A review of marine phylogeography in southern Africa

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The southern African marine realm is located at the transition zone between the Atlantic and Indo-Pacific biomes. Its biodiversity is particularly rich and comprises faunal and floral elements from the two major oceanic regions, as well as a large number of endemics. Within this realm, strikingly different biota occur in close geographic proximity to each other, and many of the species with distributions spanning two or more of the region's marine biogeographic provinces are divided into evolutionary units that can often only be distinguished on the basis of genetic data. In this review, we describe the state of marine phylogeography in southern Africa, that is, the study of evolutionary relationships at the species level, or amongst closely related species, in relation to the region's marine environment. We focus particularly on coastal phylogeography, where much progress has recently been made in identifying phylogeographic breaks and explaining how they originated and are maintained. We also highlight numerous shortcomings that should be addressed in the near future. These include: the limited data available for commercially important organisms, particularly offshore species; the paucity of oceanographic data for nearshore areas; a dearth of studies based on multilocus data; and the fact that studying the role of diversifying selection in speciation has been limited to physiological approaches to the exclusion of genetics. It is becoming apparent that the southern African marine realm is one of the world's most interesting environments in which to study the evolutionary processes that shape not only regional, but also global patterns of marine biodiversity.

Introduction

Phylogeography is the study of the historical and phylogenetic components of the spatial distribution of gene lineages within and amongst closely related species.[1,2] Many phylogeographic studies have focused on species of conservation concern,[3] whilst others have used the approach to investigate species complexes[4] or address questions in invasion biology.[5] In many instances, results have been interpreted in a somewhat narrative manner, linking genetic disjunctions with past climates or physical barriers and limited dispersal. More rigorous interpretations can be obtained when phylogeography is used in a comparative context; if the genetic structure of co-distributed but evolutionarily independent populations is congruent, then this reveals common processes that have driven genetic divergence.[6,7] If focused on multiple taxa, phylogeographic studies can thus be a very powerful tool in the identification of locations and processes central to the origin and maintenance of biological diversity.[8,9]

In a recent review of phylogeographic studies, Beheregaray[10] highlighted challenges for the Southern Hemisphere, noting that 77% of all studies were on boreal taxa, whilst biodiversity-rich developing nations are lagging in their use of this powerful method. South Africa was listed as 21st out of the 100 most productive countries in terms of publishing phylogeographic studies, with a total of 68 papers at that time. South Africa was also the 4th most productive country in the Southern Hemisphere, after Australia, Brazil and New Zealand. In light of the imbalance between the North and South, it is timely and appropriate that an assessment of the discipline in southern Africa is undertaken. Here we present a synthesis of key findings and a candid look ahead for phylogeographic research on marine organisms, which we hope can be used to identify research gaps, motivate for new studies and drive new directions, not only in regional, but also global marine biological research.

Southern Africa has a long and diverse coastline, comprising rocky and sandy shores, kelp forests, estuaries and coral reefs, yet marine phylogeography lags behind phylogeographic research on terrestrial biota. Although papers that could be considered to have a phylogeographic component were sporadically published during the 1980s[11,12] and 1990s,[13,14] a concerted effort to study the region's marine biota began less than a decade ago.[15,16] In recent years, marine phylogeography has primarily been driven by three South African research groups, based at Rhodes University, Stellenbosch University and the University of Pretoria. Each group has its

own focus: the group at Rhodes University focuses primarily on coastal invertebrates, the group at Stellenbosch University on coastal and deep-water fishes, commercially exploited crustaceans and other coastal invertebrates, and that at the University of Pretoria focuses exclusively on commercially important fish species. As southern Africa is of great interest from a biogeographic point of view because of its location at the transition zone between the Atlantic Ocean and Indian Ocean biomes, it has also featured prominently in a number of key phylogeographic studies with a global focus.[17,18] In this review, we highlight several areas of research where southern African marine organisms have featured prominently, identify significant gaps in terms of both sampling design and technical aspects, and discuss how these shortcomings can be addressed in the near future.

Coastal phylogeography

Of the different fields of marine phylogeography that are being studied in southern Africa, coastal phylogeography can be considered the one about which we know most. Since 2000, 23 papers dealing with the phylogeography of coastal taxa have been published and several more are either in press or in preparation. Papers authored by South African researchers understandably dominate the literature; access to coastal sites is easy, sampling is relatively simple and cheap, and usually many samples can be obtained in a short period of time. A recent review paper examined the phylogeographic patterning of southern African coastal taxa[19] and some of the general trends identified are briefly discussed below.

