Significant Population Structure and Little Connectivity in South African Rocky Shore Species: Implications for the Conservation of Regional Marine Biodiversity

DANIEL B. WRIGHT

Supervisors:
Dr Jacqueline Bishop
Department of Zoology, University of Cape Town

Dr Sophie von der Heyden
Department of Botany and Zoology, University of Stellenbosch

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Percy FitzPatrick Institute of African Ornithology,
University of Cape Town,
Rondebosch,
Cape Town
South Africa 7701,
e-mail: dan.wright@uct.ac.za

ABSTRACT

South Africa has 3650 km of coastline that spans the boundary between the Atlantic and Indo-Pacific biomes. The coastal waters boast a remarkable array of biological diversity and high levels of species abundance and endemism. Currently around 23% of the coastline is formally protected via marine protected areas (MPA) with 9% enforced as no-take zones. Even with this relatively high level of protection (as compared to other nations globally) the MPA network is still relatively sparse with protected areas that are on average ~110 km apart and unevenly distributed with the majority of MPAs situated along the species-rich east coast. This has led to concerns that the current MPA network is not protecting a representative sample of the genetic diversity among marine species nor is it sufficiently genetically connected via dispersal and gene flow to ensure their long-term persistence. To test a number of questions regarding the distribution of genetic diversity and degree of population genetic structuring along the South African coast we analyzed mitochondrial DNA sequence data for 10 sessile rocky-shore species and one reef-fish that represent three distinct life history strategies. We find that the distribution of genetic diversity across the South African coastline closely mirrors the distribution of species richness, increasing from west to east. We also find similar levels of population genetic structure among brooders, broadcast spawners and live-bearers, demonstrating that life histories are a poor predictor of genetic connectivity for South African marine species. Finally, we find that estimates of effective dispersal distance for taxa from each of the life history categories are low (~0.5-1.5 km per generation) suggesting that populations within MPAs are reliant on populations in unprotected areas via a stepping-stone model of genetic connectivity. In light of these findings, we discuss a number of recommendations to enhance the role of the existing South African MPA network and echo previous calls for the establishment of protected areas along the west coast.

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CHAPTER 1

Literature Review

Role of Molecular Ecology in Marine Conservation

An ongoing question facing marine geneticist is what role can conservation genetics play in marine conservation? Is the role simply to identify areas of high genetic diversity to complement (and to some degree, counter) traditional measures of species richness as a prioritization tool? Can conservation genetics test the potential link between genetic diversity, genetic connectivity, and the occurrence of inter-population genetic structure to offer insight into the processes that explain patterns in population dynamics? Does conservation genetics have a role in the design and implementation of conservation efforts (e.g. fisheries management, mining regulations, marine protected areas) and if so, to what degree?

In some parts of the world, researchers have begun to grapple with these questions and develop a number of methods and tools to address them. In particular, a number of recent studies have been conducted in the United States (Buonaccorsi et al. 2004, Duvernell et al. 2008, Johansson et al. 2008, Kelly & Palumbi 2010) and Australia (Miller & Ayre 2008, Curely & Gillings 2008, Coleman et al. 2011) exploring the extent to which genetic research can inform conservation action. With each additional study, patterns are emerging and the methods themselves are being refined (Weersing & Toonen 2009, Kelly & Palumbi 2010). The efforts are not without their challenges though, and given the general lack of expertise in translating findings from genetic research into on-the-ground solutions to the myriad of challenges in modern-day conservation biology, genetic criteria are rarely considered in conservation planning (von der Heyden 2009, Laikre et al. 2010). Regardless, an increasing number of studies are producing compelling results and it may be only a matter of time before the importance of genetic diversity in the marine environment is fully embraced and the role that conservation genetics has to play in its persistence is crystallized.

Conserving Genetic Diversity

Biodiversity has become a ubiquitous term in the field of conservation, and its preservation is often the stated goal of conservation action. It is, in many cases, defined simply as species richness or the number of species in a given area (Turpie et al. 2000, Awad et al. 2002). This definition largely ignores the individual components of biodiversity and in particular, overlooks genetic diversity and the evolutionary processes leading to biodiversity. If biodiversity is the variance between species, then genetic diversity should be thought of as the variance within a species (Salm et al. 2000).

There are a multitude of reasons to concern oneself with the protection of genetic diversity. Most fundamentally, genetic diversity has been correlated with species fitness (Reed & Frankham 2003, Beebee & Rowe 2008). Genetic diversity underpins adaptability to environmental change over ecological time scales and individuals with high genetic diversity have been shown to have higher survival rates and reproductive success than genetically depauperate individuals (Reusch & Hughes 2006). Genetic diversity is equally important at the community level. Individuals aggregate to form populations and interact with other species to form functioning ecosystems. High genetic diversity helps maintain the natural variety and integrity of functioning ecosystems and all of the economic and sociological benefits that come from them (Allendorf & Luikart 2007).

Genetic diversity and adaptability is not only important across ecological time scales, but over evolutionary time scales as well. It can be thought of as the raw material for the maintenance of a species over time, the raw material for the emergence of new species, and a measure of a species ability to respond to environmental change (Bell & Okamura 2005). As selection favors some traits over others, populations will diverge enough to constitute distinct species, and in doing so, add to the species richness component of biodiversity. Even if the degree of change is not sufficient to constitute a new species, it can still contribute to the persistence of the species (Rocha et al 2007), which is the ultimate goal of any conservation plan.

The preservation of genetic diversity is of particular importance in marine ecosystems. Unlike terrestrial systems, instances of endemism (when a species range is confined to a relatively small geographic area) are comparatively rare (Salm et al. 2000). As a result, examples of species extinction in the marine environment are relatively few when compared to land (Powles et al. 2000). Human activities such as fishing, mining, and all sources of pollution have however led to the eradication of some populations (Norse 1993), and ergo, the unique genetic diversity therein. This loss of genetic diversity leaves the remaining populations more susceptible to the accumulation of deleterious gene mutations and stochastic demographic changes (Lynch et al 1995, Reed & Frankham 2003). It can be argued then that genetic impoverishment is in fact a greater threat to the persistence of marine species than global extinction, and should be of the high concern for conservation (Salm et al. 2000).

Genetic Research Methods

Though clearly an important component of biodiversity and conservation efforts, measures of genetic diversity have generally played a lesser role in conservation planning than the research outputs from phylogenetic systematics and community ecology. Phylogenetic systematics has traditionally borne the burden of informing our understanding of priority areas using the primary tools of endemism, abundance, and morphological diversity. There has, however, been a recent surge in techniques for genetic research allowing conservationist to identify areas of high genetic endemism, evolutionary significant units (ESU) (Moritz 1994, Teske et al. 2009b), and cryptic species (Dawson & Jacobs 2001, Amato et al. 2007, von der Heyden 2009) amongst other applications. Data from such techniques assist for example in the identification of barriers to gene flow and thereby shed light on the processes that underpin species distribution (Teske et al. 2011a).

There are several ecologically important attributes which traditional phylogenetic systematics is not equipped to elucidate that population genetic and phylogeographic studies now can. The identification of genetically distinct units is one such case (Moritz 2002). Panmixia (or the even distribution of alleles across a species entire range) is extremely rare, even in marine environments, which are thought to have fewer barriers to dispersal (Caley et al. 1996, Neethling et al. 2008). Consequently there are some populations which will harbor a collection of alleles that is unique to the species either as a result of adaptation or long term isolation. Each such population constitutes a genetic unit and arguably warrants protection as its own management unit (Moritz 2002, von der Heyden 2009).

Genetic research is also able to assist in the identification of cryptic species, or species that are morphologically identical, but genetically differentiated from each other (Knowlton 2000). Historically, species identification has been almost exclusively based on morphology (Rocha et al. 2007), but it is possible for a population to diverge genetically enough from other populations to warrant being categorized as a new species without developing a distinguishable morphological trait. The reverse situation is possible too, where populations exhibit morphological variation and are considered unique taxonomic units, but are genetically homogenous (Rocha et al. 2007). In both cases, a traditional systematics approach to prioritization would likely mislead and thereby fail in identifying the areas richest in biodiversity.

Possibly the most powerful information that is now available through genetic studies is insight into the process of dispersal and migration together with the resulting patterns of genetic connectivity between populations and within species. These processes underpin the distributional pattern across a species range (von der Heyden 2009) and an understanding of the movement of genes between populations is a powerful tool in the identification of priority areas for conservation (Palumbi 2003, Roberts et al. 2003, Coleman et al. 2011). Prior to the development of genetic studies, connectivity data had been limited to direct observation and mark-recapture studies, which are riddled with logistical challenges, especially in the marine environment.

Because of the vastness of area in the world's oceans, mark-recapture rates are extremely low among marine species, particularly for highly mobile species (Shanks 2009). The use of tracking devices and human made tags is also difficult and expensive as they have to be able to withstand the high pressures and corrosive environment of the sea. Adding to this complexity is that most coastal marine species are largely sessile as adults and disperse during their larval period (Cowen et al. 2006, Sale 2004) where it is technically difficult to track them. There is a fundamental lack of ability to taxonomically identify species in their larval state, and the difficulty of identification is compounded by the sheer number of larvae that can be collected in one field sample (Grantham et al. 2003). The diminutive size of marine larvae make it virtually impossible to use traditional tagging methods (Eble et al. 2011) and leaves only chemical tags as means to track the movement of an individual from birth to recruitment. Even if the migration and recruitment of larvae is observed, there is no method for determining if the individual has successfully bred, thereby genetically connecting geographically disparate populations (Shanks 2009).

Faced with the multiple challenges of direct observation, researchers have turned to the use of surrogates to try and determine migration patterns and connectivity between populations. Surrogates offer many advantages over direct observation methods, and as the chemical identifier that all creatures carry with them naturally, DNA has become the preferred surrogate for connectivity studies (Shanks 2009). The use of genetic markers has largely eliminated the issues of taxonomic identification, even in the difficult larval stage (von der Heyden et al. 2007). Another key advantage of genetic research over direct observation is that it focuses on the collective effect of migrants that have successfully reproduced and contributed to the process of gene-flow between populations (Slatkin 1987, Hellberg et al. 2002). Scale is a particularly important component of connectivity research though. If the scale of the study does not match the scale at which a species displays variability, the results can overestimate dispersal and potentially misinform conservation priorities (Bohonak 1999).

A well established genetic measurement of population structuring and connectivity amongst and between populations is that of Wright's F-statistics (Wright 1965). F-statistics are a method of measuring levels of inbreeding (F_{IS}) or conversely the level of genetic differentiation (F_{ST}) at different hierarchies. Initially F-statistics were measured in terms of deviation from Hardy-Weinberg equilibrium, which estimates an expected heterozygosity within and across populations (Grosberg & Cunningham 2001). Any population that has a lower observed level of heterozygosity than that expected under the Hardy-Weinberg model is considered to be isolated to a degree from other populations. A number of analogues of F_{ST} have been developed over the years, including G_{ST} (Nei 1973, 1978), R_{ST} (Slatkin 1993) and N_{ST} (Lynch & Crease 1990). Most recently Jost (2008) proposed quantifying genetic diversity using the effective number of alleles rather than heterozygosity, resulting in the measure D_{ST}. Ryman and Leimar (2009) claim that Jost's D has the same, or even more pronounced dependencies on average within population heterozygosity, making it no more accurate than G_{ST}. All versions of F-statistics are now collectively referred to as measures of genetic distance and, when viewed in a pairwise configuration, allow researchers to identify genetic barriers that may not be obvious visually (as is often the case in marine systems) and to understand the scale at which species experience genetic differentiation (Grosberg & Cunningham 2001).

