BIODIVERSITY RESEARCH

Genetic isolation by distance reveals restricted dispersal across a range of life histories: implications for biodiversity conservation planning across highly variable marine environments

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ABSTRACT

Aim Isolation by distance (IBD) analyses are an effective tool for determining genetic connectivity among populations, providing a basis for estimating dispersal and thus contributing to spatial biodiversity planning. Here, we use an IBD approach to determine patterns of connectivity to infer dispersal distances for a phylogenetically diverse range of marine species.

Location Two thousand and eight hundred kilometre of South African coastline.

Methods mtDNA data sets for 11 rocky shore and reef-dwelling marine species with diverse life history strategies (broadcast spawning, brooding and live-bearing) were used to quantify intraspecific genetic connectivity by means of global and pairwise Φ_{st}. Mantel tests were used to assess the significance of genetic structure with geographic distance. Significant, positive slopes were used to estimate dispersal distances. For all species, we also plotted genetic diversity along the coast and compared this to patterns of species richness.

Results For seven of the 11 species tested, we report positive IBD relationships, with patterns of IBD of similar magnitude in broadcast spawners and live-bearers. Dispersal estimates were low, with effective distances of < 10 km per generation. We find discordance between pelagic larval development and population structure and that genetic structure and the physio-geographic features of the coastline considered to be important biogeographic barriers do not overlap. Genetic diversity and species richness show congruent patterns, with both variables lowest on the west coast, and increasing towards the east.

Main conclusions Our study highlights the complexity of marine systems and the clear need for regional assessments of connectivity, rather than more general management plans which may not otherwise effectively encompass area-specific conservation needs. Importantly, we show that the current marine protected area (MPA) network in South Africa is not effective in protecting evolutionary processes and strongly recommend a network of more closely spaced MPAs in the region that reflects the low average connectivity between distant marine populations.

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INTRODUCTION

Dispersal, the movement of larval, juvenile or adult stages, is an important driver of ecological and evolutionary processes in marine environments that affects population dynamics and demography, as well as ecosystem functioning (Grosberg & Levitan, 1992; Caley *et al.*, 1996). Given the importance of understanding the movement of species through relatively open systems such as oceans and the potential impact on recruitment, dispersal is a fundamental variable in determining connectivity between populations with impacts on fisheries management, the spread of alien and invasive species and the spatial planning of marine reserve networks (Shanks *et al.*, 2003; Fogarty & Botsford, 2007; Sorte *et al.*, 2010). Dispersal and connectivity in marine systems are, however, difficult to measure given the small size of larvae, generally large population sizes and large geographic ranges inhabited by marine species.

There is broad consensus among biologists that understanding population genetic structure and gene flow within and between populations (i.e. genetic connectivity) is fundamental to the development of effective conservation strategies (Hellberg *et al.*, 2002; Gerber *et al.*, 2003; Palumbi, 2003; Gaines *et al.*, 2010). This is particularly true for spatially explicit, ecosystem-based conservation strategies such as terrestrial protected area networks and marine protected areas (MPAs) (Botsford *et al.*, 2003). Long-term gene flow is not only critical to the process of adaptive evolution and thereby the persistence of species (Salm *et al.*, 2000), but patterns in gene flow can also aid in identifying the processes leading to contemporary species distributions (Slatkin, 1993; Grosberg & Cunningham, 2001; von der Heyden, 2009). Because distribution patterns of taxa are a result of the complex interplay between the life histories of species and their specific responses to environmental change, for example vicariance, range expansions and colonization (Grosberg & Cunningham, 2001; Eble *et al.*, 2011), unravelling local and regional driving forces are critical for effective conservation decision-making and implementation. Genetic approaches, including estimates of gene flow and measures of genetic diversity, are, however, rarely incorporated into planning scenarios (Beger *et al.*, 2014; von der Heyden *et al.*, 2014), despite genetic diversity being recognized as one of the core foundations of biodiversity conservation (Laikre *et al.*, 2010).

Understanding genetic connectivity among geographically proximate populations is of particular importance in marine ecosystems where hydrodynamic regimes fluctuate dramatically over spatio-temporal scales; this is particularly relevant in regions with increasing reliance on MPAs for conservation of economically important resources (Lubchenco *et al.*, 2003). The presence of ocean currents capable of carrying larvae long distances, together with few obvious barriers to dispersal, initially led to the assumption that marine systems were largely panmictic (Caley *et al.*, 1996). There is now, however, a growing awareness that marine species are far more genetically structured than previously believed and that

low levels of structure are not necessarily an indication of high gene flow (Cowen *et al.*, 2006; Marko & Hart, 2011). Many marine species, particularly coastal rocky shore species, disperse primarily during their larval stage, becoming sessile as adults (Sale, 2004; Cowen *et al.*, 2006). Extended larval durations undoubtedly increase dispersal potential (Kinlan & Gaines, 2003); however, a number of studies support spatially limited realized dispersal in species with long larval periods (Miller & Ayre, 2008; Ayre *et al.*, 2009; Puebla *et al.*, 2012) and suggest that life history alone is not always an accurate predictor of dispersal distance (Kelly & Palumbi, 2010). Indeed, studies using tagging, microchemistry and molecular data across a range of species suggest dispersal distances in marine organisms of between 10 and 100 km, rather than 1000s of kilometres (Palumbi, 2003; Levin, 2006), and these findings have influenced an important shift in the design of some MPAs from large, stand-alone MPAs to smaller connected networks (Hastings & Botsford, 2003; Largier, 2003; Shanks, 2009), especially in coastal regions.