Location of coastal phylogeographic breaks

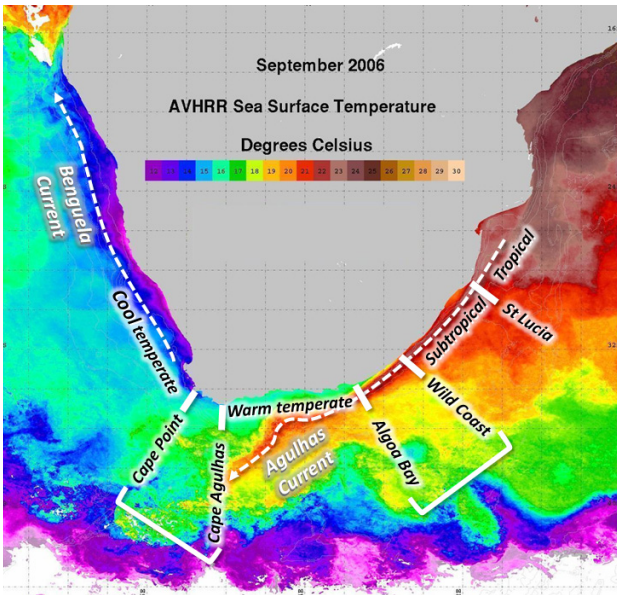
Most coastal species are divided into regionally confined genetic lineages whose distributions in many cases are linked with southern Africa's marine biogeographic provinces.[20,21] Phylogeographic breaks separating such lineages have been identified in three regions (Figure 1).[19]

On the south-west coast, phylogeographic breaks that coincide with the biogeographic disjunction between cool-temperate and warm-temperate biota[22] have been reported near Cape Point[23,24] and Cape Agulhas.[25,26] The region between these sites is sometimes considered a transition zone,[27] and several species have phylogeographic breaks at both sites, with distinct lineages that are endemic to this transition zone.[20,23]

Phylogeographic breaks on the south-east coast, at the disjunction between warm-temperate and subtropical biota,[22] have been difficult to define because their exact locations differ considerably for different species, and, in some, there is considerable overlap of genetic lineages.[23,28] The continental shelf in this region gradually widens from north to south, deflecting the warm Agulhas Current away from the coast, limiting its influence on coastal biota (Figure 1).[29] The northernmost breaks in this region have been identified on the Central Wild Coast (Transkei region)[20,30] and the southernmost breaks were reported near Algoa Bay.[24,31]

The third area where phylogeographic breaks have been identified coincides approximately with the transition zone between subtropical and tropical biotas on the east coast;[32] some species have phylogeographic breaks in north-eastern South Africa near St Lucia[21,33] and others have breaks farther north in Mozambique.[34,35]

An important finding is that not all species that occur in more than one marine biogeographic province exhibit genetic structure, and those that do need not have phylogeographic breaks at the same localities. Some species are not genetically structured across one or more biogeographic disjunctions,[20] and several taxa show no genetic structuring along their entire ranges.[36,37] In addition, several species with low capacity for dispersal exhibit phylogeographic breaks that do not coincide with present-day marine biogeographic disjunctions,[20,23] suggesting that in these, historical patterns are retained by limited gene flow.[38] Also, although planktonic dispersers usually do not have any phylogeographic breaks within marine biogeographic provinces, this does not necessarily imply that all are panmictic within provinces. Whilst panmixia has been identified in a highly philopatric coastal fish that disperses primarily by means of planktonic larvae,[37] significant genetic structure was found in the brown mussel, *Perna perna*.[39] Populations of this species residing in different bays in the warm-temperate province were not only genetically distinct from each other on the basis of differences in haplotype frequencies, but they were also distinct from populations on the open coast.



Source: SST image, Marine Research Institute, University of Cape Town

FIGURE 1: Southern African oceanography and location of coastal phylogeographic breaks. The region is dominated by two boundary currents: the warm, southward-flowing Agulhas Current on the south-east coast, and the cold, northward-flowing Benguela Current on the west coast. The region can be divided into four major marine biogeographic provinces – cool temperate, warm temperate, subtropical and tropical – each of which has its own assemblage of species. Coastal phylogeographic breaks between provinces have been identified at three major localities that in most cases coincide with the disjunctions between the provinces: south-west coast (westernmost – Cape Point, easternmost – Cape Agulhas), south-east coast (southernmost – Algoa Bay, northernmost – Wild Coast) and northern east coast (St Lucia).

