Genetic and Biophysical Models Help Define Marine Conservation Focus Areas

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Ecological and environmental variables play a major role in the genetic structure of marine populations, but how oceanography affects their dispersal and associated connectivity remains far from being understood. To account for the effect of different dispersal strategies in terms of pelagic larvae and non-pelagic reproduction, we utilize the power of comparative phylogeographic analyses of five phylogenetically and functionally diverse intertidal species along the west coast of South Africa using population genetics and biophysical models within the Benguela Current system. Some broadcast spawners exhibit genetic panmixia, others show genetic structure similar to direct-developing species, suggesting complex recruitment patterns in rocky shore environments. Patterns of genetic structure do not correspond with pelagic larval competency period, with a broadcast spawning urchin displaying the highest levels of population structure. Biophysical models of larval dispersal reveal mixed dispersal patterns, with the strongest connections in a northward direction following the Benguela Current, yet most modeled species also show the capacity for southward (albeit weaker) migration among some sample localities. Some sites, particularly the most northern areas, show very low levels of potential connectivity. Lastly, we synthesized our results to highlight key areas for the development of Marine Protected Areas (MPAs) that capture the evolutionary patterns of marine species of the west coast and find that the results from our molecular and biophysical analyses are coherent with previous suggestions for a network of protected areas.

Keywords: marine spatial planning, gene flow, marine protected area, conservation planning, population structure, rocky shore, comparative phylogeography, South Africa

INTRODUCTION

Dispersal, the movement of individuals across land-and-seascapes, is important in maintaining ecological and genetic connectivity between geographically disjunct populations (Cowen and Sponaugle, 2009; Baguette et al., 2012). Connectivity is an important consideration under ongoing changes in climate and ocean conditions, particularly given the potential for altered dispersal pathways, which in turn may erode signals of local adaptation and impact the ability of populations to persist into the future (Lett et al., 2010; Sgro et al., 2011; Doney et al., 2012; Coleman et al., 2017). In marine systems, connectivity is challenging to measure because the connectedness of populations depends on several factors such as the directionality of larval transport, the number of individuals moving within a system and their settlement success, as well as the spatio-temporal

dynamics and the physical and ecological features of the seascape (Baguette et al., 2012; Pfaff et al., 2015; Treml et al., 2015a,b; Wright et al., 2015). Therefore, in order to capture connectivity at different spatial and temporal scales, analyses should ideally incorporate species with different dispersal strategies (Baco et al., 2016), because this captures a wider range of genetic patterns (Nielsen et al., 2017).

Phylogeographic studies, mapping genetic differentiation across land, or seascapes, have the power to resolve broad-scale connectivity patterns, whilst allowing for the incorporation of multi-species data to provide relative estimates of connectivity (Kelly and Palumbi, 2010; Wright et al., 2015; Baco et al., 2016) and associations with environmental factors (Selkoe et al., 2016a). Where shared patterns across multiple species are revealed, these can provide particular insights into the processes that shape populations and communities in space and time (Selkoe et al., 2016b). Additionally, in combination with molecular analyses, modeling approaches in marine systems have been used for inferring parameters such as the strength and directionality of larval dispersal and estimating dispersal distance (Wright et al., 2015; Baco et al., 2016), unraveling the processes linking dispersal and environmental features such as oceanographic regimes (White et al., 2010) as well as predicting biotic and abiotic variables that help explain observed patterns of structure (Benestan et al., 2016; Selkoe et al., 2016a). Models of larval dispersal can also help identify areas that benefit fisheries and biodiversity conservation (Krueck et al., 2017).

The genetic structure of marine populations and their larval connectivity are known to be greatly influenced by environmental and ecological variables, with the influence of oceanographic and environmental features in determining large-scale biogeographic patterns of marine species becoming better understood (Bowen et al., 2016; Selkoe et al., 2016a). For example, studies overlaying larval dispersal estimates with ocean current data have shown that this approach helps disentangle the effects of hydrographical features shaping population dynamics (Gilg and Hilbish, 2003; White et al., 2010; Davies et al., 2015). The benefit of this approach is that it allows one to compare and contrast conservation strategies derived from classic ecological data, with those from molecular and dispersal-based data, revealing complementary yet often very different management priorities (Beger et al., 2014; Nielsen et al., 2017; von der Heyden, 2017).

Understanding the spatial and temporal patterns in connectivity is becoming increasingly important in the context of marine reserves, with several studies suggest that some existing regional marine protected area (MPA) networks are poorly connected, for example in the Mediterranean (Andrello et al., 2013), temperate Australia (Coleman et al., 2011) and in South Africa (Wright et al., 2015). In South Africa, previous studies suggest that for some species genetic boundaries align with broad biogeographic breaks (von der Heyden, 2009; Teske et al., 2011). However, the absence of obvious dispersal barriers across some region along an almost linear coastline, suggest local-scale oceanographic features (such as eddies or near-shore counter currents; see for example Teske et al., 2015) also act to maintain regional population divergence, in combination with

physiological adaptations, historical events, and availability of habitat (von der Heyden, 2009; Teske et al., 2011; Toms et al., 2014).