The shift to marine resource management via a network approach calls attention to the importance of reliable measures of connectivity that can be extended to a large range of taxa. The focus of numerous recent marine phylogeographic studies has largely been directed towards identifying barriers to gene flow and understanding the role of life histories, particularly larval duration, in determining the extent to which marine taxa exhibit spatial genetic structuring (Ayre *et al.*, 2009; Shanks, 2009; Weersing & Toonen, 2009). To date, biogeographic barriers have been shown to be poor proxies for population genetic patterns in the marine environment, most likely because of the inherent assumption that over evolutionary time-scales, multiple taxa will have been influenced to the same degree by specific geographical features, although this has rarely been shown to be the case (Kelly & Palumbi, 2010; but see Kuo & Avise, 2005), even for phylogenetically closely related species (von der Heyden *et al.*, 2013). With a fair amount of the variation in realized dispersal unexplained by, for example, life history features and biogeographic barriers to dispersal (Selkoe *et al.*, 2014), there remains a continued need for geographically explicit studies across multiple co-occurring taxa. Patterns of dispersal and population structure can vary significantly between species, even in shared habitats, and analyses focused on single species or life history strategies are in many instances purely descriptive with limited power to inform regional management of marine biodiversity (von der Heyden, 2009; Toonen *et al.*, 2011). Further, the links between species richness and genetic diversity are poorly understood; terrestrial examples show patterns both of congruence (Tolley *et al.*, 2011) and disjunction (Forest *et al.*, 2007; Taberlet *et al.*, 2012). To our knowledge, only one example exists for marine species; Messmer *et al.* (2012) showed that for 11 species of coral reef fishes, declines in genetic diversity were correlated with declines in species diversity across the Pacific Ocean. However, identifying whether areas that are high in biodiversity are also high in

genetic diversity and examining the processes driving such patterns can lead to more effective conservation planning.

The South African oceanographic regime, like its biodiversity, is unique, as it is influenced by two major boundary currents: the warm, nutrient-poor Agulhas Current on the east coast and the cold-water, upwelling dominated system of the Benguela Current on the west coast (Fig. 1). Not only have these two contrasting current systems helped shape the rich biodiversity of the region (Awad *et al.*, 2002; Griffiths *et al.*, 2010), but they also play important roles in population genetic structure of marine species (reviewed in von der Heyden, 2009; Teske *et al.*, 2011a,b). However, connectivity across this highly variable system is poorly understood, although preliminary analyses suggested that the MPA network may not provide sufficient connectivity for the meta-

population dynamics of the majority of marine biodiversity (von der Heyden, 2009).

Several techniques exist for inferring dispersal and quantifying connectivity in marine species, for example trace element signatures, models of larval dispersal, tagging studies (mostly of adult individuals) and genetic approaches. Of these, the latter is most commonly utilized, because numerous data sets are available that include pairwise measures of genetic differentiation, which can be compared across multiple species and regions (Kelly & Palumbi, 2010; Weersing & Toonen 2009; Selkoe & Toonen 2011; Durrant *et al.*, 2013). Given the growing number of available data sets, comparative estimates of dispersal are now a valuable alternative for improved understanding of connectivity in marine systems.
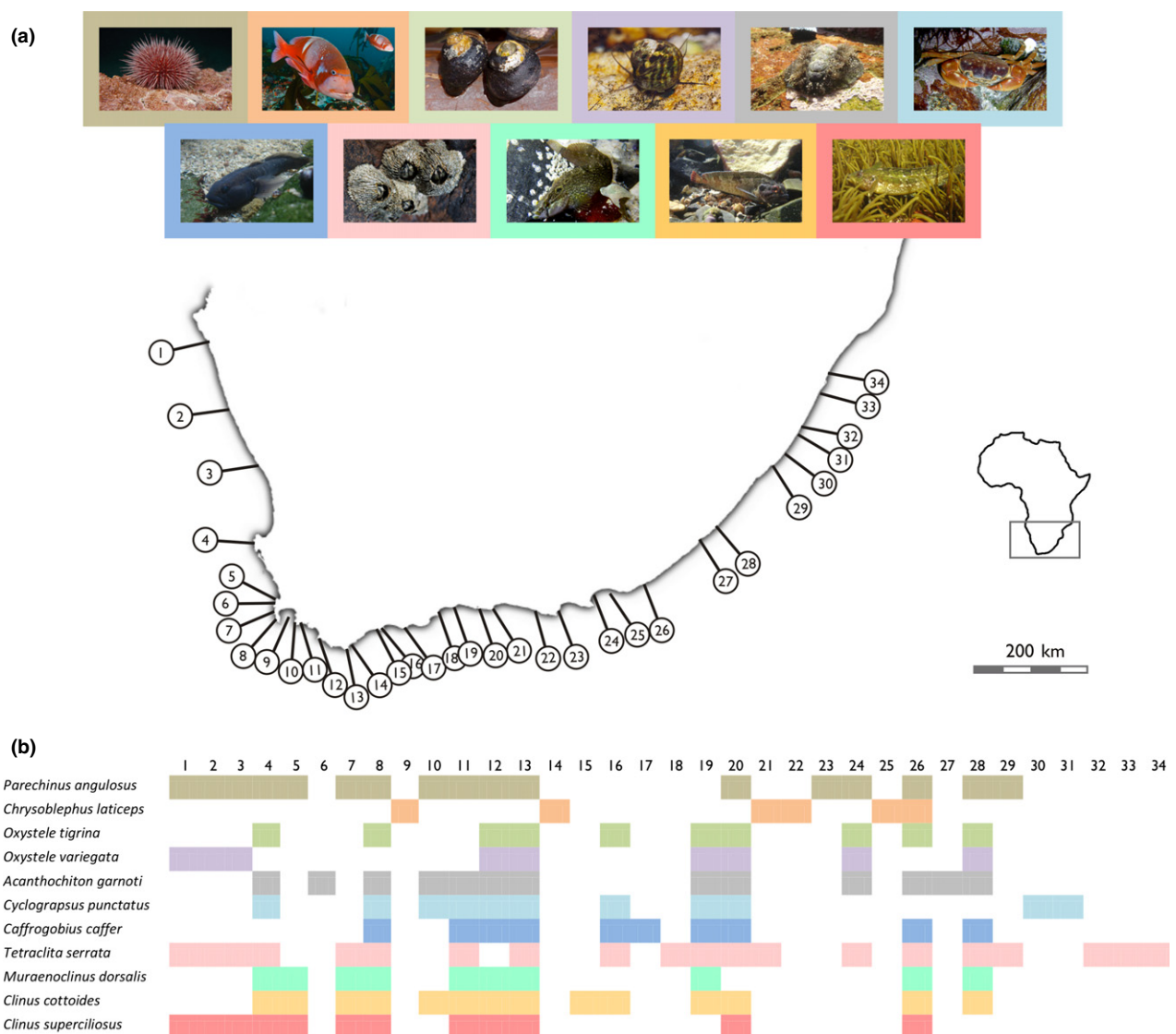