The primary advantage of measures of genetic diversity is that they reduce a lot of the complexity inherent in studies of connectivity and allow a common measure by which to compare multiple species and life histories (Gillespie 1998). They are not however without their criticisms. There are several assumptions underlying F stats and other measures of genetic distance and these are often cited as weaknesses to the approach. A basic assumption is that the sub-populations are approximately the same size and have similar levels of variance in allelic frequencies (Whitlock & McCauley 1999). Similarly, it is assumed that populations have reached equilibrium between migration and drift (Felsenstein 1982). Allelic frequency and genetic equilibrium can both be influenced by historic events, such as the last glacial maxima (Grosberg & Cunningham 2001) or recent colonization events (Eble et al. 2011) and can effectively mask recent patterns of gene flow (Rousset 1997). It therefore requires careful interpretation to distinguish between genetic variance that is occurring on an ecological time scale (e.g. oceanographic barriers to dispersal) versus variance as the legacy of events occurring on an evolutionary scale (Grosberg & Cunningham 2001). It is important to note, however, that the use of multiple markers (mtDNA and nDNA) (Rocha et al. 2007) or the use of a single marker across several taxa (Vandergast et al. 2008) can help differentiate between these scales. One has to consider the danger in potentially under-interpreting a genetic signal when using just the maternal lineage (mtDNA) especially in species that display sex-biased dispersal. Barrowclough and Zink (2009) have however argued that mtDNA is sufficient for identifying population structure and that given the lower cost of sequencing and the breadth of available analytical tools, that mtDNA is currently a superior marker than nuclear DNA microsatellites.

An even more recent addition to the arsenal of tools to measure population genetic structure is isolation-by-distance (IBD) (Slatkin 1993, Bohonak 2002). IBD is a model built on the principle that if the dispersal potential of a species' propagules is shorter than the species range, then even at equilibrium, drift will lead to genetic divergence between sub-populations (Slatkin 1993, Rousset 1997, Grosberg & Cunningham 2001). This suggests that species with limited dispersal capabilities should show a stronger IBD signal over shorter distances than species with high dispersal potential (Ayre & Dufry 1994). Isolation-by-distance requires a measurement of genetic distance (F-statistic or analogue such as Φ_{ST}) and an independently calculated measure of geographic distance between the sampling locations. A Mantel test (Mantel 1967, Legendre & Fortin 2010) is then used to determine if there is a statistically significant autocorrelation (or covariance) between the two matrices and a reduced major axis (RMA) regression is used to determine the slope of the relationship (Bohonak 2002). IBD adds a valuable complement to F stats as it explicitly considers geographic distance making it possible to see if geographically distant populations are also genetically distinct (Bohonak 2002) and to test areas identified as genetic breaks between populations (areas of high genetic variation and short geographic distance). IBD has also been shown to help establish if populations are at equilibrium between migration and drift (a concern for studies using F-statistic alone) as an isolation-by-distance signal should not be possible unless the population is approaching equilibrium (Hutchinson & Templeton 1999, Eble et al. 2011).

Because IBD uses F-statistics as its measure of genetic distance, it is subject to the same criticisms. It has however been shown to match observed data (Shanks 2009) and has become an increasingly common and trusted method of research in recent years (for examples see Bollmer et al. 2007, Zickovich & Bohonak 2007, Addison et al. 2008). More recent statistical developments include use of the slope from IBD together with information on species density to calculate dispersal distances (Palumbi 2003, Buonaccorsi et al. 2004, Pinsky et al. 2010) thereby providing a more exact measure of connectivity between sub-populations. Quantifying the realized dispersal distance for species will augment the number of studies that can be compared to observed data and will allow for the further refinement of genetic techniques to accurately measure average dispersal ability.

Marine Protected Area Design

Genetic studies have gone a long way in helping identify populations with high genetic diversity and to understanding the processes of connectivity that explain their existence, distribution, and persistence, but a mechanism is still required to protect these populations. Genetic diversity can be protected in an *ex situ* manner for some species (such as seed banks for plant species) but this is impractical for many fauna, and especially so for marine species. Genetic diversity in the sea requires habitat protection and this is best accomplished by *in situ* protection, in the form of marine protected areas (MPA) (Salm et al. 2000).

There are a lot of variables to consider when designing an MPA, the most basic of which are how big should they be, and how many? Similar to the SLOSS (single large or several small) debate for terrestrial reserves (Burkey 1989), there are questions about the most effective design for MPAs (Hastings & Botsford 2003). The question of dispersal capability is central to this debate (Palumbi 2003). In order for a marine reserve to be self-seeding, it needs to be sufficiently large to capture most of the resident species' propagules (Lockwood et al. 2002, Hastings & Botsford 2003), but for species with high dispersal potential, this is impractically large (Botsford et al. 2003, Gaines et al. 2010). For species that are able to disperse longer distances (10 to 100s of kilometer) it has been suggested that a network of MPAs is a more practical design (Palumbi 2003, Avasthi et al. 2005, Fernandes et al. 2005, Eble et al. 2011, McCook et al. 2010, Coleman et al. 2011). A network of smaller reserves may be easier to establish along heavily populated areas than one large reserve. A moderately spaced (10 to 100 km) network of small reserves may provide an aggregate (synergistic) benefit over a single reserve through increased connectivity and may even benefit commercial fishing along with conservation efforts (Gaines et al. 2010).

Another basic question is where should MPAs be located? MPAs are commonly placed in areas of high species richness (such as coral reefs), areas with rare or unique habitat (such as mangroves), or areas that are productive for commercially valuable species, especially fishes (Teske et al. 2011a). The majority of MPAs tend to include a section of shoreline and only extend a relatively short distance into open water (10s of kilometers) and there are a number of reasons for this. One is that MPAs often coincide with terrestrial reserves and serve to extend their boundaries into the sea (Turpie et al. 2000), but there are biologically practical reasons as well. Much of the ocean's natural biodiversity occurs in the marine portion of the coastal zone (Ray & Grassle 1991) and as such, should be targeted for protection. Similarly, many of the sessile, benthic species require near-shore habitats. Sessile species tend to benefit most from MPAs as they are unlikely to move out of the protected area during their lifetime. Highly mobile species are more likely to benefit from other forms of protection, such as limitations on fishing effort (Shanks 2009).

There is also a basic question of level of protection that should be enforced in MPA design. There are examples of MPAs across the entire range of possibilities from very few restrictions (typically restricting commercial activities such as mining and large-scale fisheries), to absolute no-take regulations, which prevent recreational use as well (Lubchenco et al. 2003). Decisions about the level of protection as well as the size, location and spacing are based on the intent for which the MPA was designed. However, as more is understood about the complexity of the marine environment, it is becoming clear that MPAs cannot be set up in isolation, but need to be part of a network with overarching conservation goals (Hastings & Botsford 2003).

There has been some recent acknowledgement that connectivity between protected areas needs to be a consideration in MPA design (Jones 2002, Palumbi 2003, Almany et al. 2007, 2009, Kelly & Palumbi 2010). The International Union for the Conservation of Nature (IUCN) has defined an individual MPA as “a clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values’ (Tunley 2009). They do however recognize that it is important for an individual MPA to be part of a greater network and defined a “network of marine reserves” as "a set of marine reserves within a biogeographic region, connected by larval dispersal and juvenile or adult migration." (IUCN 1994, NRC 2000a). In addition to the IUCN, several studies have noted the importance of connectivity to achieving MPA goals whether they be for the protection of biodiversity, the enhancement of fisheries, or both (Gaines et al. 2003, Gerber et al. 2003, Largier 2003, Hellberg et al. 2002).

Conservation genetic research approaches have a lot to offer in the way of testing hypotheses about the location and spacing of MPAs to best protect the full range of biodiversity (species and genetic diversity). The common finding in the literature is that marine systems are much more closed than previously thought (Cowen et al. 2006, Levin 2006). Whether it is hydrodynamics, life-histories, pelagic larval duration, larval behavior or fragmentation of habitat, there are clearly barriers to dispersal in marine environments. The high level of heterogeneity in dispersal abilities and seascapes has complicated the identification of a reliable proxy for connectivity (Kelly & Palumbi 2010). The best approach is for researchers to make conservation recommendations based on studies of an array of species in the specific region to be protected. This offers that best chance for the persistence of healthy, functioning, sustainable marine ecosystems.

CHAPTER 2

Genetic Diversity, Genetic Structure, and Dispersal for South African Marine Taxa

INTRODUCTION

There is broad consensus among molecular ecologists and conservation biologists that understanding gene-flow within and between populations (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 conservation strategies such as gazette terrestrial protected area networks and marine protected areas (MPA). 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 help identify the processes that have led to contemporary species distributions (Slatkin 1987, Grosberg & Cunningham 2001, von der Heyden 2009). There is an inherent temporal disjunction between ecological estimates of connectivity (migration) and genetic connectivity (gene flow). Measures of observed migration can overestimate genetic connectivity as not all migrants successfully reproduce (Lowe & Allendorf 2010). Similarly, measures of genetic connectivity can underestimate migration rates since alleles must repeatedly be introduced into a population over generations for the signal to be detectable using molecular analysis (Bohonak 1999). Because distribution patterns are the result of a complex mix of evolutionary events (e.g. glacial maxima, Benguela upwhelling) and ecological phenomena (geographic barriers, life-history traits, demographic stochasticity) (Rousset 1997, Grosberg & Cunningham 2001, Eble et al. 2011), unraveling the local driving forces in a region is critical for effective conservation management decision making and implementation.

Identifying patterns of gene-flow is of particular importance for marine environments where hydrodynamic regimes can fluctuate dramatically and there is an increasing reliance on marine protected areas for the conservation of economically important resources (Kelly & Palumbi 2010). The presence of rapid ocean currents, capable of carrying larvae long distances and few visible barriers to dispersal initially led many to believe that marine systems were largely open (Caley et al. 1996). There is now, however, a growing awareness that marine species are far more structured than previously believed (Cowen et al. 2006, Levin 2006). For example, estimates of average dispersal for marine species between 10 and 100 km are common (Palumbi 2004) and this has led to a paradigm shift in MPA management from large, stand alone MPAs to smaller connected networks of MPAs (Hastings & Botsford 2003, Largier 2003, Kelly & Palumbi 2010).

The shift to management of marine resources via a network approach has further emphasized the importance of reliable connectivity measures and researchers have searched for a proxy that could apply to a large range of taxa. The focus of these efforts has been predominantly directed towards identifying biogeographic barriers and understanding the role of life-histories (particularly larval duration) in determining the extent to which marine taxa exhibit spatial genetic structuring (Weersing & Toonen 2009). Nonetheless, biogeographic barriers have proven a poor proxy as this approach assumes that multiple taxa will react similarly to the same geographical features, but this has rarely been shown to be the case (Kelly & Palumbi 2010). Many marine species (particularly coastal rocky shore species) are sessile as adults and disperse primarily during their larval stage (Sale 2004, Cowen et al. 2006). One prediction regarding the role of life histories in determining the extent of population structuring in marine organisms has been that the longer the larval duration, the greater the potential for dispersal (Kinlan & Gaines 2003). A number of studies have however shown that even long larval durations can lead to spatially limited dispersal (Miller & Ayre 2008, Ayre et al. 2009) and that the use of life-history only works as an effective predictor of dispersal distance for species without a larval phase i.e. brooders or viviparous species (Kelly & Palumbi 2010).

With a fair amount of the variation in realized dispersal unexplained by life history and biogeographic barriers to dispersal, there continues to be a need for geographically explicit studies that identify patterns in dispersal across multiple taxa with shared habitat. A number of recent studies have attempted to dissect patterns of dispersal and population structure along the coast of South Africa, most notably von der Heyden et al. (2007, 2008, 2010) and Teske et al. (2003, 2006, 2009a, 2011b). There are however many more studies on abundance and species richness in the region with a bias towards commercially valuable fish species (see Turpie et al. 2000). This bias has led to a local marine protected network designed to protect target species or areas of highest species richness measured as the number of species present per 100 km of coastline (Fig. 2). The result is a network that is heavily skewed toward protecting the species rich east coast (Griffiths et al. 2010) with no protection for the west coast (Attwood et al. 1997), where species are less abundant. At present, considerations for genetic connectivity are completely absent from the design process, largely due to a lack of available data describing patterns in genetic structure for the region (von der Heyden 2009, Laikre et al. 2010). A gap persists in the scientific community's understanding of population genetic patters for a broad set of species along the dynamic coastline of South Africa, leaving an opportunity for research across a mosaic of taxa and environmental gradients.

A detailed understanding of the processes that are driving patterns of population genetic structure of a region is a vital component to the design of a marine reserve network that can effectively protect the full range of marine biodiversity (species and genetic diversity) (Salm et al. 2000). Patterns of genetic structure and dispersal can vary significantly between species even in a shared habitat, so analysis of a single species or life history strategy has limited power to inform conservation design and management.

