5.260
XX	22	6.048	0.621	0.614	5.460
FD	29	6.619	0.644	0.626	5.660
BR	19	5.476	0.616	0.577	5.240
TM	19	5.095	0.551	0.549	4.920
SB	30	6.048	0.588	0.594	5.110
PSJ	20	5.667	0.591	0.590	5.400
MB	21	6.000	0.631	0.597	5.540
PHH	43	6.571	0.585	0.578	6.550
PHM	53	7.762	0.627	0.621	7.690
PHR	175	8.667	0.607	0.613	8.630

Table 3. AMOVA results for the populations grouped by the STRUCTURE results. Bold values indicate statistical significance.

Source of variation	Degrees of freedom	Sum of squares	Variance components	Fixation indices	% Variation
Among groups	2	100.71	0.29	<b>0.045</b>	<b>4.54</b>
Among populations within groups	13	116.11	1.48	<b>0.015</b>	<b>1.48</b>
Within populations	526	3130.28	5.95	<b>0.060</b>	<b>93.98</b>

## Figures

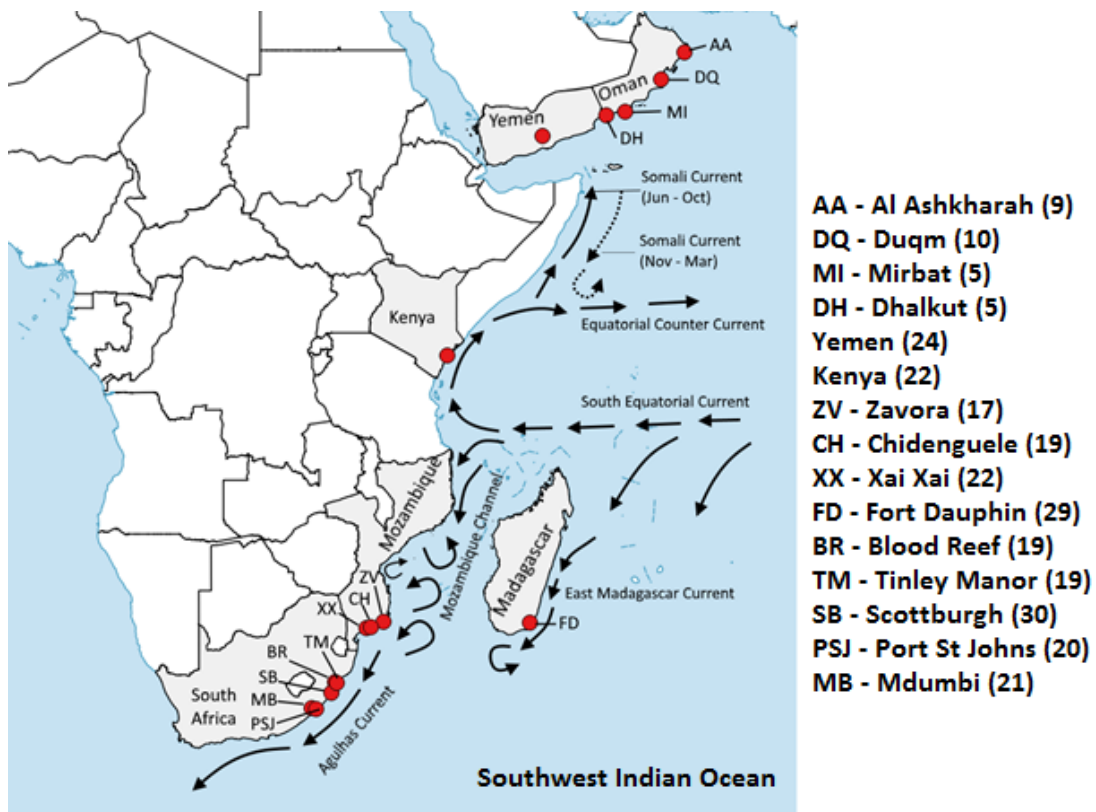
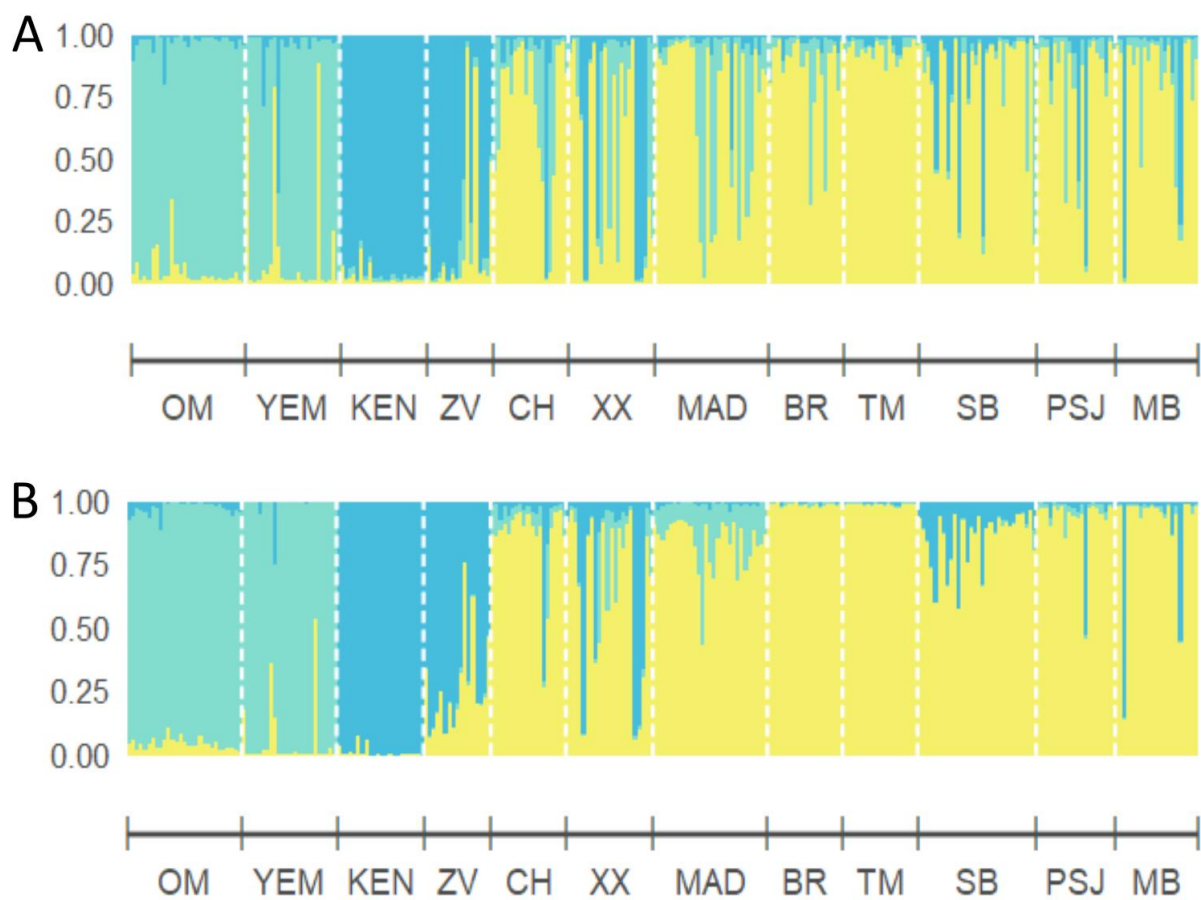


Figure 1. Map of *Panulirus homarus* sampling locations and the number of samples collected per locality. The major current systems (adapted from Lutjeharms, 2006) are also shown.



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36 Figure 2. STRUCTURE plots for the *P. homarus* dataset, (A) using admixture model with no locprior  
 37 and (B) admixture model with locprior.