The South African west coast is one of the most productive marine regions globally, with strong seasonal upwelling resulting in high levels of primary productivity (Nelson and Hutchings, 1983; Shannon and Nelson, 1996) that shapes a unique marine biodiversity and supports extensive pelagic and demersal fisheries. The northwards flowing Benguela Current has long been hypothesized to facilitate connectivity of marine species in this region, although these models relate to exploited demersal and pelagic fishes, which should be less influenced by inshore dynamics (Stenevik et al., 2008). For coastal species in this region, the interplay between hydrodynamics and gene structure have not been assessed, contributing to the theory that the west coast should broadly display population genetic homogeneity facilitated by the Benguela Current.

This study contributes toward better understanding the forces acting on population structuring of multiple intertidal species, with a particular emphasis on invertebrates that are traditionally under-represented in such studies (Selkoe et al., 2016a). To do this, we make use of methods that estimate genetic structure and biophysical connectivity, specifically to provide preliminary insights whether regional large-scale oceanography influences extant population genetic structuring in marine species. We utilize a comparative phylogeographic approach, focusing on five phylogenetically diverse rocky shore species inhabiting the coastline of the southern Benguela Current system. This region is an ideal place to test hypotheses concerning the directionality of dispersal, due to the linear geography of the coastline that lacks major offshore islands and is characterized by a relatively simple oceanography. Specifically, we test the hypothesis (1) that species with long pelagic larval competency periods and broadcast spawning dispersal show the highest connectivity and lowest levels of genetic structure compared to brooding and live-bearing species and (2) that the predominant direction of gene flow (i.e., migration) of larvae will be northwards along the shore, aligned with the primary flow direction of the Benguela, as has been suggested by previous egg and larval surveys and limited genetic studies (von der Heyden et al., 2008, 2011; Teske et al., 2011; Muller et al., 2012, but see also Teske et al., 2015). Overall, we evaluate our research to assess the potential management implications toward prioritizing areas for marine reserves and help to identify shared genetic breaks across multiple taxa in one of the most productive marine regions globally.

METHODS

Sampling Protocol, DNA Extraction, and PCR

Four different intertidal species (the limpet *Scutellastra granularis*, and topshell *Oxystele tigrina*; the cushion star *Parvulastra exigua* and the clinid fish *Clinus superciliosus*) with differing reproductive strategies, ranging from broadcast spawning to live-bearing (**Tables 1**, **2**), were sampled from the major, representative rocky shore habitats on the west coast

(684 samples in total, **Tables 1**, **2**). An additional 162 urchin, *Parechinus angulosus*, sequences were obtained from Muller et al. (2012). Sampling was conducted across seven, equally spaced sites (except for sites 6 and 7 on the Cape Peninsula) spanning ∼740 km of the South African west coast (**Table 1**; **Figure 1**). The number of individuals collected for each species varied between 20 and 34 (although for one site nine individuals of *C. superciliosus* were collected; **Table S1**). We chose species living across similar shore heights in the intertidal zone (although all species can also be found in very shallow sub-tidal environments but at lower densities; with an exception being *S. granularis*, which is an obligate high shore species), as previous studies suggest that species confined to the different parts of the shore can show varying levels of population genetic structuring (Bird et al., 2007; von der Heyden et al., 2013). Field collection was approved by the Department of Agriculture, Forestry and Fisheries of South Africa (permit reference number: RES2012/13) and ethics approval was provided by Stellenbosch University Ethics Committee, reference SU-ACUM13-00014.

Given that the southern Benguela, although of global and local significance, is highly understudied, we chose to provide a broad overview of genetic structuring across multiple species, and focussed on mtDNA markers. MtDNA resolves large-scale population structuring and is particularly suitable for multi-species studies, thus proving suitable for critical insights into the evolutionary history of a region and offering a foundation for future studies (Bowen et al., 2014). A partial fragment of the mtDNA cytochrome oxidase I (COI) gene was amplified for the four invertebrate species, whereas for the fish, *C. superciliosus*, a fragment of the mtDNA control region was targeted (despite several attempts and different primer combinations, it was not possible to amplify mtDNA COI consistently for all fish samples). DNA extraction, primer sequences and PCR protocols followed Muller et al. (2012) and von der Heyden et al. (2011) respectively. For *P. exigua* and *O. tigrina*, species-specific primers were designed (**Table S2**). Trimmed fragment lengths range from 250 to 300 bp. New sequences were deposited in GenBank (KU640409–KU640590, KU640591–KU640755, and KU640756–KU640952).