Figure 1 (a) Map of South Africa showing the 2800 km of geographic range sampled in this study (Port Nolloth to Umhlanga Rocks), (b) sampling localities for each of the eleven species studied. (refer to Appendix S2 for sample sizes at each locality, as well as sampling locality name).

Globally, there remains an urgent need for the inclusion of genetic and connectivity data not only in MPA design (Beger *et al.*, 2014), but in all aspects of conservation planning (Diniz-Filho *et al.*, 2013). No multispecies studies have thus far solely examined Southern Hemisphere regions and, few studies exist from developing nations where marine biodiversity and especially genetic studies are scarce (Behegaray, 2008). Indeed in southern Africa, there is a distinct lack of population genetic data for the majority of species along a highly exploited and eco-geographically dynamic coastline where contrasting oceanographic regimes shape high levels of marine biodiversity across a mosaic of taxa and environmental gradients (Griffiths *et al.*, 2010; von der Heyden *et al.*, 2011; Teske *et al.*, 2011a,b).

Here, we explore connectivity at evolutionary time-scales and the role of life history in determining the spatial distribution of genetic variation across a range of phylogenetically diverse marine organisms. Using a comparative mitochondrial DNA data set for 11 species sampled across their full distributional ranges, and which encompass diverse life history strategies, we address the inherent limitations of understanding regional diversity based on population genetic inference from single species. For each species, we test for isolation by distance (IBD) and whether life history is a reliable predictor of genetic connectivity. We then estimate effective dispersal distances for each species and ask whether the current MPA network in South Africa is sufficiently connected to protect and maintain metapopulation dynamics. Our data set also gives us the opportunity to examine the relationship between genetic and species diversity across this highly variable coastline.

METHODS

Data collection

DNA sequence data on 11 intertidal marine species were taken from published works (Neethling *et al.*, 2008; Teske *et al.*, 2010; von der Heyden *et al.*, 2011, 2013; Muller *et al.*, 2012; Reynolds *et al.*, 2014), as well as unpublished data (Muteveri, 2013); two new data sets (*Acanthochiton garnoti* and *Cyclograpsus punctatus*; Appendix S1 in Supporting Information) were generated for this study (Table 1; Appendix S1). Sampling sizes for each species and locality are given in Appendix S2. To minimize the effects of unequal sampling, all animals were sampled at the same geographical localities where possible and efforts were made to obtain similar samples sizes per site. Further, we chose species that are all abundant members of South African rocky shore intertidal communities and thus make the assumption that all have relatively high effective population sizes.

Taxa were chosen to represent the range of life history strategies found within marine coastal communities and comprised predominantly sessile species that included five broadcast spawners, three brooders and three live-bearers (Table 1). The reef-living red roman *Chrysoblephus laticeps*

was the only vagile and commercially exploited fish species included in the study. Sampling sites included 34 locations between Port Nolloth on the west coast of South Africa and Umhlanga Rocks on the east coast, spanning more than 2800 km of the South African coastline (Fig. 1); note that not all species were collected at each of the 34 sampling sites (Appendix S2 lists sampling locations and sizes). All individuals were analysed at the cytochrome *c* oxidase subunit I (COI) mtDNA locus with the exception of the clinids (*Clinus superciliosus*, *Clinus cottoides* and *Muraenoclinus dorsalis*) and the red roman, *C. laticeps*, which were analysed using the mtDNA control region. Partial DNA sequences ranged from 493 to 790 bp.

Population genetic analysis and dispersal estimates

For all data sets, we calculated a number of diversity measures and quantified genetic structure using both non-spatial and spatial models of population structure. Using Arlequin 3.5 (Excoffier & Lischer, 2010), we estimated genetic diversity including unique number of haplotypes, haplotype diversity (h) and nucleotide diversity (π). Analysis of molecular variance (AMOVA; Excoffier *et al.*, 1992) and pairwise Φ_{ST} were used to explore the extent of genetic structuring across species' ranges based on sampling locations.