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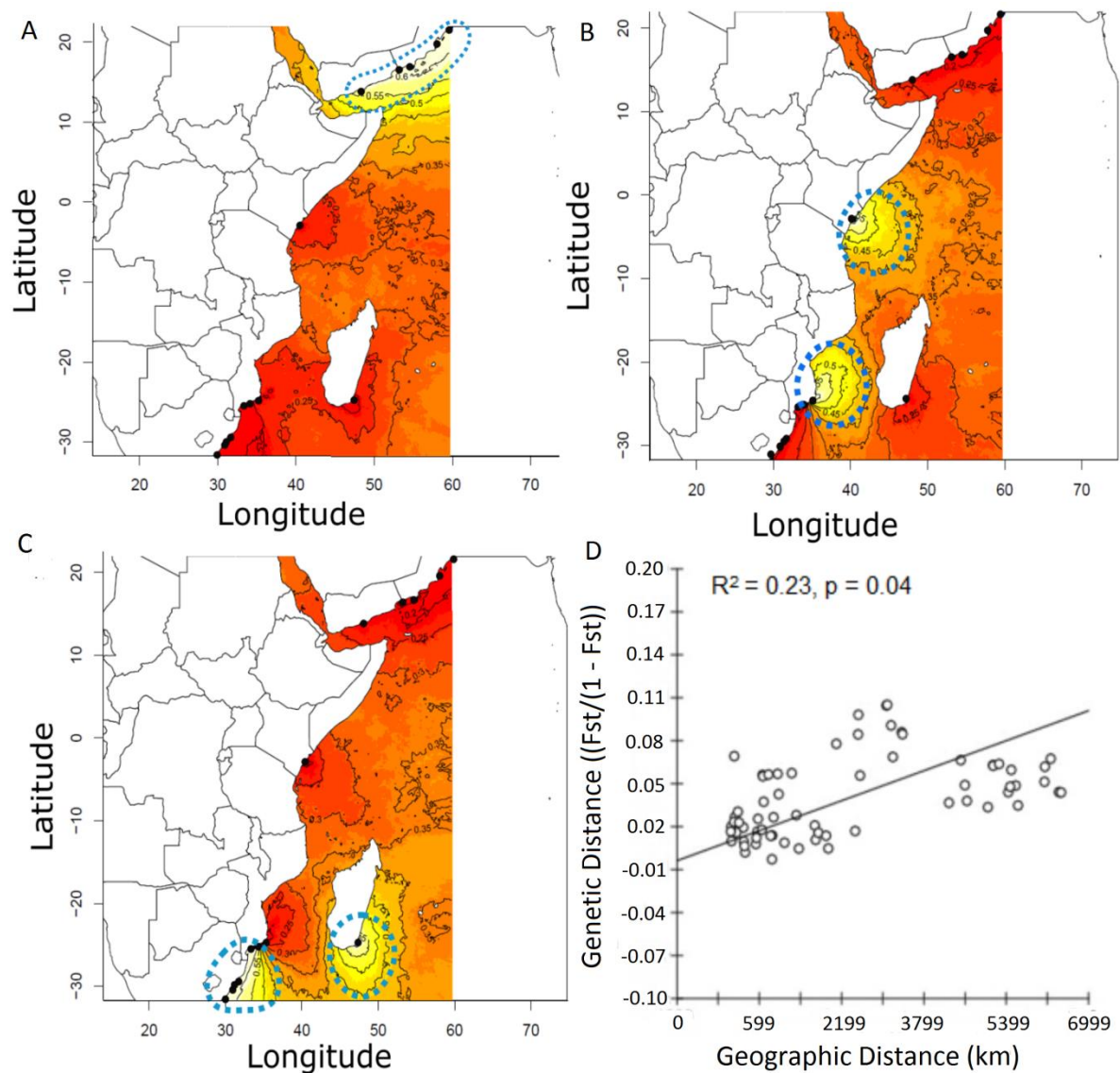
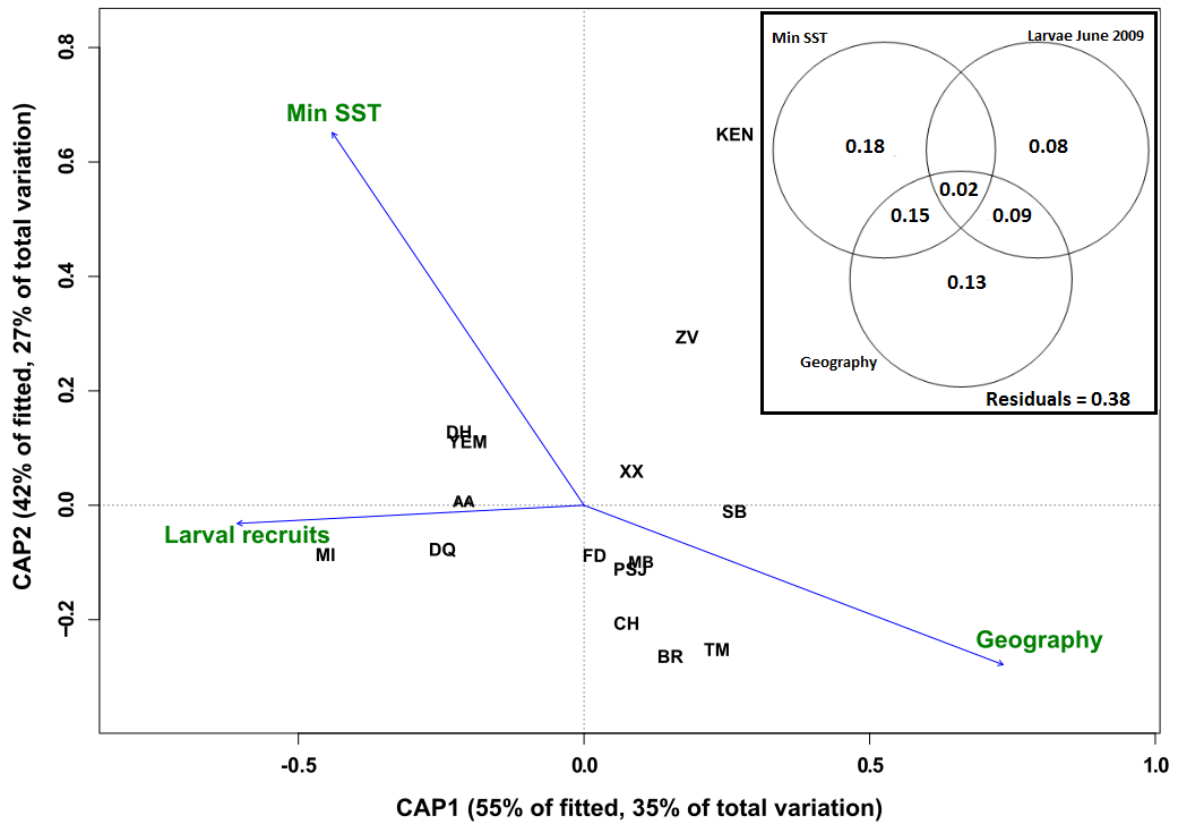