To address the limitations of population inferences from single species, we analyze mtDNA sequence data for 10 rocky shore species and one reef-fish species that are representative of all the life history strategies found within marine coastal communities in South Africa. By analyzing multiple species and life history strategies we are able to explore how a range of taxa are genetically structured along the coast of South Africa. We use a measure of haplotype diversity at each sample location to test whether or not genetic diversity and species diversity overlap and explore explanations for the observed relationship. We then assess whether or not life history can be used as a reliable predictor of genetic connectivity by testing patterns of population genetic differentiation against a model of isolation-by-distance. Finally, to address whether or not the current MPA network in South Africa is sufficiently connected to protect extant genetic diversity, we estimate an average dispersal distance per generation for representative taxa from each life history category. The ultimate goal of this study is to use the observed patterns in our data to better understand how to most effectively conserve South Africa's coastal marine biodiversity.

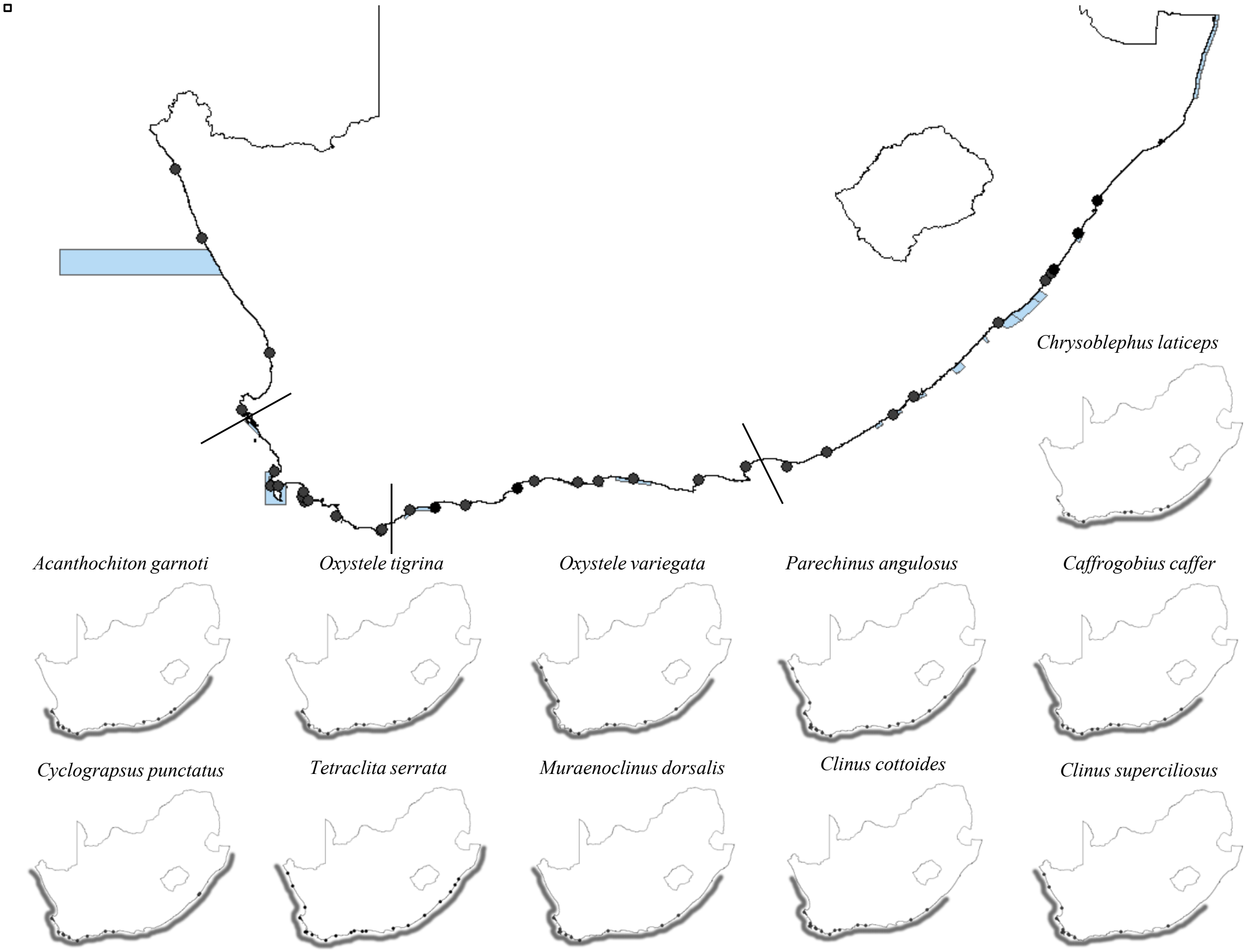

Figure 1. Map of South African with the full range of sample locations for all species represented. Lines indicate observed genetic breaks among study taxa (from west to east Jacobsbaai, Cape Agulhas, Port Elizabeth). Marine protected areas are represented in blue, including the proposed Namaqualand MPA (top left). Smaller maps indicate sample locations for individual species and species range in grey (modified from Branch et al. 1994)

METHODS

Data collection

DNA sequence data on 11 intertidal marine species were provided by von der Heyden and Teske from published and unpublished works (including von der Heyden 2008, Teske et al 2009a). Taxa were chosen to represent a range of life histories and were predominantly sessile species that included five broadcast spawners, three brooders and three live bearers (Table 1). *Chrysoblephus laticeps* was the only vagile and commercially exploited fish species included in the study. Data were collected across 34 sample locations spanning more than 2400km between Port Nolloth and Umhlanga Rocks (Fig. 1).

Genetic analysis

In order to make comparisons and validate patterns of diversity across multiple taxa and life histories, we used mtDNA sequence data for all 11 species. Data files were compiled into populations by sample location using DNASP (Librado & Rozas 2009) and exported for analysis into Arlequin v.3.5 (Excoffier & Lischer 2010) file format. Standard measures of diversity (haplotype (*h*) and nucleotide (π)) were calculated in Arlequin v.3.5 to identify areas of high genetic diversity across each of the species. An analysis of molecular variance (AMOVA) and pairwise Φ_{ST} (an analogue of F_{ST} that uses (*h*) to estimate genetic distance) was generated to explore the extent of genetic structuring within and between sampling locations.

Geographic distance between sample locations was calculated using an atlas provided by C. Attwood detailing the South African coastline at 10m intervals. Natural features (rivers and bays) and man-made features (towns) were listed at their location along the coast. Each sample location was identified in the atlas, and the distance between each site calculated. Due to the difficulty of assessing how micro-organisms experience a three dimensional marine environment and the lack of studies quantifying the impact of currents on geographic distance, a simple measure was selected as the best option.

To analyze the relationship between genetic isolation and geographic distance an isolation-by-distance analysis was performed in the program IBD Web Services (Bohonak 2002, Jensen et al. 2005; available online at http://ibdws.sdsu.edu/~ibdws/). For each data a Mantel test (Mantel 1967) was used to assess the significance of the relationship between genetic distance and geographic distance between all sample locations. The slope and intercept of the relationship was calculated using a reduced major axis regression (RMA). Genetic distance between sampling sites was estimated using Φ_{ST} with 10,000 simulations. The pairwise Φ_{ST} table produced by IBDWS was compared to the output of Arlequin v.3.5 to check for consistency. For each species file the analysis was performed using both the full data set together and with data subdivided as closely as possible given the study sample locations into the representative marine biogeographic regions of South Africa described in Griffiths et al. (2010) (i.e. Namibia border to Jacobs Bay, Mouille Point to Cape Agulhas, Cape Infanta to Port Elizabeth, and Port Alfred to Mozambique border).

To compare estimates of genetic diversity for the 11 taxa with published estimates of species diversity the South African coastline was divided into 400km sections and a mean haplotype and nucleotide diversity calculated across all species for every sample location that fell within each 400km section.

Estimating Dispersal

Mean dispersal distance was calculated using the methods developed by Buonaccorsi et al. (2004). The variance of parental position relative to offspring position (σ^2) can be calculated using the following formula.

$$\sigma^2 = \frac{1}{4D\mathcal{M}}$$

where D is the effective population density per km and $\mathcal{M}$ is the slope of the relationship between geographic distance and genetic distance per 1000km. This formula assumes a linear habitat which is defined by Rousset (1997) as a habitat where the scale of genetic differentiation is longer than the width. This is appropriate for our data as the sample range is thousands of kilometers long, but habitat for coastal species is limited to hundreds of meters wide.

Once σ^2 is calculated, the individual mean dispersal distance (α) can then be calculated using the relationship.

$$\alpha = \sqrt{\frac{\sigma^2}{2}}$$

Following Buonaccorsi et al. (2004) mean dispersal distance per generation was calculated using a range of effective densities from 10 to 10000 for one or more representative taxon from each of the life history groupings (*Parechinus angulosus* and *Oxystele variogata* for broadcast-spawners, *Cyclograpsus punctatus* for brooders and *Clinus cottoides* for live-bearers) (Table 2).

Table 1. List of study taxa with measures of haplotype (h) and nucleotide (π) diversity and results from AMOVA and IBD analysis. Percent of haplotypes unique to one sample location for each species reported as unique h. Dashes are indicated for species that do not fit the IBD model.

						AMOVA		**IBD**			
Life-history	**Common Name**	**Scientific Name**	h	π	**unique** h	**overall** Φ**ST**	**p**	**slope**	**r**	**r sq**	**p**
Broadcast Spawner	Spiny Chiton	*Acanthochiton garnoti*	0.95	0.042	84	0.07	< 0.001	0.10	0.23	0.05	0.04
	Tiger Topshell	*Oxystele tigrina*	0.93	0.054	76	0.07	< 0.001	-	-	-	-
	Variegated Topshell	*Oxystele variegata*	0.68	0.032	82	0.34	< 0.001	0.55	0.79	0.63	< 0.001
	Cape Urchin	*Parechinus angulosus*	0.91	0.022	84	0.41	< 0.001	0.55	0.53	0.28	< 0.001
	Red Roman	*Chrysoblephus laticeps*	0.98	0.054	86	0.01	0.09	-	-	-	-
Brooder	Banded Goby	*Caffrogobius caffer*	0.96	0.009	51	-0.01	0.90	-	-	-	-
	Highshore Crab	*Cyclograpsus punctatus*	0.73	0.009	80	0.49	< 0.001	0.65	0.89	0.79	< 0.001
	Volcano Barnacle	*Tetraclita serrata*	0.98	0.041	80	0.07	< 0.001	-	-	-	-
Live-bearer	Super klipfish	*Clinus superciliosus*	0.92	0.011	77	0.29	< 0.001	0.52	0.70	0.49	< 0.001
	Bluntnose klipfish	*Clinus cottoides*	0.52	0.002	76	0.26	< 0.001	0.68	0.80	0.65	< 0.001
	Nosestripe klipfish	*Muraenoclinus dorsalis*	0.65	0.005	82	0.89	< 0.001	0.64	0.30	0.09	0.04

RESULTS

Haplotype and nucleotide diversity

Average haplotype diversity (h) among species ranged from 0.52 for *Clinus cottoides* to 0.98 for *Tetraclita serrata* with the majority of species (seven of eleven) displaying genetic diversity greater than 0.90 (Table 1). *Clinus cottoides* also had the lowest nucleotide diversity (π) at 0.002 with the highest diversity of 0.054 found for both *Oxystele tigrina* and *Chrysoblephus laticeps*.

Across all sample locations with more than one species sampled, Mouille Point had the lowest mean h of 0.71 (four taxa sampled) and Cape Infanta had the highest with 0.92 (five taxa sampled). The sample location with the lowest mean (h) also had the lowest mean (π) of 0.01 (Mouille Point). Plettenberg Bay (2 taxa sampled) had the highest mean (π) at 0.06.