Maintenance of coastal phylogeographic breaks

Even though many of southern Africa's coastal species have high dispersal potential because of well-developed locomotory abilities and/or extended planktonic dispersal phases, phylogeographic breaks are often surprisingly abrupt. By linking oceanography with life history, it should be possible to establish the relative importance of the interacting factors that contribute to population genetic structuring and population connectivity.[40] Hypotheses explaining how distinct genetic patterns are maintained fall into two major categories, (1) genetic lineages are separated by barriers that limit dispersal and (2) regional genetic lineages are adapted to the environmental conditions characteristic of their marine biogeographic province and in many cases are unable to establish themselves in adjacent provinces.

Oceanic dispersal barriers

Proposed dispersal barriers that limit mixing of adjacent genetic lineages include upwelling cells,[17] river discharge,[14] coastal currents or eddies[30,41] and even a coastal dunefield.[20]

Cold-water upwelling: Numerous studies on marine species have indicated that cold-water upwelling can represent a strong dispersal barrier.[17,42] On the South African west coast, some coastal species have gaps in their distribution across a region with strong, persistent upwelling that may extend over hundreds of kilometres (e.g. the mussel *Perna perna*)[28] and dispersal of marine organisms from the Indian Ocean into the Atlantic Ocean is limited.[18,43] Some marine species show high levels of differentiation on the west coast (unpublished data), whilst in other studies, the same genetic lineages were identified on either side of the cold-water barrier,[28,44] suggesting that in these, divergence was either very recent or that populations on either side are connected by ongoing gene flow. Whether genetic disjunctions on the west coast are solely linked to upwelling cells or whether local oceanographic features such as eddies retain larvae in their natal environments has yet to be examined.

Freshwater discharge: On the south-east coast, freshwater discharge from the Mbashe River has been invoked as a dispersal barrier that prevents mixing of subtropical and temperate biota.[14] However, in many invertebrate species, the phylogeographic breaks in this region are not located near this river.[4,30] It remains to be tested whether larger rivers, such as the Tugela or the Gariep, represent dispersal barriers that limit dispersal of marine organisms along the coast.

Currents: Currents may represent dispersal barriers when water and larvae are mostly displaced offshore, away from suitable habitat in which to settle.[45] The trajectories of drifters released on the South African south and east coasts showed remarkably little overlap.[41] None of the drifters released on the south coast moved close to the east coast, and drifters released on the east coast eventually became entrained in the Agulhas Current and were moved hundreds of kilometres offshore. This suggests that large-scale regional hydrodynamics significantly reduce mixing between the temperate and subtropical biotas. However, drifters were released several kilometres offshore, so it is likely that wind-driven inshore currents facilitate some northward dispersal on the south-east coast, which would explain the presence of the temperate lineages of some coastal invertebrates as far north as the central Wild Coast (Figure 1).[26,30] Indeed, in an experiment using plastic drift cards, it was found that twice as many cards were retained in this region compared to cards released from two sites on the east coast, the majority of which were caught in the Agulhas Current.[46]

Genetic methods of analysing the strength and directionality of gene flow represent a useful additional tool for studying the role of currents in dispersal. They estimate long-term trends and only incorporate information from individuals that have dispersed and recruited successfully.

Broad-scale patterns from the different biogeographic areas show the influence of the major current systems on dispersal, and the evidence points to the importance of the interplay of the duration of larval dispersal with local current regimes. Four major gene-flow scenarios have been identified, (1) strong northward flow on the west coast with the Benguela Current, (2) strong southward flow on the east coast with the Agulhas Current, (3) some bidirectional gene flow inshore of the Agulhas Current on the south-east coast and (4) bidirectional gene flow on the south coast. These are discussed in more detail below.