Statistical Analyses of Genetic Data

Sequences were edited and aligned manually in BioEdit v.7.0.9.0 (Hall, 1999) and collapsed to haplotypes using the program Collapse 1.2 (http://darwin.uvigo.es). Standard genetic diversity (haplotype diversity h and nucleotide diversity π) indices were calculated using Arlequin v.3.5 (Excoffier and Lischer, 2010), which was also used to calculate global Φ_{ST} using an Analysis of Molecular Variation (AMOVA) and pair-wise Φ_{ST} (an analog of F_{st} that takes genetic differentiation into account) values for each species, between the different sampling sites. The relationship between genetic differentiation and geographic distance was used to test for isolation-by-distance (IBD), using a Mantel test in the online "Isolation by Distance web service v3.23" (Jensen et al., 2005) and tested for significance. To visualize the relationships between haplotypes sampled at different locations, minimum parsimony networks were constructed for each species using TCS v1.21 (Clement et al., 2000).

TABLE 1 | Summary of the diversity parameters.

Species [n]	Kommetjie		Sea point		Jacobsbaai		Lambertsbaai		Brandsebaai		Hondeklipbaai		Port Nolloth		Total haplotypes	Unique haplotypes	Ø h	Ø π
	h	π	h	π	h	π	h	π	h	π	h	π	h	π				
Oxystele tigrina [182]	0.88	0.0051	0.91	0.0052	0.92	0.0061	0.90	0.0046	0.87	0.0055	0.89	0.0049	0.91	0.0052	40	23	0.90	0.0052
Scutellastra granularis [197]	0.88	0.0040	0.83	0.0036	0.90	0.0037	0.95	0.0053	0.96	0.0044	0.89	0.0043	0.94	0.0050	67	50	0.91	0.0043
Parechinus angulosus [162]	0.95	0.0114	0.92	0.0134	0.97	0.0114	0.97	0.0163	–	–	0.84	0.0033	0.93	0.0031	73	62	0.93	0.0098
Parvulastra exigua [177]	0.08	0.0001	0.61	0.0015	0.46	0.0008	0.56	0.0015	0.80	0.0028	0.68	0.0019	0.34	0.0009	18	14	0.50	0.0014
Clinus superciliosus [128]	0.90	0.0080	0.94	0.0089	0.93	0.0059	0.92	0.0128	–	–	0.91	0.0121	0.96	0.0123	59	46	0.93	0.0100

Results for haplotype diversity (h), nucleotide diversity (π), total number and unique number of haplotypes. n, number of individuals sampled per species.

TABLE 2 | Species information used for modeling connectivity.

Species	max PLD	Pre-competency	Spawning period	Number of simulations completed	Notes
Scutellastra granularis—Granular limpet	10 days [2, 3]	1 day [1]	Annually, May to June [4]	80 (weekly)	Trochophore larvae, broadcast spawning, little known about larval stage. Can be long lived (~10 years)
Oxystele tigrina—Tiger topshell	5 days [5]	0.5 day [1]	Continuous [6, 7], but maybe twice a year [8]	200 (biweekly)	Broadcast spawning, data from genus, not species
Parechinus angulosus—Cape urchin	70 days [9]	40 days [9]	August/September and April/May [10, 6]	64 (biweekly)	Broadcast spawning, sufficient data on spawning and larvae
Clinus superciliosus—Super klipfish	0 days, live-bearing	0	Continuous [11, 12]	See notes	Live bearer; cannot be modeled
Parvulastra exigua—Cushion starfish	0 days, direct development	0	Data deficient	See notes	Crawl-away young; cannot be modeled

[1] Best Guess, [2] Dodd, 1957, [3] Wood and Gardner, 2007, [4] Branch, 1974, [5] Kilburn and Rippey, 1982, [6] Hodgson, 2010, [7] Lasiak, 1987, [8] Joska and Branch, 1983, [9] Cram, 1971, [10] Fricke, 1980, [11] Penrith, 1970, [12] Veith, 1979.