Variation across biogeographic regions

When the sample locations were broken into 400 km subsets mean haplotype diversity steadily increased from 0.77 on the west coast to its peaking at 0.89 around Port Elizabeth before dropping again slightly to 0.85 along the east coast (Fig. 2). There is a striking similarity in pattern of genetic diversity across the coast when compared to the species richness figure from Awad et al. (2002). The relatively low genetic diversity on the west coast is largely due to the low haplotype diversity of *Oxystele variegata* (*h* 0.19-0.35) and *Clinus cottoides* (*h* 0.27–0.5). The other species sampled along the west coast (*Parechinus angulosus*, *Tetraclita serrata*, and *Clinus superciliosus*) demonstrated high levels of haplotype diversity ranging from 0.84 to 0.99. Across the section of coastline with the highest mean haplotype diversity (1200-2000 km) only *Clinus superciliosus* had a measure below 0.6 ranging from 0.38 to 0.55.

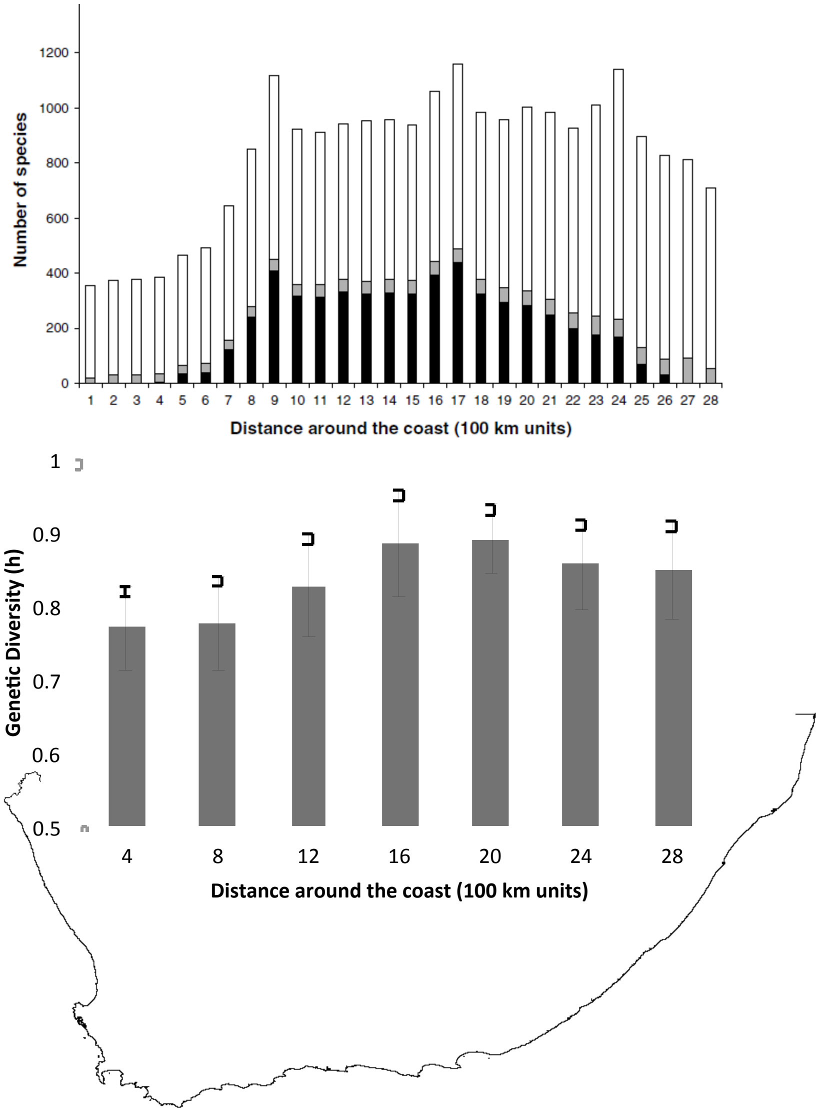

Figure 2. Graph of species richness per 100 km sourced from Awad et al. (2002) (top) and graph of haplotype diversity per 400 km (bottom) across a 2800 km range of coastline, South Africa

Unique haplotypes

It is important to note that low haplotype diversity does not necessarily translate to a low percentage of unique haplotypes per sample location. *Oxystele variegata*, despite having low average haplotype diversity, exhibits a high number of haplotypes unique to each sample site. Of the 45 haplotypes present across nine sample locations for *Oxystele variegata*, 37 (82%) are unique to one sample location (Table. 1). When sample locations are broken into the same subsets as for genetic diversity, the west coast in fact has the highest mean percentage of unique haplotypes (57%) across all species analysed (Fig. 3).

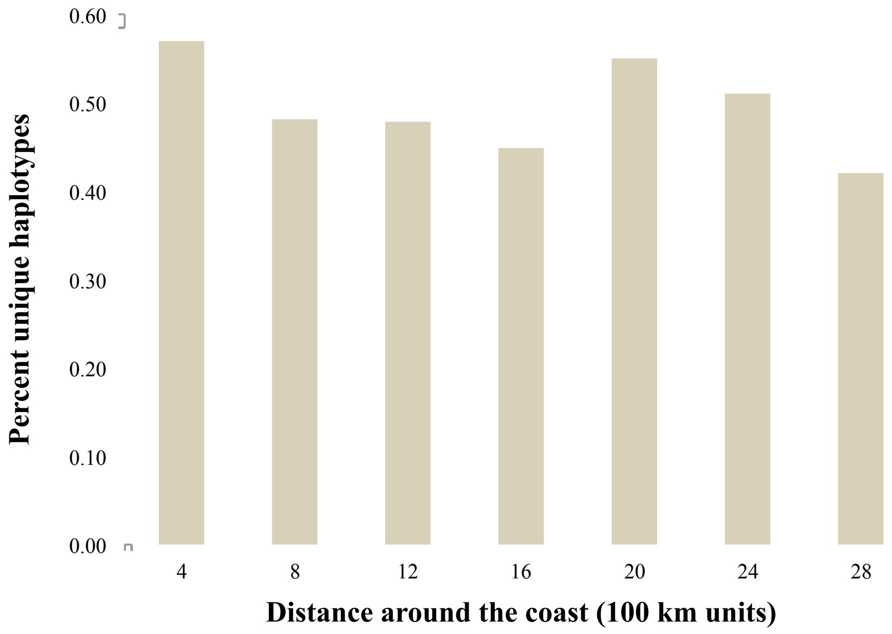

Figure 3. Graph of percent of unique haplotypes for sample taxa across a 2800 km range of coastline, South Africa

Genetic structure

The analysis of molecular variance (AMOVA) revealed a significant global Φ_{ST} for all three of the live-bearers. *Muraenoclinus dorsalis* had the highest global Φ_{ST} of any of the taxa ($\Phi_{ST} = 0.89$ $p < 0.001$) while *Clinus superciliosus* and *Clinus cottoides* revealed relatively high levels of structure at $\Phi_{ST} = 0.29$ and 0.26 respectively ($p < 0.001$ for both). Pairwise Φ_{ST} mirrored the range in global measures with *Muraenoclinus dorsalis* demonstrating structure ranging from $\Phi_{ST} = 0.17$ to 0.96 ($p < 0.001$) between sample locations. *Clinus superciliosus* and *Clinus cottoides* showed highly significant ($p < 0.001$) pairwise structure ranging from $\Phi_{ST} = 0.10$ to 0.66 and $\Phi_{ST} = 0.07$ to 0.77 respectively.

Among the brooders only two of the three taxa had a significant global Φ_{ST}. AMOVA revealed no significant structure for *Caffrogobius caffer*, while *Tetraclita serrata* had moderate but significant structure at $\Phi_{ST} = 0.07$ ($p < 0.001$) and *Cyclograpsus puntatus* showed the second most structuring of any species at $\Phi_{ST} = 0.49$ ($p < 0.001$). Highly significant pairwise Φ_{ST} ranged from $\Phi_{ST} = 0.15$ to 0.91 between locations for *Cyclograpsus puntatus* and from $\Phi_{ST} = 0.13$ to 0.28 for *Tetraclita serrata*.

The most interesting result of the AMOVA is that four of the five broadcast spawners had a significant global Φ_{ST}. *Chrysoblephus laticeps* was the only broadcast spawner for which the analysis did not find significant structure. *Oxystele tigrina* and *Acanthochiton garnoti* displayed moderate structure of $\Phi_{ST} = 0.07$ ($p < 0.001$). *Oxystele variegata* (a close relative of *Oxystele tigrina*) and *Parechinus angulosus* showed high levels of structure at $\Phi_{ST} = 0.34$ and 0.41 ($p < 0.001$). *Chrysoblephus laticeps* had no highly significant pairwise Φ_{ST} and only showed a slight significance between its two most geographically distant sample locations (False Bay and Port Alfred, $\Phi_{ST} = 0.03$ $p = .03$). In contrast *Parechinus angulosus* showed highly significant structure between sample locations, ranging from $\Phi_{ST} = 0.13$ to 0.84.

Isolation by distance

The isolation-by-distance analysis revealed a significant IBD signal at the scale of the entire sample range in seven of the nine species that had significant global Φ_{ST} values. As expected given the results of the AMOVA and pairwise Φ_{ST} analysis, all three live-bearers fit an IBD model with respect to the relationship between population genetic differentiation and geographic distance. Nonetheless, it is somewhat surprising that of the three, *Muraenoclinus dorsalis*, with the highest global Φ_{ST}, had only a marginally significant covariance ($r = 0.30$ $p = 0.04$) compared to the other live-bearers (*Clinus superciliosus* $r = 0.70$ and *Clinus cottoides* $r = 0.80$, $p < 0.001$ for both).

Amongst brooders only *Cyclograpsus puntatus* fit the IBD model, and produced the best fit of any of the taxa analyzed ($r = 0.89$ $p < 0.001$). Despite a significant global Φ_{ST} for *Tetraclita serrata* there was no support for isolation-by-distance.

Three of the five broadcast spawners fit the IBD model. *Oxystele variegata* was the best fit among broadcast spawners and the third best fit overall ($r = 0.79$ $p < 0.001$). *Parechinus angulosus* was a lesser, but highly significant fit at $r = 0.53$ and *Acanthochiton garnoti* had a marginally significant fit ($r = 0.23$ $p = 0.04$).

Interestingly, when the sample locations were subdivided into the biogeographic regions, the IBD signal was lost for six of the seven taxa that fit the model across the entire sampling range. *Clinus cottoides* was the only exception with a marginally significant IBD signal ($r = 0.52$ $p = 0.05$) between Jacob's Bay and Cape Agulhas.

Mean Dispersal Distance

An estimate of adult density (effective population size) is required to relate the IBD slope to mean dispersal distance (Rousset 1997, Buonaccorsi et al. 2004). In the absence of published density estimate for our study taxa and consistent with previous studies (Buonaccorsi et al. 2005, Cunningham et al. 2009) a range of effective populations sizes were used to calculate mean dispersal. The slope per 1000km for *Parechinus angulosus*, *Cyclograpsus punctatus*, *Oxystele variegata* and *Clinus cottoides* were steep and remarkably similar (Φ_{ST} range of 0.54-0.68) despite distinct life histories. At a density of 100 adults per kilometer, the mean dispersal distance for *Cyclograpsus punctatus* and *Clinus cottoides* was nearly identical (1.39km and 1.36km per generation respectively). The broadcast spawners *Parechinus angulosus* and *Oxystele variegata* only had a fractionally larger mean dispersal of 1.5km per generation (Table 2).

Table 2. Mean dispersal distances assuming exponential dispersal along a linear habitat

	Slope per 1000 km	**Adults per km**	**σ2**	**Mean dispersal distance (km)**
Parechinus angulosus	0.55	10	45.11	4.75
	0.55	100	4.51	1.50
	0.55	1000	0.45	0.47
	0.55	10000	0.05	0.15
Oxystele variegata	0.54	10	45.73	4.78
	0.54	100	4.57	1.51
	0.54	1000	0.46	0.48
	0.54	10000	0.05	0.15
Cyclograpsus punctatus	0.65	10	38.37	4.38
	0.65	100	3.84	1.39
	0.65	1000	0.38	0.44
	0.65	10000	0.04	0.14
Clinus cottoides	0.68	10	36.96	4.30
	0.68	100	3.70	1.36
	0.68	1000	0.37	0.43
	0.68	10000	0.04	0.14

DISCUSSION

Genetic structure along 2800km of South African coastline

Broadly, this study reveals that life-history is a poor predictor of dispersal and population genetic structure along the South African coastline, with broadcast spawners *Parechinus angulosus* and *Oxystele variegata* showing similar levels of structure as live-bearers *Clinus superciliosus* and *Clinus cottoides*. In this data set, the best demonstration of the heterogeneity in genetic structure is the contrasting patterns observed in *Oxystele variegata* and *Oxystele tigrina*. These two species of *Oxystele* topshell share the same reproductive strategy, have similar habitat requirements with overlapping ranges, and yet they are characterized by strikingly different levels of genetic structure, challenging the hypothesis that life-history can be used as a predictor of dispersal and population structure in the marine environment.