The west coast, which is dominated by the northward-flowing Benguela Current, shows the strongest signal of asymmetrical or unidirectional gene flow patterns.[24] Very little information on gene flow is available from the east coast, but the limited data there are support the idea that long-distance dispersal is mostly facilitated by the southward-flowing Agulhas Current.[23]

On the south and south-east coasts, migration is not as clear. In the barehead goby, *Caffrogobius caffer*, gene flow was shown to be predominantly with the Agulhas Current,[36] but in another rocky shore fish, the bluntnose klipfish (*Clinus cottoides)*, most gene flow occurred in the opposite direction.[24] In invertebrates, bidirectional gene flow was identified on the south coast, with more eastward than westward dispersal,[23] and gene flow on the south-east coast was also bidirectional, indicating that much dispersal takes place by means of nearshore currents.[30] Together, these somewhat contradictory examples illustrate why life history plays an important role in determining population genetic structuring. For example, like many other gobioid fishes, *C. caffer* probably has a long larval dispersal phase[47] whereas adult fishes are confined to high-shore rock pools and probably do not disperse at all.[48] Dispersal is therefore only by larvae that make use of the Agulhas Current. In contrast, clinid fishes have extremely limited larval dispersal and it is highly unlikely that young fish are able to disperse by means of the offshore Agulhas Current, but likely rather use the inshore Agulhas counter-current for dispersal.[24] Further evidence for counter-current driven dispersal comes from the eastward range expansion of

the invasive Mediterranean mussel, *Mytilus galloprovincialis*.[49] It is also likely that strengthening of the current during the winter months facilitates the annual sardine run in South Africa.[50]

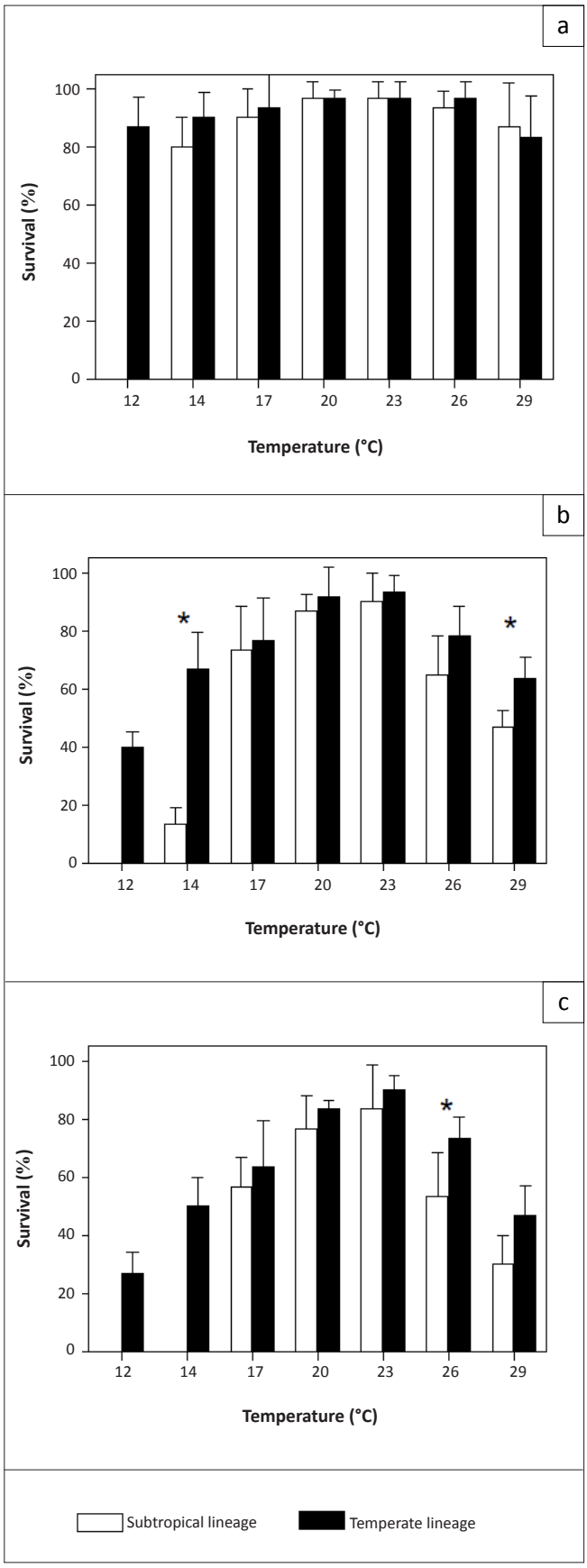
Dunefields: Dunefields seem to be an unlikely dispersal barrier for marine species, but their importance has also been documented elsewhere.[51] A possible explanation is that, in addition to coastal dunefields representing long stretches of unsuitable habitat for rocky shore and estuarine species, regions where these are located are characterised by strong, persistent onshore winds, which may limit long-shore dispersal of plankton in the surface water.