To resolve the degree to which spatial connectivity informs population structure along South Africa's coastline, we then tested patterns of population structure for each species against Wright's IBD model (Wright, 1943; Slatkin, 1993). If the dispersal potential of a species' propagules is shorter than that of the species range, genetic drift will lead to divergence between subpopulations at equilibrium (Slatkin, 1993; Rousset, 1997; Grosberg & Cunningham, 2001). Under this model, populations that are geographically closer are predicted to be more similar genetically, leading to significant concordance between estimates of genetic and geographic distance. Moreover, species with limited dispersal capabilities should show a stronger IBD signal over shorter distances than species with high dispersal potential (Ayre & Dufry, 1994).

We analysed the relationship between genetic isolation and geographic distance for all our data sets using the program GenePop (Raymond & Rousset, 1995; Rousset, 2008). For each data set, a Mantel test (Mantel, 1967) was used to assess the significance of the relationship between genetic distance and geographic distance between all sample locations. Geographic distances between sites represent linear coastal estimates in kilometres. As the data sets comprised of haploid mtDNA sequences, which have a lower effective population size than diploid loci, we first applied a correction factor to our mtDNA (Kinlan & Gaines, 2003; B. Kinlan, pers. comm.). We analysed our data in the following way: all sampling localities combined, sampling localities split by biogeographic region and sampling localities split by oceanographic regime (i.e. Agulhas and Benguela Current).

We estimated individual mean dispersal distance for each species that demonstrated significant IBD using two different

Table 1 List of study species, including their reproductive life history

Life history	Common name	Scientific name	Phylum	Family	Fertilization type	Min. PLD	N	h	π	Unique h	AMOVA Overall Φ_{ST}	P	Source
Broadcast Spawner	Spiny Chiton	*Acanthochiton garnoti*	Mollusca	Acanthochitonidae	Spawns	7 days	13	0.95	0.042	84	0.07	< 0.001	This study
	Tiger Topshell	*Oxystele tigrina*	Mollusca	Trochidae	Spawns	4–6 (for sister species)	10	0.93	0.054	76	0.07	< 0.001	Muteveri (2013)
	Variegated Topshell	*Oxystele variegata*	Mollusca	Trochidae	Spawns	4–6 (for sister species)	9	0.68	0.032	82	0.34	< 0.001	Muteveri (2013)
	Cape Urchin	*Parechinus angulosus*	Echinodermata	Echinidea	Spawns	49–56	17	0.91	0.022	84	0.41	< 0.001	Muller et al. (2012)
	Red Roman	*Chrysoblephus laticeps*	Chordata	Sparidae	Spawns	26 days	6	0.98	0.054	86	0.01	0.09	Teske et al. (2010)
Brooder	Banded Goby	*Caffrogobius caffer*	Arthropoda	Varunidae	Brooder	16 days	10	0.96	0.009	51	−0.01	0.90	Neethling et al. (2008)
	Highshore Crab	*Cyclograpsus punctatus*	Arthropoda	Tetraclitidae	Brooding, then PL	14 days	11	0.73	0.009	80	0.49	< 0.001	This study
	Volcano Barnacle	*Tetraclita serrata*	Chordata	Gobiidae	Brooder, then PL	25 days	20	0.98	0.041	80	0.07	< 0.001	Reynolds et al. (2014)
Live-bearer	Super klipfish	*Clinus superciliosus*	Chordata	Clinidae	Internal	0	12	0.92	0.011	77	0.29	< 0.001	von der Heyden et al. (2011, 2013)
	Bluntnose klipfish	*Clinus cottoides*	Chordata	Clinidae	Internal	0	14	0.52	0.002	76	0.26	< 0.001	von der Heyden et al. (2008)
	Nosestripe klipfish	*Muraenoclinus dorsalis*	Chordata	Clinidae	Internal	0	10	0.65	0.005	82	0.89	< 0.001	von der Heyden et al. (2011, 2013)

N, number of populations sampled; *h*, haplotype diversity; π, nucleotide diversity; PLD, pelagic larval dispersal; PL, pelagic larvae.

methods, that of Kinlan & Gaines (2003) and Rousset (1997). Both attract some criticisms; Kinlan and Gaines assume constant effective population size ($N_e = 1000$), which in marine species with potentially large and stochastic N_e may well affect estimates of dispersal. The Rousset (1997) method requires an estimate of adult density. Given a general lack of such data for the South African coastline, we followed a number of recent studies (Buonaccorsi *et al.*, 2005; Cunningham *et al.*, 2009) and calculated mean dispersal distance per generation using a range of effective densities from 10 to 10,000 per km^2 for every species that showed significant IBD slopes (Table 2).

To investigate the relationship between species richness (which has distinct patterns of low diversity on the west and higher diversity on the south and east coasts; Awad *et al.*, 2002), we plotted genetic diversity, measured as haplotype diversity against geographic distance. We then compared this to published patterns of species richness as shown in Awad *et al.* (2002).