This finding is consistent with prior studies, which have found life history to be a poor predictor of dispersal (Ayre et al. 2009, Shanks 2009, Selkoe & Toonen 2011) and population genetic structure (Kelly & Palumbi 2010). Pelagic larval duration (PLD) has been the focus of much of the research seeking to explain patterns in dispersal, especially among taxa that are sessile as adults. The *a priori* hypothesis is that species with a long larval duration have a greater dispersal potential than species with a short PLD or none at all (Kinlan & Gaines 2003). Several recent studies have shown that there is in fact a poor correlation between dispersal and PLD with local recruitment levels being much higher than PLD would suggest (see Weersing & Toonen 2009). Kelly and Palumbi (2010) found that studies supporting a correlation between PLD and dispersal distance included species with no larval period in the analysis. Once these species were removed, PLD failed to explain variance in dispersal. Though PLD is poorly understood for our study taxa, our results do support the work of Kelly and Palumbi (2010) as all three of our live-bearers demonstrated high levels of genetic structure, but no pattern is detectable for the other life histories.

The pairwise Φ_{ST} analysis also failed to identify consistent biogeographic barriers to dispersal across taxa, which has been researched as a possible explanatory variable for patterns in genetic structure (Galindo et al. 2006). The South African coastline is frequently referenced as having at least three biogeographic regions with a divide between the cold upwelling west coast and temperate south coast around Cape Point and another divide between the temperate southern and subtropical east coast near Port St. Johns (Harrison 2002, Griffiths et al. 2010). In this study some species showed structure around these points, but no broad pattern was present across all the taxa analyzed. This adds to a growing body of literature demonstrating that biogeography, like life history, is a poor predictor of genetic connectivity (Teske et al. 2011a). With each new study it is becoming clear that marine systems are highly complex environments and that connectivity is influenced by a combination of factors including hydrodynamics, habitat, life history, historical change, and the biology of the species. The degree to which these factors impact dispersal will certainly vary by species and location. Therefore, generalizing based on one factor risks misidentification of conservation priorities and can lead to inappropriate conservation measures.

Genetic and species diversity along the South African coast

It is impossible to miss the striking similarity in pattern of genetic diversity and species diversity across the South African coastline (Fig. 2). All of the species from our study were included in Awad et al. (2002). Given that our study taxa are abundant species, broadly span life-history patterns present in South African marine fauna, and include both vertebrates and invertebrates, it is likely that the data reported here does represent the trend for all coastal species. It is however important to point out that the genetic data analyzed in this study are derived from a much smaller sample size than that used in the species richness analysis, so it is possible that a more robust sample set would not produce as close a pattern.

Several ecological theories can nonetheless explain the observed relationship between species and genetic diversity along the South African coastline. It is theorized that environments that are stable for long periods of time tend to accumulate genes and species. Vellend and Geber (2005) developed a model, hypothesizing that locality characteristics can lead to a parallel effect influencing both the genetic diversity within populations and species diversity within communities. Environmental conditions and levels of isolation along the South African coast may have impacted communities such that genetic diversity and species diversity increased or decreased in parallel.

It is important to note however, that despite the relatively low levels of diversity along the extreme west coast, the region is characterized by the highest percentage of unique haplotypes across the taxa studied. For an example see the distribution of haplotype diversity in *Oxystele variegata* (Fig 4). Measures of diversity are commonly used to prioritize conservation efforts (Meyers et al. 2000), but they are not sufficient to cover the full range of conservation concerns. Therefore, only taking diversity indices into account would likely lead to prioritization of the east coast, which is indeed the situation presently (see Griffiths et al. 2010). This approach currently fails to protect a representative sample of the total genetic diversity for the broad range of marine taxa studied here and highlights the importance of regional approaches to conservation efforts, particularly when it comes to spatially explicit management. High numbers of unique haplotypes are not only important for local adaptation and ecological processes, but reflect the impact of long-term evolutionary scale processes as well (Floeter et al. 2008). The loss of diversity from ecological scale process can be recovered from to a degree in reasonable timeframes, but there is no recovery possible for the loss of diversity from evolutionary processes, at least not in the timeframe of human interests (Moritz 2002).

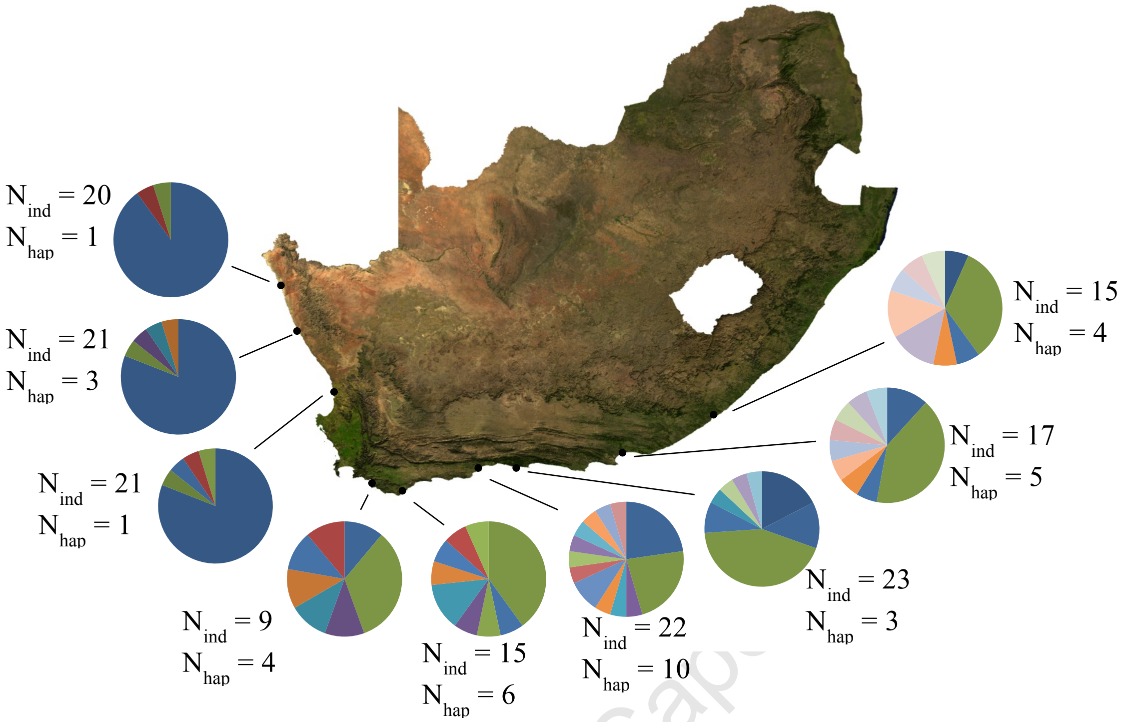

Figure 4. Map of haplotypes per sample location and their frequencies across the sampled range for *Oxystele variegata*. Number of individuals sampled per location indicated as N_{ind}. Number of private haplotypes per sample location indicated as N_{hap}. Sample sites from west to east are Port Nolloth, Hondeklipbaai, Gansbaai, Cape Agulhas, Herold's Bay, Knysna, Port Elizabeth and Haga Haga

Isolation by distance predicts poor dispersal for coastal marine species in South Africa

The IBD analysis revealed that the taxa we would have expected to have a signal based on the AMOVA did indeed fit the IBD model across the entire sampling range, though largely failed to produce a signal at a finer scale when divided into biogeographic regions. It is possible that this is the result of a recent range expansion: the continental shelf is narrow along the east and west coast of South Africa with a large plateau (Agulhas bank) along the south coast (Griffiths et al. 2010). The west and east coast likely experienced greater habitat loss during the last glacial maxima and have only recently (10000 to 12000 years) been recolonized (Teske et al. 2011a): indeed a number of recent phylogeographic studies support this model (von der Heyden 2008, 2011). At a fine scale, this could reduce the signal of IBD observed across the species range, and the lack of local population genetic structure along the west coast is the result of recent colonization events (Teske et al. 2011a). It is also possible that there simply are not enough sampling points for a significant fit and more sample locations in each of the regions are needed to detect signal of fine-scale geographic structuring. Additional research is required to fully investigate this result.

For the seven species characterized by IBD the regression analysis produced very steep slopes when compared to taxa from other published works. Palumbi (2003) reviewed five reports on marine invertebrates that produced an IBD slope with genetic distance increasing at a range from 0.01 to 0.31 per 1000 km. Only one of our study species fell within this range, the other six had a slope between 0.55 and 0.68 per 1000 km, roughly double the steepest slope of the Palumbi study (Table 1). The steep slopes are not surprising given the profound levels of structure seen in the pairwise tables, but it does highlight that South African has a highly dynamic marine environment, requiring an equally dynamic conservation management for its protection.

The steepness of slope is responsible for the remarkably short dispersal estimates produced for our sample taxa. The most likely estimates of adult density produced dispersal distances of between ~0.5 – 1.5 km per generation. These measures are low when compared to the 10 to 100 km range that is frequently cited for marine species (Palumbi 2003) but is not out of the range of other studies using this technique: Buonaccorsi et al. (2005) published a study on three species of rockfish, and at the same density of adults, calculated a mean dispersal per generation between two and 13 km. Pinsky et al. (2010) reported a range of four to 27 km per generation in coral reef fish (*Amphiprion clarkia*) and highlighted that the calculation for dispersal is sensitive to the estimate of effective density used. Our study tests a wide range of densities, but we cannot be certain that it is broad enough to reflect reality, and we recommend that observed density data be used in future studies. It is however, unlikely that any of the sample species, which are common in rocky shore habitats, have an adult density lower than 10 per km, making ~5 km the highest dispersal potential given the IBD slope.

It is also important to interpret these results in light of the assumptions inherent in the model and their associated limitations. An isolation-by-distance estimate assumes a linear habitat and a constant distribution of effective densities (Pinsky et al. 2010). The assumption of a linear habitat is relatively appropriate given that the area of coastline studied is 1000s of km long and the habitat for our study species is effectively only 100s of meters wide. Densities certainly vary along the coast, and are likely to occur on a gradient as the required rocky-shore habitat is more continuous on the west coast than the east (Teske et al. 2011a). As with any theoretical model, output must be carefully interpreted in context with other techniques. In our study, the high levels of population genetic structure across taxa and life histories support low mean dispersal estimates. It is important though, that these techniques are incorporated into future studies to increase opportunities to refine confidence levels and compare outcomes to observed data.

Despite the limitations of the IBD and associated dispersal model, the results from this study points to the fact that marine systems can have profound levels of genetic structure driven by shorter dispersal potentials than classic ecological theory would suggest. With each new study that is published there is a growing understanding that there is simply too much heterogeneity in dispersal ability between taxa to assume levels of connectivity based on any one species or environmental factor (Weersing & Toonen 2009, Kelly & Palumbi 2010). The strength of the approach used here is that it identifies patterns in connectivity among multiple species and life histories in shared habitat (von der Heyden 2009). Given the level of variation (topographic, oceanographic, species assemblages, evolutionary age and history) between studies on coastal marine population genetic structure, the application of findings from studies carried out elsewhere in the world cannot reliably inform local prioritization efforts. To the extent possible, studies should be conducted on a broad range of taxa in the specific region of concern (Carson et al. 2010).