Dispersal Modeling in the Southern Benguela Current

A biophysical larval dispersal model (Treml et al., 2012) was parameterized for the Benguela system to quantify the dispersal potential for the three taxa with a pelagic larval stage (*S. granularis*, *O. tigrina*, and *P. angulosus*). Parameter values (e.g., pelagic larval duration, competency, and spawning periodicity) were estimated by empirical data from the literature and expert opinion (**Table 2**), as many details for the species' parameters are unknown or uncertain. The model domain was set to the study area (**Figure 1**) using high-resolution shoreline data, rocky shore habitat data [taken from (South African National Biodiversity Institute, National Biodiversity Assessment (NBA), 2011), http://bgis.sanbi.org/SpatialDataset/Detail/414], our sample sites, and interpolated hydrodynamic data (based on depth, rugosity, winds, geostrophic forcing, etc.) for the region using best available (long time-series, regionally consistent, ~7 km spatial resolution, 1992–2012) oceanographic data (HYCOM, hycom.org). Although this hydrodynamic model cannot resolve the very fine-scale coastal (or intertidal) dynamics, it is adequate in resolving meso-scale eddies and the local structure of the Benguela Current system (Chassignet et al., 2007). All nearshore rocky habitat patches were used as potential sources (37 patches with mean of 33 ± 16 km^2 rocky habitat) and destinations during the biophysical larval dispersal modeling. Note, although we released virtual larvae from all possible source patches, we summarized results as the cumulative migration between the seven samples sites (including through stepping-stone habitat patches between sampled populations). As a result, our approach attempts to represent local-scale (i.e., within/among patches) to seascape-level (throughout entire Benguela system) dispersal potential through all habitat patches in the system. A single dispersal simulation consisted of modeling the advection and transport of a cloud of virtual larvae (equivalent to more than 10^7 larvae) released from an individual rocky shore habitat patch (sample sites and unsampled habitat patches) and tracks this larval cohort as it moves downstream,

directed by the biological parameters, and coastal currents. See Treml et al. (2012) for detailed numerical methods and sensitivity testing. Cumulatively, we completed 840 dispersal simulations across each of 37 potential source sites (**Figure 1**) averaged across 20 years of oceanographic data (1992–2012). Long-term average species-specific dispersal networks were developed from the modeled migration matrices to map the emergent patterns of potential population connectivity across species (connection values represent the proportion of downstream settlement that came from each potential upstream source). These dispersal networks highlight the geographic location and the strength of dispersal corridors and barriers along the west coast of South Africa.