RESULTS

The distribution of genetic variation along South Africa's coastline

The distribution of mean haplotype diversity showed a clear and steady increase from the west to the east coast. Across the 400 km subsections, mean haplotype diversity steadily increased from 0.77 (SD ± 0.06) on the west coast, peaking at 0.89 (SD ± 0.05) around Port Elizabeth before dropping again slightly to 0.85 (SD ± 0.07) along the east coast (Fig. 2). The relatively low levels of genetic diversity estimated for the west coast region are strongly influenced by the low diversity of *Oxystele variegata* ($h = 0.19–0.35$) and *C. cottoides* ($h = 0.27–0.5$). The other species sampled at multiple loca-

tions along the west coast (*Parechinus angulosus*, *C. superciliosus* and *Tetraclita serrata*) demonstrated relatively high levels of haplotype diversity ranging from 0.74 to 0.99. Along the section of coastline with the highest mean haplotype diversity (1600–2000 km), only *C. cottoides* had a measure below $h = 0.6$, ranging from 0.35 to 0.55. *Parechinus angulosus*, *C. superciliosus* and *T. serrata* for the same region had
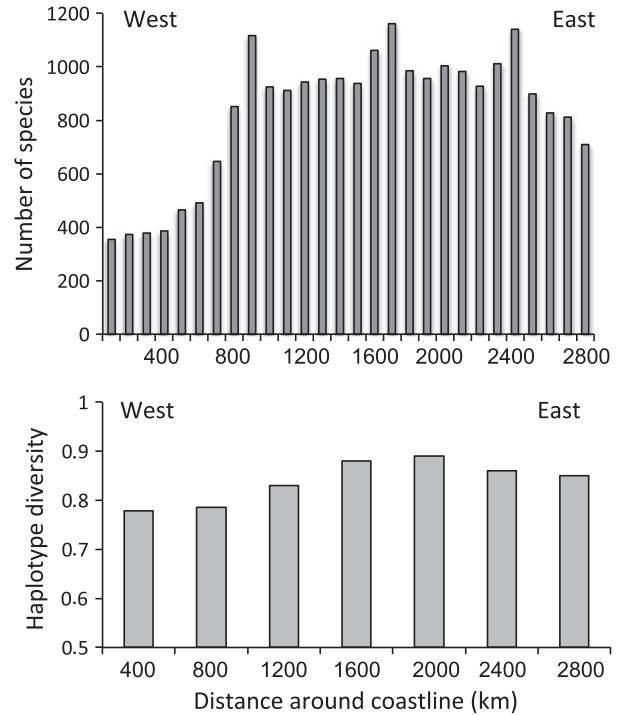

Figure 2 Graph showing species diversity (above) and genetic diversity (below – measured as haplotype diversity, h) across the geographic scale of the study. The species richness graph is after Awad *et al.* (2002).

Table 2 Isolation by distance slopes and dispersal estimates using both Kinlan & Gaines (2003) and Rousset (1997); D = effective density

Species	Slope (F_{st} vs. km)	Dispersal estimate using Kinlan & Gaines (2003) (km)	Slope ($F_{st}/1−F_{st}$) vs. km	Dispersal estimate using Rousset (1997) (km)	
				$D = 10$	$D = 10\,000$
Broadcast spawning					
Acanthochiton garnoti	0.0015	1.1	0.0015	9.17	0.09
Chrysoblephus laticeps	−0.00000057		−0.00000057		
Oxystele tigrina	−0.00112398		−0.00112398		
Oxystele variegata	0.1149	0.01	0.1149	1	0.01
Parechinus angulosus	0.0002	8.45	0.0004	17.5	0.18
Brooding					
Caffrogobius caffer	−0.00014381		−0.00014381		
Cyclograpsus punctatus	0.1279	0.01	0.1279	0.99	0.01
Tetraclita serrata	−0.00015781		−0.00015781		
Live-bearing					
Clinus cottoides	0.0003	5.8	0.0004	9.17	0.17
Clinus superciliosus	0.0686	0.02	0.0686	1.35	0.01
Muraenoclinus dorsalis	0.0002	8.44	0.0011	10.8	0.11

haplotype diversity values ranging from 0.84 to 1.00. Notably, genetic diversity and species richness show congruent patterns, with lowest species richness and genetic diversity on the west coast, which increases on the south coast and decreases slightly for both variables on the east coast (Fig. 2).

Results from AMOVA revealed diverse ranges in overall population genetic structure across different life histories (Table 1). Significant global Φ_{ST} characterized all three live-bearers in the study, of these *M. dorsalis* had the highest global Φ_{ST} ($\Phi_{ST} = 0.89$; $P < 0.001$), while *C. superciliosus* and *C. cottoides* revealed lower but comparatively still high and significant levels of structure ($\Phi_{ST} = 0.29$ and 0.26, respectively; $P < 0.001$). Pairwise Φ_{ST} estimates mirrored the range in global measures across the study (Appendix S3). Among the brooders, two of the three taxa sampled had a significant global Φ_{ST}. AMOVA revealed a lack of structure in *Caffrogobius caffer*, while the barnacle *T. serrata* had low but significant structure at $\Phi_{ST} = 0.07$ ($P < 0.001$) and the highshore crab *C. punctatus* had the second highest degree of genetic structuring of all species ($\Phi_{ST} = 0.49$; $P < 0.001$). Perhaps the most interesting outcome from this analysis is our finding that four of the five broadcast spawners support a significant global Φ_{ST}; the red roman *C. laticeps* was the only broadcast spawner (and non-rocky shore species) for which our analysis did not support significant genetic structure,

revealing minimal differences between its two most geographically distant sample locations *c.* 1000 km apart (Appendix S3). The molluscs *Oxystele tigrina* and *A. garnoti* displayed low but globally significant levels of population structure (both species $\Phi_{ST} = 0.07$; $P < 0.001$), while *O. variegata* (a close relative of *O. tigrina*) and the urchin *P. angulosus* revealed considerably higher levels of structure at $\Phi_{ST} = 0.34$ and 0.41 ($P < 0.001$), respectively.