Conservation of evolutionary processes

Patterns of genetic structure are the result of both ecological scale demographics and evolutionary scale phenomena, and there is a healthy debate on how to differentiate between the two (Rousset 1997, Bohonak 2002). From a conservation perspective, both ecological and evolutionary processes are important to the persistence of biodiversity. Much of the conservation effort to date has been focused on maintaining targeted species at particular levels of abundance through protection of critical habitat (McNeely et al. 1990). Genetic connectivity and the identification of barriers to gene-flow have become an important component of these efforts to understand the ecological processes of migration and drift and ensure the ability of species to adapt in the face of changing environments. What is often overlooked though is the importance of protecting evolutionary processes themselves (Laikre et al. 2010). Life histories and survival strategies develop and change over evolutionary timescales, and are as important, if not more important, to conserve than ecological processes alone (Moritz 2002). The extinction of a species is potentially damaging to the persistence of local biodiversity, but the loss of an entire evolutionary strategy would be devastating. Areas of high genetic diversity and genetic isolation should therefore be of conservation concern, regardless of whether the pattern is the result of ecological or evolutionary process.

MPA design in South Africa

The incorporation of findings from connectivity studies into the realm of conservation practice is a complicated process and this is particularly true for marine conservation efforts in South Africa. The South African MPA network is in some respects advanced compared to other nations. The existing network covers ~23% of the coastline, with 9% of the coastline managed as no-take reserves (Griffiths et al. 2010). Even with this relatively high degree of protection, MPAs are increasingly employed as the preferred strategy for marine conservation (Tunley 2009), adding pressure and scrutiny to the effectiveness of their design and management.

Species with low dispersal potential are generally thought to be well protected by MPAs since they experience high levels of local recruitment and are unlikely to leave the confines of the protected area as adults (Palumbi 2003). The majority of taxa in this study certainly fit the description of sessile and low dispersers and therefore, population numbers are likely being well protected for species that are present in the existing South African MPA network. Protection of the genetic diversity of marine taxa is a different matter. Despite the assumptions of the analysis used here, the extremely low dispersal distances indicated by the analysis suggest that, given the current spacing of MPAs (~110 km on average) (von der Heyden 2009), species are reliant on populations in the non-protected expanses between MPAs to maintain genetic connectivity. As such, the effectiveness of South African MPAs is to a degree, dependent on the persistence of biodiversity in unprotected areas.

Along the west coast there is a well documented gap in South Africa's existing MPA network, where presently only a single MPA has been proposed (Hockey and Buxton 1989, Attwood et al. 1997). Given our findings on the high levels of genetic structure and unique mitochondrial haplotypes present along the west coast, this is of particular concern (Fig 3). It is clear that those populations are not directly genetically connected with the eastern coast (where the highest density of MPAs is located) via dispersal, but rather follow a stepping-stone model of connectivity, and therefore the genetic diversity therein is completely unprotected at present. As such, we echo previous recommendations for the establishment of protected areas along the west coast (Hockey and Buxton 1989, Attwood et al. 1997).

In light of our very low dispersal estimates increasing the level of genetic connectivity among protected areas is clearly very challenging. Buonaccorsi et al. (2005) points out that this model produces an average dispersal distance in a typical generation, but that there are likely periodic events (e.g. storms, wind, current reversals) that can lead to instances of much higher realized dispersal. In addition to this, relatively low levels of migration have been shown to maintain genetic connectivity (Grosberg & Cunningham 2001). The exact distances needed for the maintenance of genetic diversity, including long periodic dispersal events, are outside the scope of this study and should be the subject of future research. The low average dispersal distances do however provide further support for a number of conclusions from previous studies and we recommend a network of small, moderately spaced MPAs (Eble et al. 2011, McCook et al. 2010, Coleman et al. 2011) as stepping stones to increase genetic connectivity among existing protected areas.

We acknowledge that there are very real logistical challenges to the establishment of MPAs. Economic interests and community and cultural claims to marine resources are all important considerations that inform the placement, implementation, and management of an MPA (Attwood et al. 1997) and restrict the degree to which they can be established based on criteria for the conservation of biodiversity alone. Recommendations that call for additions to the extent of the MPA network are understandably balanced against concerns that management of such a network would overwhelm already stretched management resources (Attwood et al. 1997). It is our hope that the findings presented here (and future such research) can be integrated with more traditional research to strengthen the overall case for the establishment of additional MPAs and help protect the array of extant biodiversity present in South Africa's marine ecosystem.

Conclusion

Worldwide, there remain many unanswered questions on how marine systems function over both ecological and evolutionary timescales. This study demonstrates the degree to which genetic structure can vary from one species to the next over the same habitat and how genetic connectivity could be used to inform spatial marine conservation planning. There are currently few studies that analyze genetic structure for multiple taxa across their range (Kelly & Palumbi 2010), making it difficult to interpret our results in light of other studies. This encourages bold interpretation of the data to formulate hypotheses that can be tested in future studies. There is clearly an urgent need for detailed, regionally specific research on marine systems that are being increasingly degraded by human activities. As techniques are tested and refined, there will be greater confidence in the interpretation of outcomes, and this will undoubtedly lead to more specific, actionable guidance for the conservation management of marine resources. Studies on the effectiveness of MPA networks are also required to better demonstrate the benefits of careful conservation management and design on the health of our marine ecosystems.

CHAPTER 3

Study Review and Synthesis

Challenges with the study

The primary challenge of this study was dealing with the volume of data and choosing which analytical techniques to use in a tight timeframe. There were some additional analyses that are often included in published works from similar studies that would have made a nice complement to our approach. Coalescent-based inference methods (e.g. variable population size model) and analyses such as Fu's Fs test (Fu 1997) are commonly used to test if populations have undergone a recent range expansion (Drummond et al. 2005). An understanding of the demographic history of the study species would have helped address one of the criticisms of tests of genetic structure; that they assume equilibrium between gene flow and drift (Rousset 1997).

It would also have been appropriate to run a spatial analysis of molecular variance (SAMOVA) to identify the spatial scale at which species are structured into 'populations' along the South African coast line. In this study, we treat each sample location as a population. This was acceptable since we were looking for broad scale patterns across multiple taxa and trends between sample locations, but grouping the sample locations into genetically meaningful populations may have strengthened the power to detect genetic structure.

The inclusion of observed effective density data would have contributed to the strength of the mean dispersal calculation. Effective density is extremely difficult data to gather, and it simply does not exist for many South African species. This is what led us to the approach of testing a range of densities in accordance with the approach of Buonaccorsi et al. (2005). For publication of this study, population data on klipfish will be used together with habitat requirements to approximate adult densities and hence, realized dispersal distance in the species.

Future Research

There are many exciting opportunities for future research using the same techniques as those used in this study. Given that the strength in our approach stems from the inclusion of multiple taxa and life histories, future studies should aim to sample different assemblages of species to add to the breadth of taxa studied in the South African marine environment. To the extent possible, studies should include data on population density, pelagic larval duration and habitat depth. Kelly and Palumbi (2010) used a multivariate analysis to test the explanatory power of 22 correlates of genetic structure and found that habitat depth best described variation in dispersal ability. It would be very interesting to see if that pattern held in a South African context.

Future studies should also include more densely sampled distributions of study taxa. In our study, the isolation-by-distance signal was not detectable when samples were broken into broad biogeographic regions. Subtle population differentiation can occur between geographically close populations, highlighting the importance of representative sampling across the species range in an IBD analysis. Theory suggests that the correlation between genetic and geographic distance should be detectable for genetically structured taxa at finer scales than the full species range, provided there are enough values to correlate. It would be informative to increase the sampling density for a species that fits the IBD model at a coarse scale to test if the regression produces the same slope at a finer scale.

A study that specifically sampled within and between two protected areas is also recommended (e.g. between Table Mountain National Park MPA and De Hoop MPA). This would make the measures of genetic structure more specific to an area of conservation management and therefore make recommendations more meaningful and actionable for stakeholders.

Finally, future studies should look to perform analysis across mitochondrial and nuclear DNA markers. The relative ease of use and availability of universal mtDNA markers strongly influences its preferred use over nuclear markers. It is however possible to run the same analyses used in this study on other markers (e.g. microsatellites). Investigating patterns across multiple markers would complement this study and provide greater insight into determinants of population structure and effective dispersal distances along the South African coast.

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Appendix A. Table with number of individuals sampled for each species and location. Blank cell indicates that at no samples were collected for a species at that location.

	Parechinus angulosus	*Chrysoblephus laticeps*	*Oxystele tigrina*	*Oxystele variegata*	*Acanthochiton garnoti*	*Cyclograpsus punctatus*	*Caffrogobius caffer*	*Tetraclita serrata*	*Clinus cottoides*	*Muraenoclinus dorsalis*	*Clinus superciliosus*
Port Nolloth	26			20				12			16
Hondeklipbaai	29			21				17			34
Lamberts Bay	26			21				19			8
Jacobsbaai	26		22		14	13		20	13	24	29
Mouille Point	30								33	18	20
Sea Point					21						
Kommetjie	30							24	18	22	18
Kalk Bay (Wooley's Pool)	28		21		13	16	22	11	24	6	4
False Bay		30									
Rooiels	23				15	13			42		13
Betty's Bay (Aasbank)	45				22	15	22	17	28	22	38
Gansbaai	30		18	9	20	5	25		26	6	20
Cape Agulhas	30		18	15	16	20	26	16	18	8	
Struisbaai		16									
De Hoop									35		
Cape Infanta			22			8	26	19	20		
Jongensfontein							26				
Mossel Bay								19			
Herolds Bay			17	22	11	13	26	18	32	3	
Knysna	31		23	23	10	20	24	19	17		2
Plettenberg Bay		17						22			
Tsitsikamma National Park		33									
Jeffrey's Bay	20										
Port Elizabeth	30		24	17	9			14			
Bird island		21									
Port Alfred	22	20	22		15		24	19	26	12	15
East London					13						
Haga Haga	39		24	15	9		21	18	11	11	
Port St Johns	24							20			
Munster						19					
Margate						8					
Shelley Beach								21			
Clansthal								20			
Umhlanga Rocks								24			

Appendix B. Table with haplotype diversity (h) for all species and sample location.

	Parechinus angulosus	*Chrysoblephus laticeps*	*Oxystele tigrina*	*Oxystele variegata*	*Acanthochiton garnoti*	*Cyclograpsus punctatus*	*Caffrogobius caffer*	*Tetraclita serrata*	*Clinus cottoides*	*Muraenoclinus dorsalis*	*Clinus superciliosus*
Port Nolloth	0.94			0.19				0.95			0.98
Hondeklipbaai	0.84			0.35				0.98			0.93
Lamberts Bay	0.98			0.35				0.99			0.89
Jacobsbaai	0.97		0.93		0.74	0.54		0.98	0.50	0.59	0.93
Mouille Point	0.92								0.27	0.72	0.93
Sea Point					0.97						
Kommetjie	0.95							0.96	0.47	0.64	0.88
Kalk Bay (Wooley's Pool)	0.90		0.93		0.97	0.68	0.95	0.96	0.69	0.33	1.00
False Bay		0.98									
Rooiels	0.90				0.98	0.74			0.65		0.78
Betty's Bay (Aasbank)	0.94				0.97	0.79	0.97	0.99	0.54	0.74	0.85
Gansbaai	0.96		0.95	0.92	0.98	0.40	0.97		0.34	0.33	0.95
Cape Agulhas	0.93		0.99	0.85	0.90	0.79	0.96	0.98	0.69	0.93	
Struisbaai		0.95									
De Hoop									0.75		
Cape Infanta			0.93			0.96	0.97	0.99	0.72		
Jongensfontein							0.96				
Mossel Bay								0.99			
Herolds Bay			0.96	0.91	1.00	0.87	0.95	0.97	0.55	0.67	
Knysna	0.89		0.96	0.78	0.93	0.86	0.98	0.96	0.38		1.00
Plettenberg Bay		0.99						0.97			
Tsitsikamma National Park		0.97									
Jeffrey's Bay	0.84										
Port Elizabeth	0.85		0.90	0.84	1.00			0.98			
Bird island		0.99									
Port Alfred	0.97	0.99	0.90		0.93		0.93	0.96	0.35	0.80	0.92
East London					0.97						
Haga Haga	0.77		0.90	0.89	0.97		0.97	0.97	0.35	0.71	
Port St Johns	0.92							0.99			
Munster						0.87					
Margate						0.46					
Shelley Beach								0.98			
Clansthal								0.99			
Umhlanga Rocks								0.96			

Appendix C. Table with nucleotide diversity (π) for all species and sample location.