RESULTS

Diversity Analyses and Population Structure

After editing and trimming, sequence lengths varied by species (*C. superciliosus* = 373 bp, *P. angulosus* = 790 bp, *S. granularis* = 611 bp, *P. exigua* = 651 bp, *O. tigrina* = 473 bp). Haplotype diversity and the number of unique haplotypes (those restricted to only one site) is provided in **Table 1**, which shows that diversity indices vary between the five intertidal species. Both h and π were lowest in the cushion star *P. exigua*, whereas all other species showed relatively high levels of diversity (overall range $h = 0.5$–0.93; $\pi = 0.0014$–0.01; **Table 1**). This is clearly shown by the number of unique haplotypes found in each species. Fourteen of 18 are unique for *P. exigua*, whereas for the other four species the proportion of unique haplotypes is much lower (**Table 1**; **Figure 2**). Analyses of molecular variance showed no congruent pattern of life history and population genetic structure. The broadcast spawning urchin, *P. angulosus* had the highest global Φ_{ST} ($\Phi_{ST} = 0.32$, $P < 0.001$), followed by the cushion star *P. exigua* (crawl-away young) and clinid fish *C. superciliosus* (live-bearing) ($\Phi_{ST} = 0.27$ and 0.14 respectively, $P < 0.05$). The other two broadcast spawning species, *O. tigrina* and *S. granularis* did
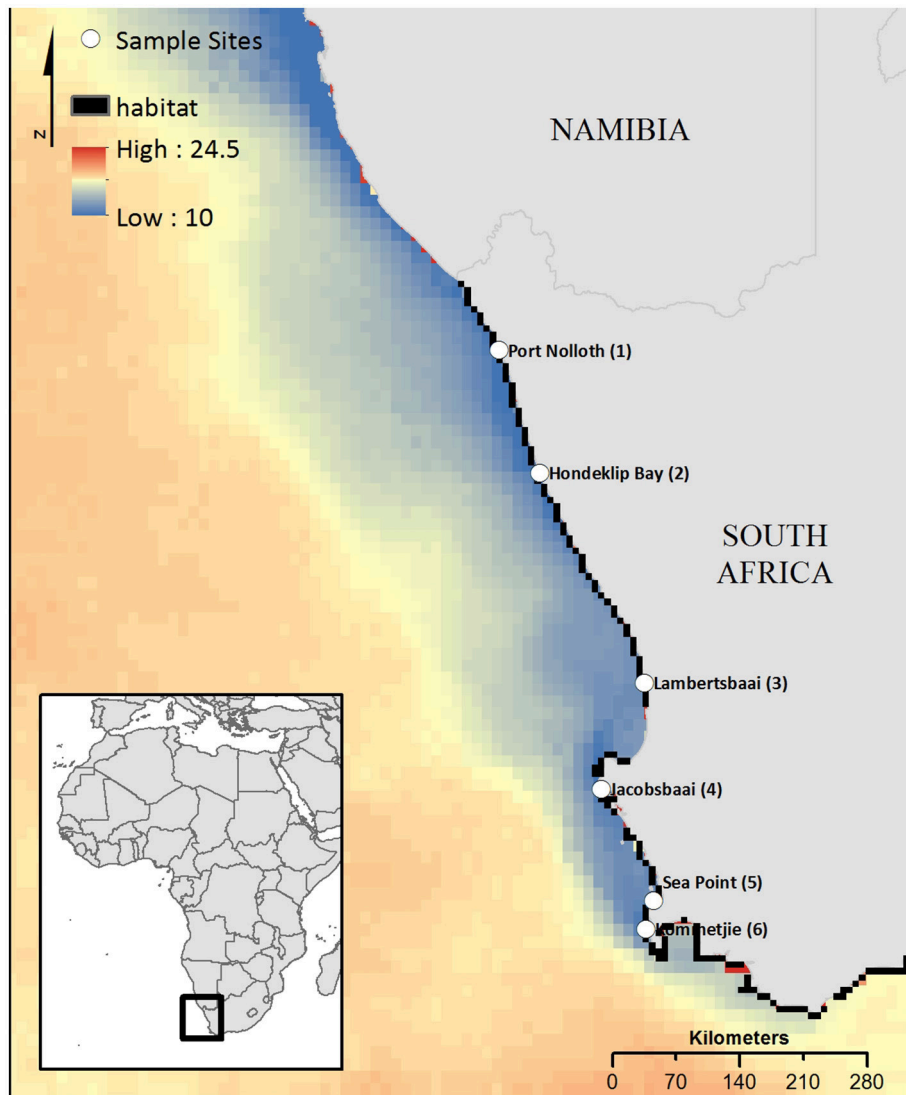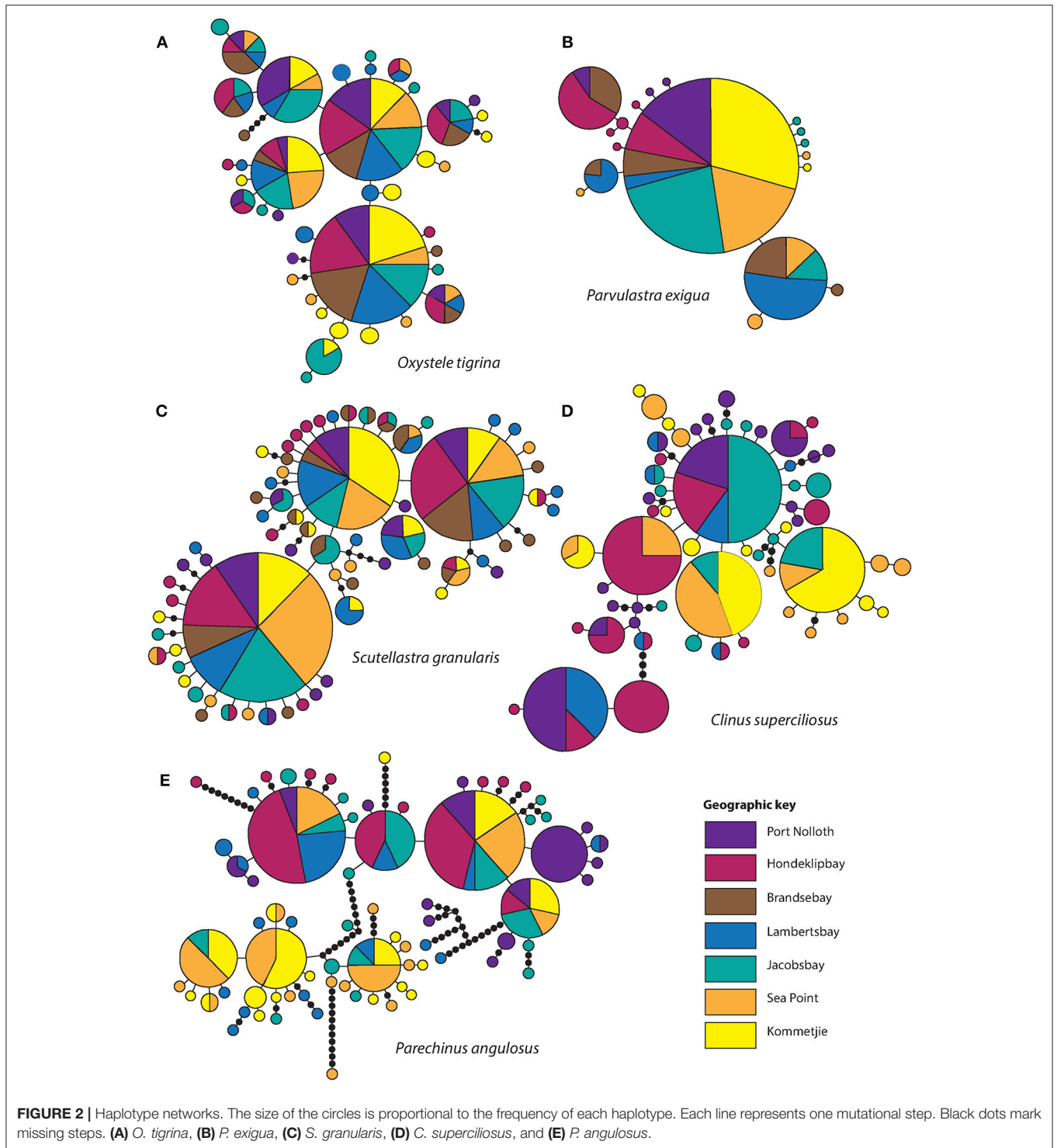
FIGURE 1 | South Africa's west coast with the sampling locations and the study area used for biophysical modeling. Site names feature the site IDs, which are used in the network plots. Mean sea surface temperature illustrates temperature differences. Modeled habitat patches, including rocky coast, and mixed shore, are shown in black.