Province-specific adaptations

Although there is little doubt that dispersal barriers limit gene flow between provinces, many can be considered to be incomplete. For example, many upwelling cells affect the surface waters for only short periods of time,[52] and many wind patterns (such as the shoreward south-easterly) are seasonal.[53] Maintenance of genetic structure in the absence of strong dispersal barriers is possible only when levels of selection are high.[54] An alternative hypothesis explaining the maintenance of coastal phylogeographic breaks suggests that although many species can reach adjacent provinces, they do not establish themselves permanently, either because they are ill-adapted to local environmental conditions or because they are outcompeted by their sister taxa. Adaptation of genetic lineages to environmental conditions that differ between provinces has been documented in several recent studies. The larvae of the subtropical lineage of the mudprawn, *Upogebia africana*, cannot survive the colder water temperatures that are typical of the temperate province during winter (Figure 2).[30] This observation suggests that, even though they can potentially settle outside their own province during summer,[23] they are unable to establish themselves in the temperate provinces. Differences in osmoregulatory abilities of warm-temperate and subtropical lineages of the estuarine sandprawn, *Callianassa kraussi*, may reflect adaptation to differences in the salinities of the estuaries of each region, and therefore limit dispersal of each genetic lineage into adjacent provinces.[21] Lastly, the fact that the temperate lineage of the brown mussel, *Perna perna*, is less tolerant of sand inundation and high temperatures than its subtropical sister lineage may partly explain its absence from the east coast.[41]

Origin of coastal phylogeographic breaks

Most studies on southern African coastal taxa that describe phylogeographic breaks limit themselves to suggesting factors that are likely to maintain them. Explaining how such patterns have arisen is proving more challenging. Molecular dating indicates that coastal phylogeographic breaks are the result of historical processes that precede the beginning of the present interglacial period.[20,55] However, such estimates are mostly based on few loci, which limits accuracy, and the markers used may not provide sufficient resolution to detect very recent divergence events (discussed below). The ages of congruent genetic disjunctions may differ considerably for



Source: Teske et al.[30]
*, significant difference in survival of larvae from different lineages ($p < 0.05$, Student's t-test).

FIGURE 2: Cumulative survival (mean + s.d.) of successive larval stages (Zoea 1–3; a–c) of the mudprawn's (*Upogebia africana*) subtropical and temperate lineages as a function of temperature.

different species, and genetic differentiation between sister lineages in adjacent provinces may range from differences in haplotype frequencies in recently diverged lineages[24,34] to lineages being so distinct that each can be considered to be a distinct species.[21,33] For example, divergence time estimates that were based on more than one locus indicated that in the brachyuran crown crab species complex, *Hymenosoma orbiculare*, a split into temperate and subtropical lineages occurred at least 16 million years ago,[4] whereas congruent regional genetic units of the clinid fish *C. cottoides* diverged as recently as 60 000 years ago.[24]

In contrast to south-eastern Australia[56] or Indonesia,[57] there are no geological features in southern Africa that could have acted as land bridges during episodes of low sea level and that could have completely isolated populations of coastal taxa. There is consequently no compelling evidence for any geological vicariance events along the coast that could have driven simultaneous divergence in multiple species. The region's coastal morphology nonetheless changed considerably as a result of climate oscillations during the Pleistocene. For example, during the Last Glacial Maximum (26 500 – 19 000 years ago),[58] when the sea level was about 120 m lower than it is today,[59] large areas of continental shelf were exposed, particularly south of Cape Agulhas.[60] Also, the region's sea surface temperatures cooled as a result of intensified upwelling on the west coast[61] and a reduced influence of the Agulhas Current.[62] How these changes may have affected habitat availability and the amount of gene flow along the coast is poorly understood, but the role of oceanic dispersal barriers (discussed in the previous section) in driving the evolution of regional lineages needs to be assessed in this context. The exposure of the Agulhas Bank during the Last Glacial Maximum resulted in the southern tip of Africa being about 200 km south of where it is today, and, in combination with colder water temperatures in the region during that time, this may have presented a cold-water dispersal barrier similar to that on the west coast. The Agulhas Current weakened during glacial phases and may have ceased to flow during winter,[62] suggesting that advection of larvae away from the coast would have been considerably reduced, with stronger bidirectional longshore dispersal by means of nearshore currents. This possibility suggests that the role of the Agulhas Current in limiting mixing of regional biotas may never have been substantially more important than it is today. The fact that species from the east coast can temporarily establish themselves in the eastern portion of the temperate province during the summer months[63] indicates that, even today, it represents a highly permeable barrier. The same can be said of upwelling cells and the freshwater plumes of large rivers. Also, some dispersal barriers have formed more recently than the genetic lineages they separate,[20] suggesting that they only contribute towards maintaining genetic structure that was already present. Population genetic theory suggests that even a small amount of migration between populations will prevent genetic divergence by drift,[64] which indicates that southern Africa's historical oceanic dispersal barriers may be insufficient to explain the origin of marine phylogeographic breaks.