	Parechinus angulosus	*Chrysoblephus laticeps*	*Oxystele tigrina*	*Oxystele variegata*	*Acanthochiton garnoti*	*Cyclograpsus punctatus*	*Caffrogobius caffer*	*Tetraclita serrata*	*Clinus cottoides*	*Muraenoclinus dorsalis*	*Clinus superciliosus*
Port Nolloth	0.016			0.004				0.048			0.012
Hondeklipbaai	0.009			0.009				0.051			0.012
Lamberts Bay	0.069			0.015				0.046			0.013
Jacobsbaai	0.032		0.059		0.059	0.005	0.005	0.042	0.001	0.003	0.008
Mouille Point	0.038								0.001	0.006	0.009
Sea Point					0.028						
Kommetjie	0.032							0.046	0.002	0.002	0.008
Kalk Bay (Wooley’s Pool)	0.016		0.049		0.027	0.003		0.044	0.004	0.001	0.011
False Bay		0.045									
Rooiels	0.025				0.107	0.004			0.003		0.008
Betty’s Bay (Aasbank)	0.023				0.038	0.007	0.011	0.052	0.003	0.003	0.011
Gansbaai	0.017		0.050	0.041	0.059	0.013	0.010		0.001	0.009	0.013
Cape Agulhas	0.012		0.054	0.050	0.023	0.009	0.010	0.048	0.003	0.019	
Struisbaai		0.033									
De Hoop									0.003		
Cape Infanta			0.059			0.011	0.010	0.038	0.003		
Jongensfontein							0.009				
Mossel Bay								0.030			
Herolds Bay			0.052	0.069	0.039	0.018	0.009	0.031	0.002	0.002	
Knysna	0.012		0.057	0.040	0.037	0.017	0.011	0.032	0.001		0.018
Plettenberg Bay		0.073						0.040			
Tsitsikamma National Park		0.049									
Jeffrey’s Bay	0.017										
Port Elizabeth	0.010		0.048	0.033	0.038			0.045			
Bird island		0.041									
Port Alfred	0.035	0.081	0.062		0.036		0.009	0.033	0.001	0.003	0.012
East London					0.034						
Haga Haga	0.007		0.052	0.027	0.023		0.010	0.039	0.001	0.002	
Port St Johns	0.012							0.043			
Munster						0.006					
Margate						0.002					
Shelley Beach								0.038			
Clansthal								0.038			
Umhlanga Rocks								0.037			

Appendix D. Pairwise phi-st table for each of the study taxa. Highly significant values are bolded (p < 0.001).

Parechinus angulosus

Port Nolloth	**0.00**																	
Hondeklipbaai	**0.17**	**0.00**																
Lamberts Bay	**0.16**	**0.16**	0.00															
Jacobsbaai	**0.20**	**0.15**	0.02	0.00														
Mouille Point	**0.49**	**0.50**	**0.11**	**0.20**	0.00													
Kommetjie	**0.59**	**0.61**	**0.17**	**0.30**	-0.01	0.00												
Kalk Bay (Wooley's Pool)	**0.77**	**0.81**	**0.35**	**0.55**	**0.15**	0.07	0.00											
Rooiels	**0.71**	**0.74**	**0.27**	**0.46**	0.08	0.03	0.00	0.00										
Betty's Bay	**0.72**	**0.73**	**0.34**	**0.50**	**0.13**	0.06	0.00	0.01	0.00									
Gansbaai	**0.77**	**0.80**	**0.36**	**0.55**	**0.16**	0.08	-0.01	0.02	0.00	0.00								
Cape Agulhas	**0.81**	**0.84**	**0.40**	**0.60**	**0.21**	**0.13**	0.01	0.04	0.02	0.01	0.00							
Knysna	**0.81**	**0.84**	**0.40**	**0.60**	**0.19**	0.11	0.00	0.02	0.02	0.02	0.03	0.00						
Jeffrey's Bay	**0.78**	**0.82**	**0.34**	**0.55**	0.16	0.09	0.01	0.01	0.04	**0.03**	0.06	-0.01	0.00					
Port Elizabeth	**0.82**	**0.85**	**0.40**	**0.61**	**0.19**	0.12	0.01	0.02	**0.04**	0.03	0.06	-0.01	-0.02	0.00				
Port Alfred	**0.72**	**0.75**	**0.34**	**0.52**	**0.21**	**0.16**	**0.12**	**0.09**	**0.14**	**0.11**	**0.15**	**0.16**	**0.10**	**0.15**	0.00			
Haga Haga	**0.85**	**0.87**	**0.44**	**0.65**	**0.23**	**0.14**	0.01	0.03	**0.03**	0.03	0.03	0.01	0.03	0.01	**0.20**	0.00		
Port St Johns	**0.80**	**0.84**	**0.37**	**0.58**	0.19	0.11	0.00	0.02	0.02	0.00	0.01	0.02	0.03	0.03	**0.12**	0.01	0.0	

Chrysoblephus laticeps

False Bay	0.00					
Struisbaai	0.01	0.00				
Plettenberg Bay	0.01	0.01	0.00			
Tsitsikamma National Park (	0.02	0.00	0.01	0.00		
Bird island	0.00	-0.01	0.02	0.01	0.00	
Port Alfred	0.03	0.00	-0.01	0.00	0.02	0.00

Oxystele tigrina

Jacobsbaai	0.00									
wooley's pool	0.01	0.00								
Gansbaai	**0.22**	**0.18**	0.00							
Cape Agulhas	0.10	0.02	0.09	0.00						
Cape Infanta	0.01	-0.01	**0.21**	0.07	0.00					
Herolds Bay	0.04	-0.02	**0.20**	0.01	0.03	0.00				
Knysna Heads	0.02	0.00	0.10	0.02	0.01	0.02	0.00			
Port Elizabeth	**0.16**	**0.15**	0.02	0.12	**0.15**	**0.19**	0.07	0.00		
Port Alfred	-0.02	0.02	**0.21**	0.08	0.00	0.03	0.01	**0.15**	0.00	
Haga Haga	-0.02	0.02	**0.23**	0.10	0.00	0.05	0.01	**0.17**	-0.03	0.00

Oxystele variegata

Port Nolloth	0.00								
Hondeklipbaai	-0.02	0.00							
Lamberts bay	0.01	0.01	0.00						
Gansbaai	**0.71**	**0.67**	**0.57**	0.00					
Cape Agulhas	**0.57**	**0.54**	**0.45**	-0.02	0.00				
Herolds Bay	**0.50**	**0.49**	**0.42**	-0.04	0.01	0.00			
Knysna Heads	**0.51**	**0.49**	**0.39**	-0.01	-0.01	0.02	0.00		
Port Elizabeth	**0.67**	**0.64**	**0.55**	-0.03	-0.02	0.01	0.02	0.00	
Haga Haga	**0.68**	**0.64**	**0.54**	0.04	0.01	0.06	0.05	-0.01	0.00

Acanthochiton garnoti

Jacobs Bay	0.00												
Sea Point	0.04	0.00											
Wolley's Pool	0.02	0.03	0.00										
Rooi-Els	0.03	**0.14**	0.06	0.00									
Aasbank (Bettys bay)	**0.12**	**0.13**	0.07	0.10	0.00								
Gansbaai	**0.10**	**0.09**	0.06	0.10	**0.07**	0.00							
Cape Agulhas	**0.09**	0.08	0.01	0.08	0.01	0.05	0.00						
Herolds Bay	**0.10**	**0.11**	0.03	0.07	0.00	0.05	0.01	0.00					
Knysna Heads	0.06	0.10	0.03	0.08	0.07	0.08	0.07	0.03	0.00				
Port Elizabeth	0.09	**0.14**	0.07	0.04	0.01	0.06	0.04	-0.02	0.04	0.00			
Port Alfred	0.07	**0.11**	0.05	0.06	0.07	0.08	0.04	0.07	0.08	0.07	0.00		
East London	0.08	0.07	0.00	0.05	0.04	0.05	-0.01	-0.01	0.04	0.01	-0.01	0.00	
Haga Haga	0.12	**0.17**	**0.12**	0.06	**0.09**	0.08	0.11	0.07	**0.17**	0.08	0.07	0.03	0.00

Cyclograpsus punctatus

Jacobsbaai	0.00										
Wooleys Pool	-0.01	0.00									
Rooi-Els	0.06	0.05	0.00								
Bettys Bay	-0.05	-0.02	0.03	0.00							
Gansbaai	-0.01	0.17	0.20	-0.03	0.00						
Cape Agulhas	-0.02	0.01	0.01	-0.03	-0.04	0.00					
Cape Infanta	0.01	0.07	0.01	-0.02	-0.05	-0.06	0.00				
Herolds Bay	**0.47**	**0.57**	**0.53**	**0.45**	0.21	**0.41**	0.33	0.00			
Knysna	**0.15**	0.22	**0.18**	0.12	-0.02	0.08	0.00	0.13	0.00		
Munster	**0.82**	**0.87**	**0.86**	**0.80**	**0.72**	**0.76**	**0.75**	0.20	**0.54**	0.00	
Margate	**0.87**	**0.93**	**0.91**	**0.83**	**0.77**	**0.77**	**0.78**	0.18	**0.51**	-0.04	0.00

Caffrogobius caffer

Wooley's Pool	0.00									
Aasbank (Bettys bay)	-0.03	0.00								
Gansbaai	-0.02	-0.02	0.00							
Cape Ahulhas	-0.01	-0.01	-0.01	0.00						
Cape Infanta	-0.02	-0.02	-0.01	-0.02	0.00					
Jongensfontein	0.01	-0.02	0.02	0.01	-0.01	0.00				
Herolds Bay	-0.02	-0.02	-0.02	-0.03	-0.02	0.01	0.00			
Knysna Heads	-0.01	-0.01	-0.01	-0.03	-0.02	0.01	-0.03	0.00		
Port Alfred	-0.02	0.00	-0.02	-0.01	0.01	0.05	-0.02	0.00	0.00	
Haga Haga	-0.02	-0.01	0.01	-0.02	-0.02	0.01	0.00	-0.01	0.02	0.00

Tetraclita serrata

Port Nolloth	0.00																			
Hondeklipbaai	**0.16**	0.00																		
Lamberts Bay	0.16	-0.01	0.00																	
Jacobsbaai	**0.21**	-0.01	0.00	0.00																
Kommetjie	0.01	**0.21**	**0.19**	**0.25**	0.00															
Wooley's pool	**0.21**	0.00	0.00	-0.03	**0.24**	0.00														
Bettys Bay	0.01	**0.13**	**0.12**	**0.19**	0.00	**0.17**	0.00													
Cape Agulhas	0.13	-0.01	-0.01	-0.01	**0.19**	-0.02	**0.12**	0.00												
Cape Infanta	**0.22**	-0.02	0.01	-0.01	**0.27**	-0.01	**0.19**	-0.01	0.00											
Mossel Bay	**0.28**	0.01	0.01	0.02	**0.29**	-0.01	**0.21**	0.03	0.01	0.00										
Herolds Bay	**0.24**	0.00	0.01	0.00	**0.28**	0.01	**0.22**	0.00	-0.01	0.01	0.00									
Knysna	**0.25**	0.01	0.01	-0.02	**0.28**	-0.01	**0.21**	0.01	-0.01	-0.01	-0.02	0.00								
Plettenberg Bay	**0.26**	0.00	0.01	-0.01	**0.27**	-0.02	**0.19**	0.03	0.01	-0.01	0.02	0.00	0.00							
Port Elizabeth	**0.23**	0.00	-0.01	-0.02	**0.25**	-0.05	**0.18**	0.01	0.00	-0.01	0.01	-0.01	-0.02	0.00						
Port Alfred	**0.25**	0.01	0.00	0.01	**0.29**	0.00	**0.21**	0.02	0.01	-0.01	-0.01	-0.02	0.02	-0.01	0.00					
Haga Haga	**0.22**	0.00	0.00	-0.01	**0.26**	-0.02	**0.19**	-0.02	-0.02	-0.01	-0.02	-0.02	0.01	-0.01	-0.01	0.00				
Port St. Johns	**0.21**	-0.02	0.00	-0.01	**0.25**	-0.02	**0.18**	-0.01	-0.02	-0.02	-0.01	-0.01	0.00	-0.01	-0.01	-0.02	0.00			
Shelley Beach	**0.25**	0.01	0.01	0.00	**0.26**	-0.03	**0.21**	0.01	0.00	-0.02	-0.01	-0.02	0.00	-0.03	-0.01	-0.02	-0.02	0.00		
Clansthal	**0.23**	0.01	0.00	-0.02	**0.26**	-0.04	**0.20**	-0.01	0.00	0.00	-0.01	-0.01	0.01	-0.02	-0.01	-0.02	-0.01	-0.02	0.00	
Umhlanga Rocks	**0.21**	-0.01	0.01	-0.01	**0.27**	0.00	**0.20**	-0.02	-0.02	0.02	-0.01	0.00	0.03	0.02	0.01	-0.02	-0.01	0.01	0.00	0.00