Population structure as a function of IBD and estimates of mean dispersal distance

As expected given the results of the AMOVA and pairwise Φ_{ST} analysis, all three live-bearers revealed a significant fit to the model (Table 2, Fig. 3). Only one brooding species, the crab *C. punctatus*, showed a significant IBD slope, and despite a significant global Φ_{ST} the distribution of genetic variation in another brooding species, *T. serrata* does not appear to be the result of IBD. Notably, of the four broadcast spawners with significant global Φ_{ST} values, three of these revealed significant fit to the IBD model, *O. variegata*, *P. angulosus* and *A. garnoti*, with slopes of similar magnitude as for live-bearing species (Table 2, Fig. 3).

Given the generally steep IBD slopes for all species, estimates of average dispersal were very low (Fig. 3, Table 2),
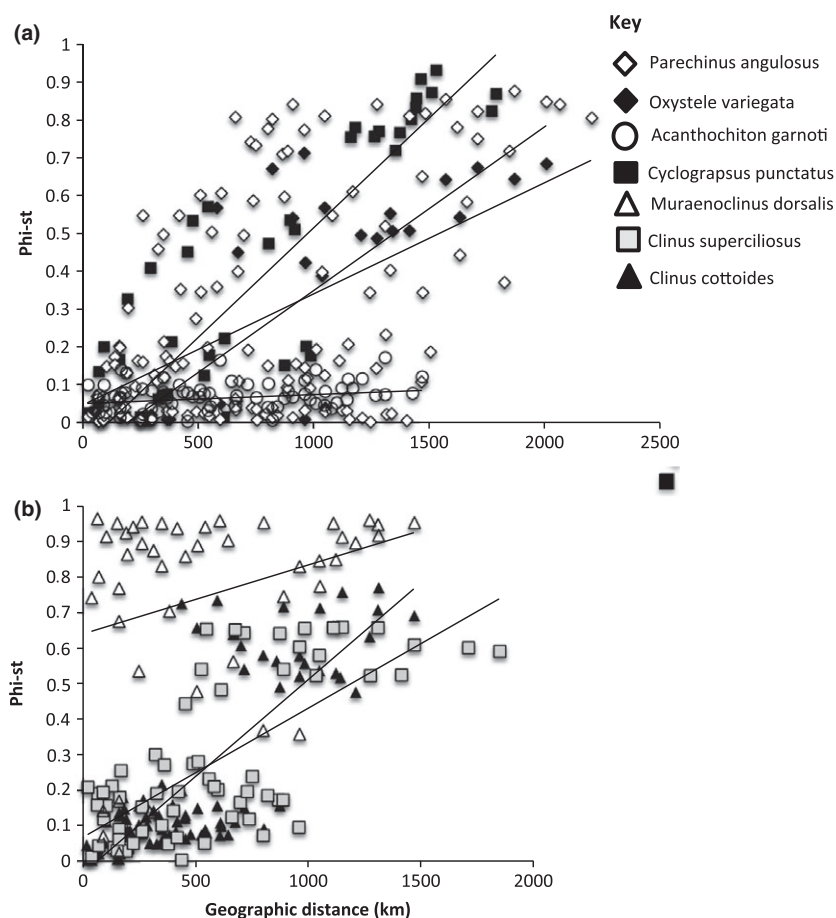

Figure 3 Isolation by distance plots of pairwise population values for geographic distance and genetic distance. (a) Plots for broadcast spawning and brooding species, (b) plots for live-bearing species. Only species for which slopes were positive and significant are shown, refer to Table 2 for species with negative slopes.

with the highest dispersal estimates for *P. angulosus* of *c.* 17 km. All other estimates were below 10 km, with some species having effective dispersal of < 1 km (Table 2).

DISCUSSION

Seven of the 11 species used in our study analyses revealed a significant fit with IBD at the scale of the whole sample range. A recent meta-analysis on 240 studies showed that a positive IBD slope can be affected by the number of populations included in the study, where the higher the number of populations included, the greater the probability of retrieving a signal of IBD (Jenkins *et al.*, 2010). The numbers of populations included in our study ranged from 6 to 20 (mean = 12; Table 1), with nine of 11 studies including 10 or more sampling sites. As species with similar population numbers showed both positive and negative slopes, we can assume that the signal of IBD for seven of the species included in this study is biologically meaningful. Further, positive IBD slopes are influenced by the presence of genetically structured populations (Meirmans, 2012). This can be problematic in overinflating signals of IBD and can be overcome by testing for IBD within subgroups that are shown to be genetically differentiated. When substructure was taken into account for our data, only the *C. cottoides* and *P. angulosus* subgroups retained a weak signal of IBD, but this may well be confounded by low statistical power resulting from a low number of populations of < 4 per subgroup for other species (Jenkins *et al.*, 2010). Notably, in *T. serrata* and *O. tigrina*, we did not recover a positive IBD slope despite significant structure in the data set, which lends support that the signals of IBD recovered for other species are true.

Genetic structure, diversity and species richness along 2800 km of South African coastline

Our findings support an emerging trend in marine phylogeographic studies that reveal life history traits to be poor predictors of both dispersal (Ayre *et al.*, 2009; Shanks, 2009; Weersing & Toonen, 2009; Riginos *et al.*, 2011; Selkoe & Toonen, 2011) and population genetic structure (Kelly & Palumbi, 2010; Selkoe *et al.*, 2014). Our data reveal unexpectedly that broadcast spawners, for example the urchin *P. angulosus* and mollusc *O. variegata*, have similar levels of population differentiation as live-bearers, the clinid fishes *C. superciliosus* and *C. cottoides*. Our study also reveals the unexpected degree of heterogeneity in genetic structure along the South African coastline, as observed in the contrasting patterns of two closely related topshells *O. variegata* and *O. tigrina*. These two species share similar reproductive strategies and habitat requirements with largely sympatric distributions and yet are characterized by strikingly different levels of genetic structure, providing a solid challenge to the hypothesis that life history can be used as a general predictor of dispersal and population connectivity in the marine environment.