The association of genetic lineages with marine biogeographic provinces could point to ecological factors driving genetic divergence. Two recent studies have indicated that divergence could be driven by climate oscillations. In the first study, a range expansion from the south-east coast to the south-west coast that occurred during the previous interglacial period (~120 000 years ago) was identified in the coastal snail *Nassarius kraussianus* by means of coalescent-based molecular dating of mitochondrial DNA (mtDNA) sequence data (Figure 3).[31] Westward range expansions of warm-water molluscs during this period are well documented in the fossil record.[65] However, in contrast to other coastal molluscs, subsequent climatic cooling did not result in a range contraction in *N. kraussianus*, whose shells were used as ornaments by humans living on the south-west coast during the last glacial period.[66] This lack of range contraction suggests that the species' western populations adapted to cooler water. The species is today represented by a younger temperate lineage and a more ancient lineage that occurs in the subtropical and tropical provinces, with a phylogeographic break located near Algoa Bay (Figure 1). Congruent but much older divergence events that could be linked to range expansions during warm climatic phases, followed by adaptation and speciation during cooler phases, have also been reported in the *Hymenosoma orbiculare* species complex using multilocus DNA sequence data.[4]

Ecological divergence scenarios linked to climate oscillations may explain why divergence times differ considerably amongst species with congruent phylogeographic breaks. Although most species may undergo range expansions in response to shifting boundaries between marine biogeographic provinces as a result of climate oscillations,[65] adaptations to unfavourable environmental conditions during a particular range shift may only have arisen in a small fraction of the species affected, whilst the ranges of most others would have contracted.

Offshore marine phylogeography

Genetic studies of offshore populations are rare compared to coastal species. This difference can be ascribed to a number of factors, including the expense of obtaining samples, the lack of taxonomic expertise for some groups, and the lack of inclusion in multinational, large-scale research programmes. Research initiatives such as the Western Indian Ocean Marine Science Association, the Agulhas and Somali Current Large Ecosystem Project and the African Coelacanth Ecosystem Programme should have boosted such research, but, to date, little research from such initiatives has been published. There is considerable room for scientists working in southern Africa to expand into offshore phylogeographic studies, and perhaps some national strategy in this regard should be developed.

Recent offshore marine phylogeographic studies in southern Africa have primarily focused on commercially exploited species, with special emphasis on the Cape hakes that comprise the most important demersal fisheries resource