not have significant global F_{ST} values ($P > 0.05$). *Parechinus angulosus* also had the largest pairwise Φ_{ST} values (0.15–0.62, $P < 0.05$), which increase with distance between collection sites, thus resulting in a significant signal of IBD. IBD slopes for all other species were not significant (**Figure S1**). Pairwise Φ_{ST} values were relatively high for *P. exigua* (0.11–0.51, $P < 0.05$) and somewhat lower for the live-bearing fish *C. superciliosus* (0.09–0.25, $P < 0.05$; **Table S3**). The haplotype networks vary between species, with the cushion star showing the simplest network with one central haplotype, whereas the networks for the four other species are more complex. In particular the networks of the *O. tigrina* and *S. granularis* reflect the low values for population structure, displaying a high degree of shared haplotypes between collection sites (**Figure 2**).
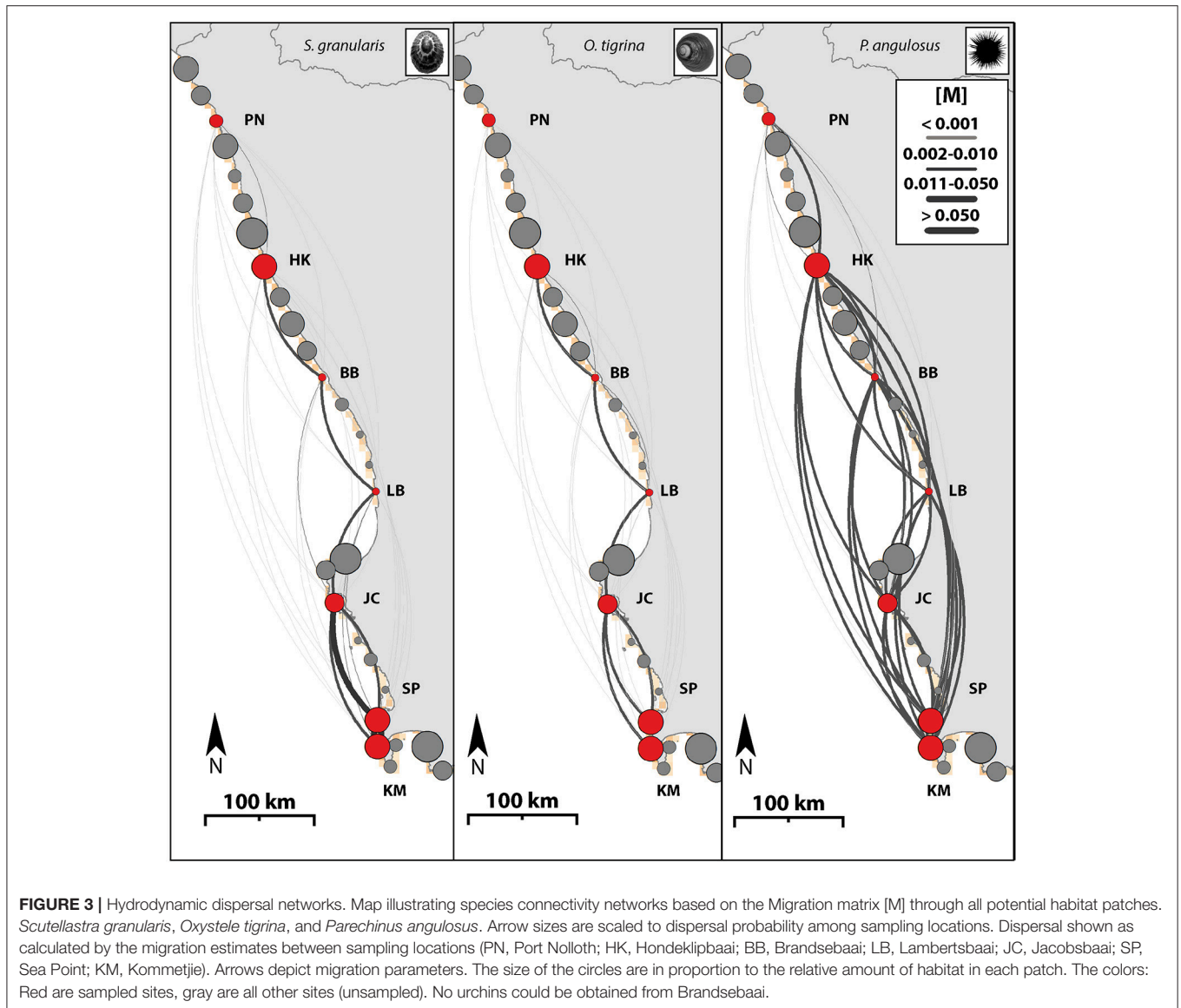
Dispersal Modeling