These findings extend to pelagic larval duration (PLD), which has been the focus of much research seeking to explain population connectivity in marine environments (see Weersing & Toonen, 2009; Selkoe & Toonen, 2011 and examples therein). The prevailing expectation is that species with longer larval durations have greater dispersal potential than species with short PLD or those that lack a larval stage (Kinlan & Gaines, 2003), yet several recent meta-analyses suggest poor relationships between PLD and genetic structure; indeed, this relationship is tenuous at best as on removal of direct developers from the analyses where PLD no longer explains the observed variance in dispersal patterns (Weersing & Toonen, 2009; Kelly & Palumbi, 2010; Riginos *et al.*, 2011). Although PLD is generally poorly understood for most taxa with a free-living larval stage, results of this study and others (Kelly & Palumbi, 2010; Selkoe & Toonen, 2011; Weersing & Toonen, 2009), generally, suggest that while life history is a poor predictor for brooders and spawners, it is a strong predictor of genetic structure in live-bearing species. In species where PLD and dispersal are poorly correlated, other ecological processes are clearly driving the observed patterns. Factors such as ecological transitions across biogeographic regions as well as egg type are known to contribute to population genetic structuring (Riginos *et al.*, 2011), yet in a study taking into account species traits, no particular variable explained patterns of F_{st} or IBD (Selkoe *et al.*, 2014). With this in mind, it is likely that other life history traits not considered in this study, such as spawning time and frequency, egg size or larval type, behaviour and larval and adult physiology, may be better descriptors of population structure.

Although evidence is accumulating for numerous species that show some degree of population genetic structuring in South Africa (Teske *et al.*, 2011a), the processes leading to genetic structuring along coastline remain poorly understood (but see e.g. Teske *et al.*, 2011b; Toms *et al.*, 2014). Disentangling the relative effects of factors driving and maintaining genetically structured populations (such as biogeographic barriers, ocean currents, palaeo-climatic events) remains a challenge in marine ecology globally and importantly for the context of this and similar studies examining genetic approaches as tools for management, generalizing based on any one factor risks misinforming regional conservation priorities.

A second exciting finding of this study is the congruent patterns between genetic diversity and species richness. Figure 2 clearly shows the west coast as having the lowest diversity in genetic variation and species richness, the latter which is well studied (Awad *et al.*, 2002), with an increase in genetic diversity and species richness towards the east coast. Despite efforts to understand congruence in patterns of genetic and species diversity in marine systems, there remains a paucity of evidence and this hinders even preliminary attempts at integrating genetic data into biodiversity planning (Beger *et al.*, 2014). However, when such data are included, they can change conservation priorities significantly (Mouillot *et al.*, 2011). In a study on genetic and fish species

diversity in the Pacific Ocean, which also saw significant correlates between the two variables, Messmer *et al.* (2012) highlight the importance of diversity signals at the edges of geographic distributions. They discuss that more isolated populations at the limits of species ranges experience reduced immigration, which in turn can reduce genetic and species diversity. This can be particularly pronounced in populations which undergo fluctuations in population sizes, which influences population bottlenecks and even extinctions. In South Africa, reduced gene flow occurs around Cape Point, a biogeographic barrier which separates the west from the southwest coast, for some species (von der Heyden *et al.*, 2008; Muller *et al.*, 2012; Reynolds *et al.*, 2014). This may well be a factor in separating populations on either side of Cape Point and contribute to reduced levels of genetic diversity for some species. Whatever the mechanisms driving the patterns of species and genetic diversity, our results do highlight that different regions of the South African coastline have distinct signals of genetic diversity, which require separate management actions to maintain them.

IBD suggests limited dispersal distances in an oceanographically dynamic region

Isolation by distance and the distribution of genetic variation across landscapes is seen as a useful tool for initial investigations into population connectivity and as a proxy for conservation planning (Durrant *et al.*, 2013). Yet, signatures of IBD are far from common in studies of marine organisms and particularly so in species with pelagic larval stages. Our analyses reveal a significant fit to a model of IBD for seven of our study species, including species with and without pelagic larval stages. Estimates of the relationship between genetic and geographic distances were relatively high, suggesting that a range of species along South Africa's coastline experience dispersal over relatively short distances. Given that high pairwise and global Φ_{ST} values characterize numerous species in the region (Teske *et al.*, 2011a,b), dispersal estimates may actually be low for many more, as yet genetically uncharacterized species.

The steepness of the IBD slope scales inversely with dispersal distance and reveals relatively short generational dispersal estimates for our sample taxa, of < 10 km, with only one value, for *P. angulosus* larger than 10 km. These estimates reflect the small scales over which dispersal may occur in the marine environment and not only in South Africa; for three species of rockfish (*Sebastes* spp.), mean dispersal distances reported range between 2 and 13 km per generation (Buonaccorsi *et al.*, 2005). Similarly for the barred hamlet, *Hypoplectrus puella*, dispersal estimates were in the order of 2–14 km (Puebla *et al.*, 2009), while for the clown fish, *Amphiprion clarkia*, values of 4–27 km per generation were estimated (Pinsky *et al.*, 2010). Together with our results, these studies highlight the importance of considering population density when estimating dispersal distances from IBD slope relationships (Puebla *et al.*, 2009; Pinsky *et al.*, 2010). In the

absence of field-based density data, we estimated dispersal distances for a range of densities, and while we cannot be certain that these values are broad enough to reflect biological reality, we feel that given their rocky shore habitat requirements and relatively high abundances, it is highly unlikely that any of the sample species have adult densities lower than 10 per km, lending support to the low dispersal values estimated here. Densities, however, certainly vary along the coast and likely occur on a gradient as rocky shore habitat becomes increasingly limited from west to east. Here, per-generation dispersal distances are low enough that a change in population density is unlikely to significantly impact on the findings; nonetheless, the inclusion of observed density data would surely enhance the accuracy of future studies and allow for more nuanced conservation recommendations.