Figure 3. Results of the Geneland analysis. Contour plots showing the posterior probabilities of the inferred clusters corresponding to populations of (A) *P. h. megasculptus*, (B) *P. h. homarus*, and (C) *P. h. rubellus*. The highest membership values are in white to yellow, and the contour lines depict the spatial position of genetic discontinuities. (D) Isolation by distance plot showing the relationship between geographic and genetic distance.

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60 Figure 4. Distance-based redundancy analysis (dbRDA) to test the effect of minimum SST, larval  
 61 recruits and geographic distance as predictor variables of genetic differentiation between the three  
 62 *P. homarus* subspecies. The arrows indicates the direction of the maximum correlation and the  
 63 length of the arrows represents the strength of the correlation.

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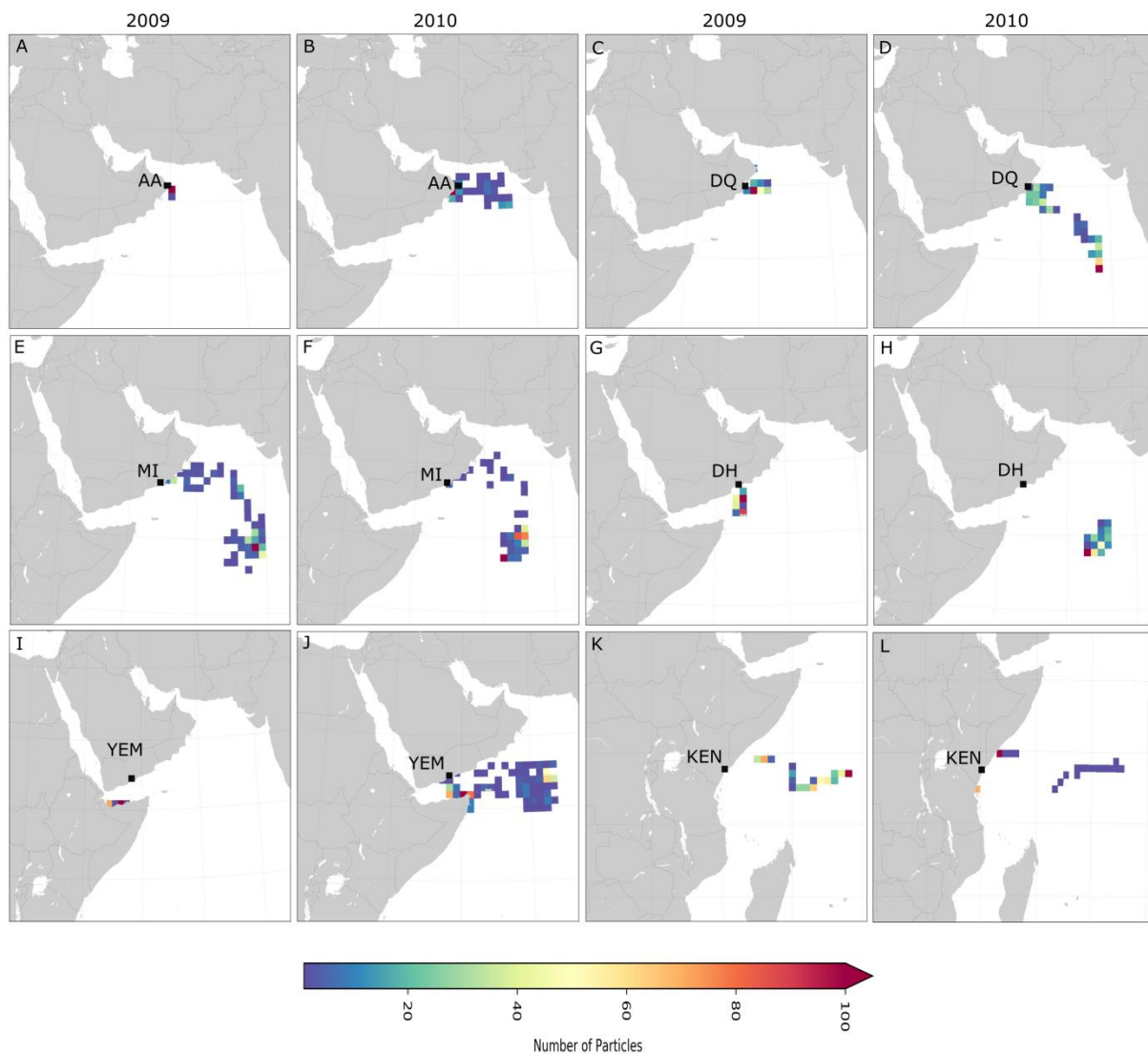


Figure 5. Particle density plots of the Lagrangian trajectories on a 1°x1° spatial grid for the northern sites for the peak breeding season in June 2009 and 2010. AA = Al Ashkharah, DQ = Duqm, MI = Mirbat, DH = Dhalkut, YEM = Yemen, KEN = Kenya.