The dispersal networks representing the three modeled taxa (**Figure 3**) clearly illustrate the complex and directed nature of dispersal potential across this seascape (dispersal strengths range from below 0.001–0.20). As the pelagic larval competency period increases, a larger number of sites become more strongly connected (see *O. tigrina* and *P. angulosus* for lower and upper extremes) and have a lower local retention rate (*O. tigrina* and *S. granularis* with 12–13% local retention; *P. angulosus* with <0.001%). Multi-species consistency can be seen in the generally stronger northward flow structure in the north (sites 1–3), and more mixed flow among the central and southern sites in the seascape. For the limpet and top shell, dispersal is generally strongest between adjacent sites, with less connectivity

FIGURE 2 | Haplotype networks. The size of the circles is proportional to the frequency of each haplotype. Each line represents one mutational step. Black dots mark missing steps. **(A)** *O. tigrina*, **(B)** *P. exigua*, **(C)** *S. granularis*, **(D)** *C. superciliosus*, and **(E)** *P. angulosus*.

between sites that are further apart. For the urchin, modeled dispersal is high between sites even if they are not adjacent to each other, except for the two most northern sites where connectivity is lower. The two most northern sites also have the lowest connectedness for in the dispersal estimates of the limpet and topshell. Connectivity matrices from all modeled taxa are available in **Table S4**.

DISCUSSION

Our study used an integrative approach, combining population genetics and biophysical modeling to investigate whether regional oceanographic conditions could contribute toward shaping the genetic structure of a diverse array of rocky shore species distributed along one of the world's most

FIGURE 3 | Hydrodynamic dispersal networks. Map illustrating species connectivity networks based on the Migration matrix [M] through all potential habitat patches. *Scutellastra granularis*, *Oxystele tigrina*, and *Parechinus angulosus*. Arrow sizes are scaled to dispersal probability among sampling locations. Dispersal shown as calculated by the migration estimates between sampling locations (PN, Port Nolloth; HK, Hondeklipbaai; BB, Brandsebaai; LB, Lambertsbaai; JC, Jacobsbaai; SP, Sea Point; KM, Kommetjie). Arrows depict migration parameters. The size of the circles are in proportion to the relative amount of habitat in each patch. The colors: Red are sampled sites, gray are all other sites (unsampled). No urchins could be obtained from Brandsebaai.

productive marine regions. The results show that three of five coastal species exhibit significant population structuring. The urchin, *P. angulosus*, that is characterized by the longest larval competency and lowest levels of local retention nevertheless displays the highest level of population structure of all species analyzed in this study. Therefore, given the mixed findings of the three broad-cast spawning species, we cannot conclusively answer our hypothesis that longer larval competency results in lower genetic structure. The biophysical model provides evidence for potential dispersal both northward, i.e., with the dominant oceanographic feature of the region, the Benguela Current, but also mixed flow in the southern and central study regions. Interestingly, the biophysical model also suggests limited gene flow across some regions along almost 800 km of linear coastline, particularly the two most northern sites. Considering our hypotheses, the findings clearly reject the hypothesis that larval dispersal would dominantly follow the flow direction of

the Benguela Current, due to the substantial migration rates toward southern localities. This could indicate the influence of near-shore countercurrents, although represented and not fully resolved in our hydrodynamic data, which might transport larvae independently of the Benguela Current.

Hydrodynamic Models and Patterns of Genetic Structure Resolved Mixed Patterns of Potential Connectivity

We recovered diverse patterns of population genetic structure across our target species, from signals of panmixia to strong population divergence. For example, analyses based on estimates of F_{ST} suggest that from an evolutionary perspective, the two mollusc species remain well connected within the near-shore Benguela Current system. In contrast, the broadcast spawning urchin, with the greatest potential for dispersal (**Figure 3**)

exhibits the highest levels of genetic structure. The direct-developing cushion star and the live-bearing clinid fish also show significant levels of population structure, although these are not as high as for the urchin. This result mirrors previous findings of multi-species genetic analyses of coastal species (Kelly and Palumbi, 2010; Wright et al., 2015) in that the duration of larval competency is generally a poor predictor of genetic structure (Weersing and Toonen, 2009).