Implications for regional MPA design: genetic diversity, species richness and limited dispersal

Terrestrial and marine systems are under severe threat of anthropogenic drivers of global change, thereby increasing the need for targeted and effective conservation of biodiversity. However, conservation prioritization based on species richness alone fails to represent the evolutionary history of species, although it is accepted that evolutionary processes have shaped extant patterns of biodiversity. This indicates a need to include genetic measures to better represent the processes that generated biodiversity (Beger *et al.*, 2014). While successful dispersal clearly remains central to the development of effective biodiversity planning in the marine environment, our understanding of the processes maintaining or limiting gene flow remains poor for a large majority of marine species (Cowen *et al.*, 2006) and little consensus on how dispersal distances and population connectivity should in fact be estimated persists in this debate (Dawson & Jacobs, 2001; Palumbi, 2003; Weersing & Toonen, 2009; Selkoe & Toonen, 2011). Despite these challenges, it is clear that the extensive heterogeneity in dispersal ability among marine taxa should be sufficient evidence to prevent the use of highly generalized patterns in regional connectivity based on any one species or environmental factor (Weersing & Toonen, 2009; Kelly & Palumbi, 2010). In South Africa, MPAs are predominantly extensions of land-based reserves or were implemented to protect commercially important fish species (Attwood *et al.* 1997), which rarely include all biodiversity. Our results across a phylogenetically variable suite of rocky shore species show that dispersal is limited and that the one commercially exploited species, *C. laticeps*, has no genetically structured populations. Therefore, basing MPA networks predominantly on inshore fisheries, which could be characterized by similar patterns of little or no genetic structure, is clearly not representative of rocky shore marine biodiversity.

Given the degree of variation (topographic, oceanographic, species assemblages, evolutionary age and evolutionary history) among studies on coastal marine population genetic

structure, the application of findings from studies carried out elsewhere in the world clearly cannot reliably inform local prioritization efforts. While the dispersal models indicate short average dispersal distances in a typical generation, stochastic events (e.g. storms, wind, current reversals) could potentially result in instances of significantly greater realized dispersal. There is also evidence for local physiological adaptation between populations, which may play an important role in the spatial maintenance of unique genetic lineages (Teske *et al.*, 2008). So while exact distances required for the maintenance of local genetic diversity, including long periodic dispersal events, are outside the scope of this study, they should be the subject of future research.

However, the low average dispersal distances reported here echo the call from numerous recent studies arguing globally for increased networks of small, moderately spaced MPAs (Shanks *et al.*, 2003; McCook *et al.*, 2010; Coleman *et al.*, 2011; Eble *et al.*, 2011) as stepping stones to increase genetic connectivity among existing protected areas. The current MPA network in South Africa has average distances of 110 km between reserves, and even the geographically closest reserves (*c.* 20 km) may not be well connected for all taxa. This suggests that the South African MPA network is likely to be poorer at protecting evolutionary processes, than it currently is at maintaining fish numbers outside of protected areas. We thus strongly recommend a network of more closely spaced MPAs in the region. Given the rapidly changing marine environment and an uncertain future for many species, more closely spaced protected area may also provide more resilience to marine communities (Gerber *et al.* 2014).

The strength of the comparative approach used in this study is clear – we have summarized discordant patterns in population connectivity among multiple co-occurring species across a range of life histories in the marine environment, an approach that allows the identification of shared processes and patterns in relatively open marine environments (von der Heyden, 2009; Toonen *et al.*, 2011). Importantly, we show extremely low rates of dispersal irrespective of mode of reproduction, which implies inadequate protection of evolutionary patterns and processes, because according to our data, the current MPA network in South Africa is failing to capture the low rates of dispersal detected. Despite the ongoing theoretical challenges in quantifying the dispersal ecology of species, results from this study undoubtedly confirm that marine systems may be characterized by unexpectedly high levels of genetic structure, shaped in part by shorter dispersal potentials than classic ecological theory would suggest. Our results highlight the complex and dynamic nature of South Africa's marine environment, one that surely deserves innovative and pioneering conservation approaches for the protection and persistence of its rich biodiversity.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Methods for novel data sets (*A. garnoti* and *C. punctatus*).

Appendix S2 Sampling localities and sample sizes for each species.

Appendix S3 Pairwise Φst values for each species.

BIOSKETCH

This work was carried out by members and colleagues of the Evolutionary Genomics Group (http://academic.sun.ac.za/botzoo/egg/index.htm), of which a particular interest is the applicability of genetic tools to the conservation and sustainable utilization of African terrestrial and marine fauna and flora.

Author contributions: S.v.d.H. and J.B. conceived the study; S.v.d.H. and C.A.M. collected the data; D.W. analysed the data and wrote the first draft; J.B. and S.v.d.H. led the writing; C.A. and D.W. contributed towards the manuscript. This work formed part of the University of Cape Town's Conservation Biology MSc requirements for D.W.

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