Clinus cottoides

Jacobsbaai	0.00													
Mouille Point	0.14	0.00												
Kommetjie	**0.09**	**0.01**	0.00											
Wooley's Pool	0.08	**0.11**	0.03	0.00										
Rooi-Els	0.05	**0.07**	0.04	0.04	0.00									
Betty's Bay	0.06	**0.07**	0.01	-0.01	0.01	0.00								
Gansbaai	0.11	**0.08**	0.07	0.04	0.06	0.02	0.00							
Cape Agulhas	0.15	**0.22**	**0.14**	0.10	**0.15**	**0.13**	**0.19**	0.00						
De Hoop	**0.16**	**0.20**	**0.16**	**0.13**	**0.17**	**0.16**	**0.18**	-0.02	0.00					
Cape Infanta	**0.11**	**0.12**	0.08	**0.09**	**0.10**	**0.09**	**0.12**	0.00	0.05	0.00				
Herolds Bay	0.09	**0.08**	**0.07**	**0.09**	**0.08**	**0.07**	0.08	0.05	**0.09**	0.00	0.00			
Knynsna	0.16	0.15	**0.11**	**0.10**	0.08	0.08	**0.13**	0.07	0.13	0.00	-0.01	0.00		
Port Alfred	**0.71**	**0.76**	**0.66**	**0.54**	**0.56**	**0.58**	**0.72**	**0.58**	**0.54**	**0.61**	**0.66**	**0.73**	0.00	
Haga Haga	**0.69**	**0.77**	**0.63**	**0.48**	**0.52**	**0.53**	**0.71**	**0.52**	**0.49**	**0.57**	**0.64**	**0.74**	0.01	0.00

Muraenoclinus dorsalis

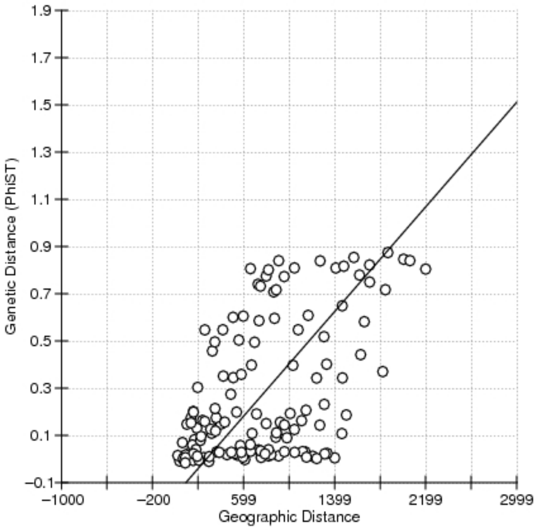
Jacobsbaai	0.00									
Mouille point	**0.17**	0.00								
Kommetjie	**0.87**	**0.74**	0.00							
Wooley's pool	**0.96**	**0.91**	**0.97**	0.00						
Bettys Bay	**0.95**	**0.93**	**0.95**	0.07	0.00					
Gansbaai	**0.94**	**0.89**	**0.94**	0.77	**0.80**	0.00				
Cape Agulhas	**0.89**	**0.83**	**0.88**	**0.54**	**0.68**	0.14	0.00			
Herolds bay	**0.95**	**0.91**	**0.96**	0.94	**0.86**	**0.71**	0.14	0.00		
Port alfred	**0.95**	**0.91**	**0.95**	**0.85**	**0.83**	**0.75**	**0.37**	**0.48**	0.00	
Haga Haga	**0.96**	**0.92**	**0.96**	**0.90**	**0.85**	**0.78**	**0.36**	0.56	0.03	0.00

Clinus superciliosus

Port Nolloth	0.00											
Hondeklipbaai	0.04	0.00										
Lamberts bay	0.05	-0.01	0.00									
Jacobsbaai	0.05	**0.14**	0.18	0.00								
Mouille Point	**0.17**	**0.23**	**0.30**	**0.09**	0.00							
Kommetjie	0.12	0.20	**0.27**	0.04	0.01	0.00						
Wooley's pool	0.07	0.13	0.20	0.16	0.16	**0.16**	0.00					
Rooi-Els	**0.17**	**0.20**	0.28	**0.19**	**0.26**	0.21	0.19	0.00				
Bettys bay	**0.17**	**0.24**	**0.28**	**0.10**	0.03	0.03	**0.20**	**0.21**	0.00			
Gansbaai	**0.10**	**0.19**	**0.21**	**0.07**	**0.09**	0.05	0.06	0.12	0.05	0.00		
Knysna	**0.53**	0.52	0.52	0.64	0.64	0.65	0.48	**0.65**	0.54	**0.45**	0.00	
Port Alfred	**0.59**	**0.60**	**0.61**	**0.66**	**0.66**	**0.66**	**0.58**	**0.66**	**0.60**	**0.54**	0.01	0.00

Appendix E. Graph of genetic distance phiST (Y axis) and geographic distance in km (X axis) for seven taxa. Values for p, r, r-squared and the slope of the regression are included.

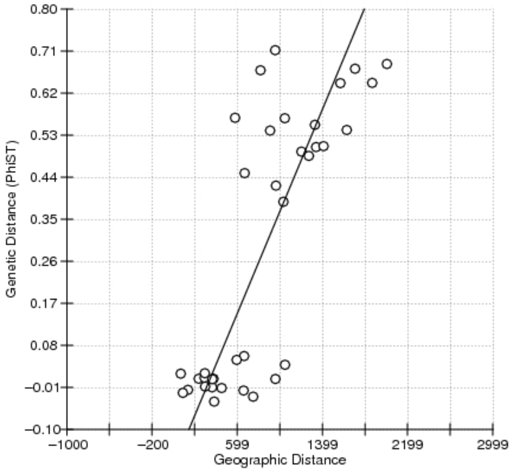
Parechinus angulosus



Z	r	p
38519.0676	0.530393	p < 0.0010

slope	slopeSE	r^2
5.54E-04	4.06E-05	2.81E-01

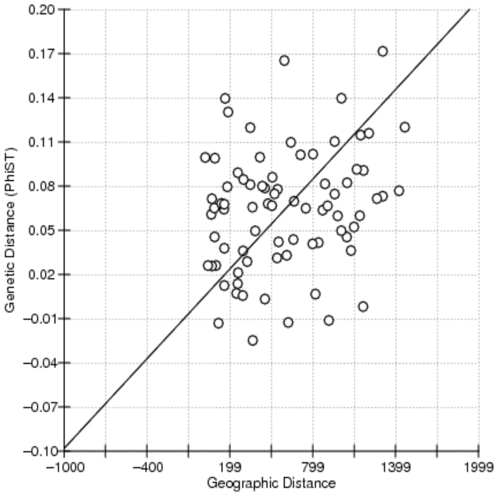
Oxystele variegata



Z	r	p
12761.30747	0.792333	p = 0.0010

slope	slopeSE	r^2
5.47E-04	5.72E-05	6.28E-01

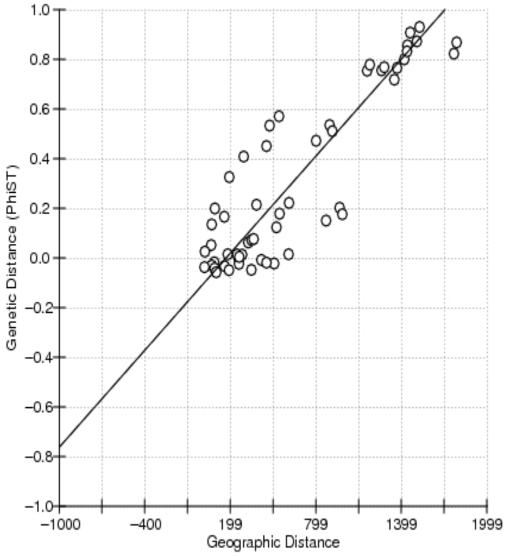
Acanthochiton garnoti



Z	r	p
3273.084595	0.232127	p = 0.0440

slope	slopeSE	r^2
1.02E-04	1.13E-05	5.39E-02

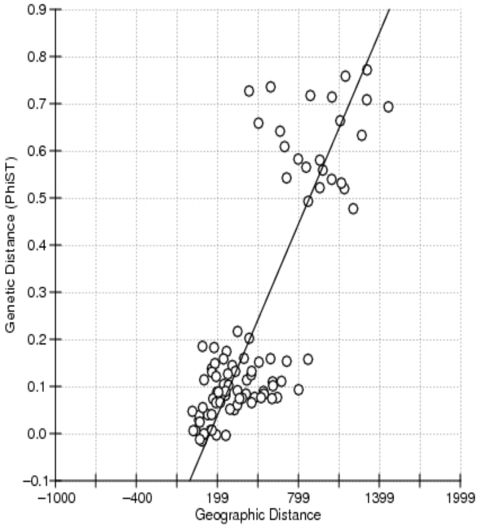
Cyclograpsus punctatus



Z	r	p
19620.14538	0.890041	p < 0.0010

slope	slopeSE	r^2
6.51E-04	4.08E-05	7.92E-01

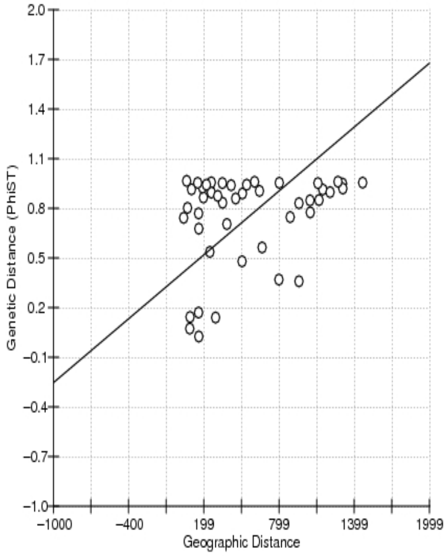
Clinus cottoides



Z	r	p
16525.89742	0.806361	p = 0.0010

slope	slopeSE	r^2
6.76E-04	4.24E-05	6.50E-01

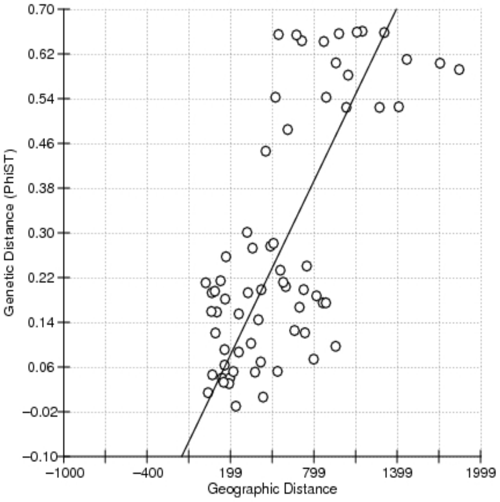
Muraenoclinus dorsalis



Z	r	p
20339.02272	0.301756	p = 0.0410

slope	slopeSE	r^2
6.44E-04	9.36E-05	9.11E-02

Clinus superciliosus



Z	r	p
14925.25747	0.701872	$p < 0.0010$

slope	slopeSE	r^2
5.18E-04	4.61E-05	4.93E-01