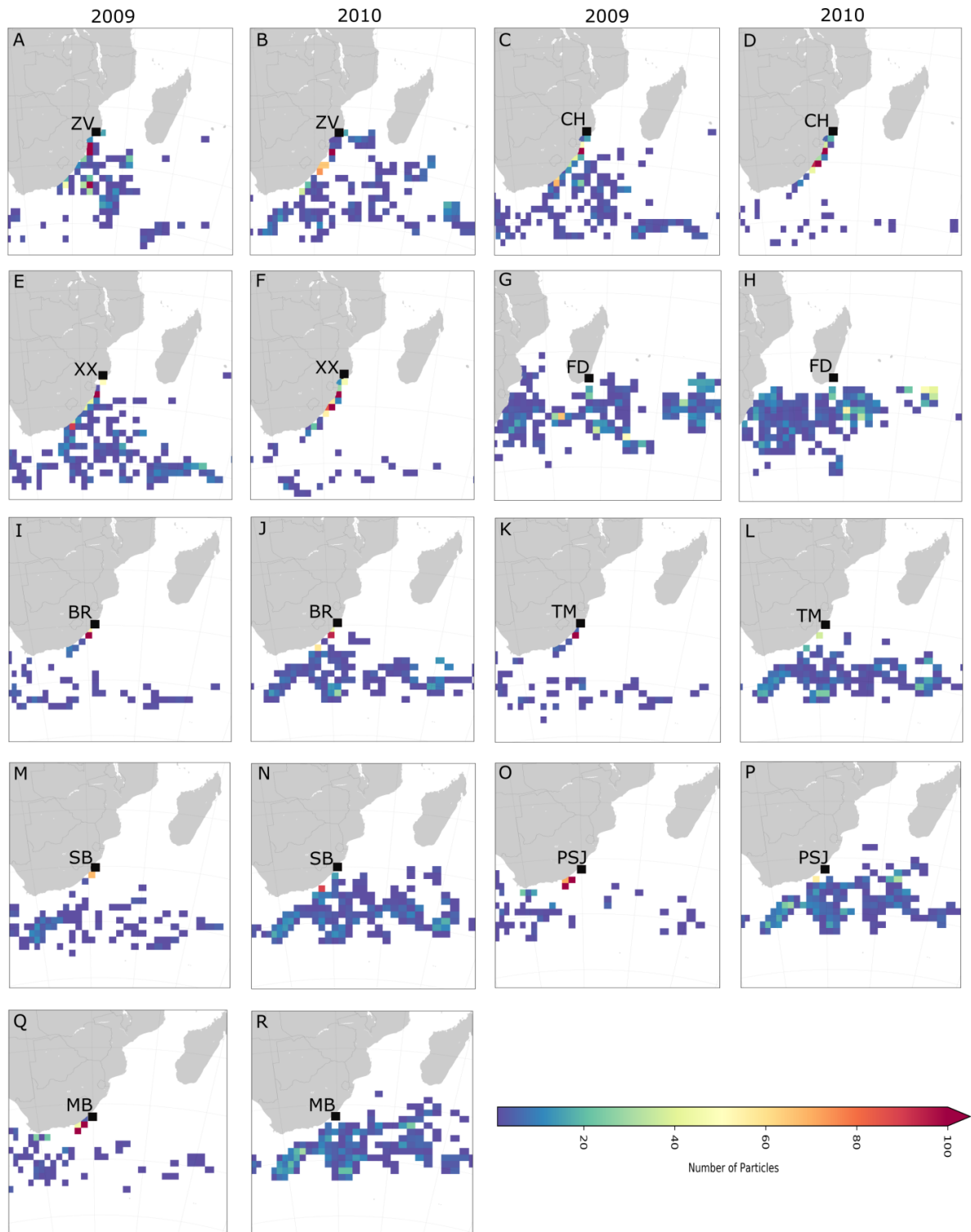


Figure 6. Particle density plots of the Lagrangian trajectories on a 1°x1° spatial grid for the southern sites for the peak breeding season in January 2009 and 2010. ZV = Zavora, CH = Chidenguele, XX = Xai Xai, TM = Tinley Manor, BR = Blood Reef, SB = Scottburgh, PSJ = Port St Johns, MB = Mdumbi.