Interestingly, the biophysical model suggested that the urchin has the highest potential of larval connectivity, with even distant populations seemingly well connected which is in stark contrast to the genetic results. This points to other, as yet unknown seascape features such as local adaptation or post-settlement processes, such as larval behavior, that maintain strong genetic structure despite high flow, which has been observed in other high gene flow marine species (Sanford and Kelly, 2011; Benestan et al., 2016). Nielsen et al. (2018) showed that *P. angulosus* populations in the region are characterized by a low number of private SNPs that indicate some population isolation. In particular, the two most northern sites are most differentiated, which may well be linked to our finding that from a larval connectivity perspective, these two sites are relatively poorly connected to the southern populations.

In contrast to the high dispersal potential and low genetic structure of the urchin, for the limpet we recover scenarios of genetic panmixia (at least measured with mtDNA COI), but hydrodynamic models that suggest lower levels of connectivity. As for the genomic study on the urchin, this is mirrored by private SNPs found in the most northern limpet populations (Nielsen et al., 2018), providing further evidence that oceanography shapes the evolutionary trajectories even in high dispersal species with large effective population sizes. Overall, our combined analyses of genetic structure and hydrodynamic models suggest a complex system of multiple drivers, including environmental variation as well as oceanography contributing toward shaping the population and dispersal dynamics of marine coastal species on the west coast.

Perspectives for the Management of Highly Variable Coastal Marine Systems

The incorporation of molecular data into management and conservation planning is a challenging process, mainly due to a lack of theoretical and practical frameworks (Beger et al., 2014; von der Heyden et al., 2014; Nielsen et al., 2017). However, integrating genetic information is particularly valuable for delineating populations and providing insights into population connectivity (Davies et al., 2015; Liggins et al., 2016; von der Heyden, 2017). Although single marker approaches, such as the one used in our study approaches cannot account for aspects such as adaptive variation, it nonetheless serves as a suitable tool for identifying broad patterns of spatial genetic structure on which further analyses can be built, especially with the inclusion of multiple species (Bowen et al., 2014; Nielsen et al., 2017). The latter is particularly important from a conservation planning perspective, especially in regions that lack capacity and are under-resourced, as multi-species mtDNA data sets such as the one in

this study, have the potential to provide valuable insights into the spatial distribution of genetic variation, which can be efficiently incorporated into the planning process (Nielsen et al., 2017).

Though South Africa is considering several new MPAs, particularly through the ocean economy development program Operation Phakisa (www.operationphakisa.gov.za), the current MPA network has been shown to be ineffective at protecting genetic population differentiation and diversity and that in general molecular data is underutilized in marine management applications in the region (von der Heyden, 2009; von der Heyden et al., 2014; Wright et al., 2015; Nielsen et al., 2017). Therefore, resolving genetic structure among multiple species has the strength to point to shared environmental and dispersal barriers, which may lead to the recognition of separate "management units." Although this term is more commonly applied to exploited species, it can also be used to delineate units of species that are not of commercial interest. Importantly, our work shows that even though previously recognized hard barriers to gene flow such as Cape Point, (Teske et al., 2011) could not be detected at the west coast for the studied species, our work suggest some regions are poorly connected from both genetic and biophysical perspectives. As we have shown here, the west coast appears to be genetically structured between sites and across taxa, suggesting that the different populations should be considered as separate management units (see **Figures 2**, **3**). For species that show strong genetic structure, such as the urchin in our study, multiple MPAs would be required to secure the unique genetic signals at each site and build resilience in the system.

Our suggestion to protect specific west coast areas to safeguard unique genetic patterns correspond to previous recommendations for spatial conservation priorities (Majiedt et al., 2013). These focus areas lie adjacent to regions for which we observed reduced gene flow, supporting that biodiversity, habitat, and genetic patterns vary considerably in this region and probably require distinct management interventions to capture their differences. Ideally, a local network of MPAs would protect the genetic, connectivity and evolutionary characteristics, although this approach would benefit from additional insights from other coastal and offshore species to test fully and across different marker types (Nielsen et al., 2018). In summary, a combination of biological, oceanographic, molecular, and available socio-economic data would greatly improve our ongoing efforts in developing an integrated spatial management strategy for the west coast of South Africa.

AUTHOR CONTRIBUTIONS

SvdH, LM, and ET designed the study, collected the data, analyzed the data, prepared figures, and wrote the manuscript.

FUNDING

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2018.00268/full#supplementary-material

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