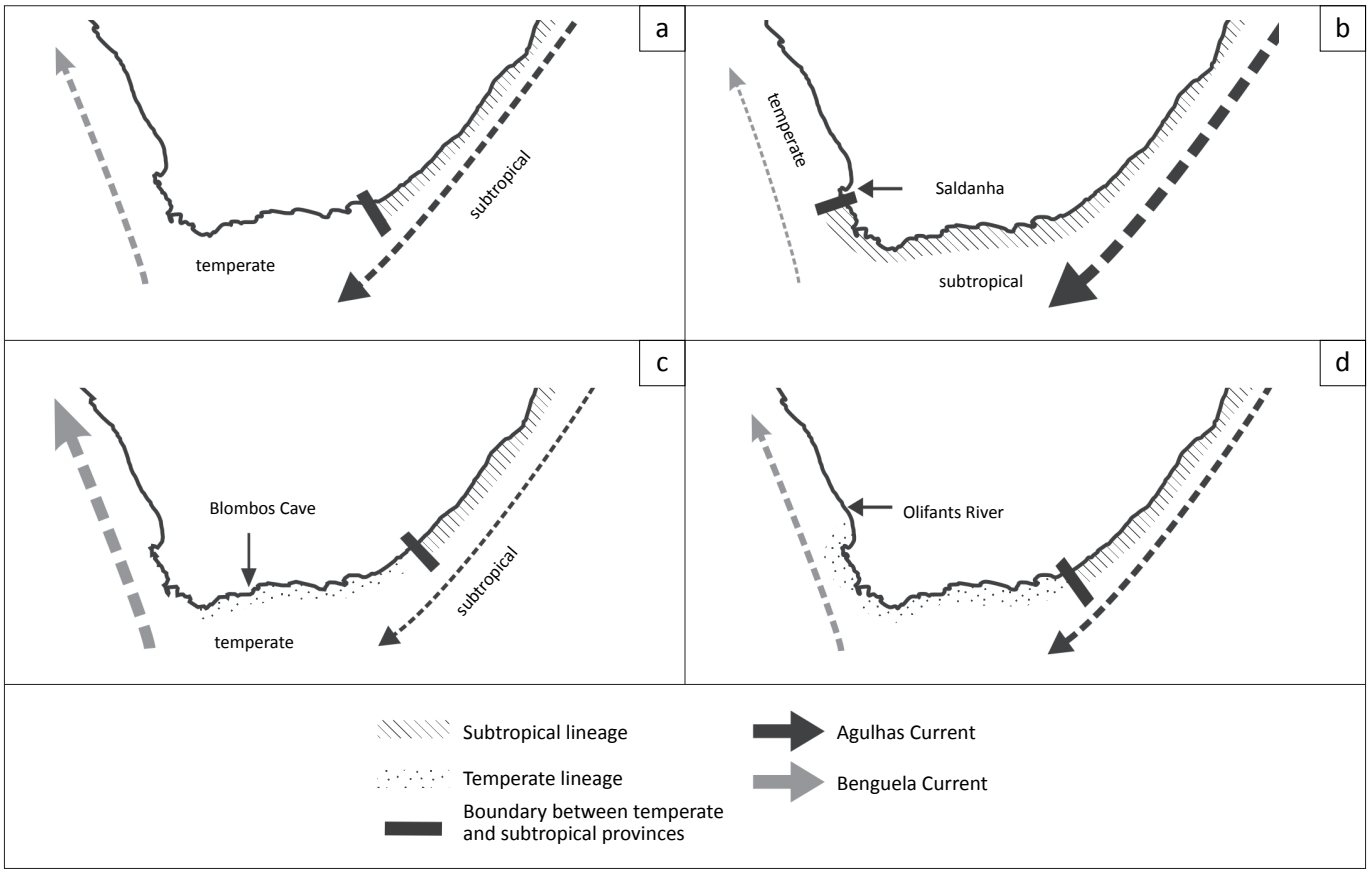


FIGURE 3: A hypothesis explaining how phylogeographic breaks associated with the disjunctions between marine biogeographic provinces can arise in the absence of absolute dispersal barriers. The example presented here is based on molecular dating and fossil data of the coastal snail *Nassarius kraussianus*.[31] Saldanha and Olifants River: approximate south-western distribution limits; Blombos Cave: Last Glacial Maximum fossil site.

in South Africa and Namibia. The major focus regarding offshore stocks is on transboundary management between Namibian and South African fish stocks. Interestingly, there appears to be genetic structure in the deep-water hake, *Merluccius paradoxus*,[55,67] between Namibia and South Africa, as well as between individuals within South Africa. However, as *M. paradoxus* was shown to only have population genetic structuring with adult fishes and no structure for juvenile non-spawning fish,[67] the focus to date has been on understanding the structuring of adult fishes. One study has examined the distribution of the eggs and larvae of *M. paradoxus* and those of its shallow-water sister taxon *M. capensis* (which in the early stages are morphologically identical) and found that spawning depth differs signficantly, but that most larvae of a certain size are found on the continental shelf at depths of about 200 m.[68] Several other studies have used molecular techniques on offshore marine species in southern Africa; for example, the lanternfish, *Lampanyctodes hectoris*, showed no significant genetic differentiation between South African and Namibian stocks.[69] There also appears to be no differentiation in the squid *Loligo vulgaris* between disparate spawning areas in South Africa.[70] In contrast, horse mackerels, *Trachurus capensis*, show slight differentiation between Namibia and South Africa based on allozyme loci.[11] Preliminary research using allozymes also suggested slight stock differentiation of orange roughy, *Hoplostethus atlanticus*, in Namibian waters.[71]

There have also been a number of studies on commercially important crustaceans, in particular rock lobsters of the genera *Jasus* and *Palinurus*. These have primarily focused on understanding population genetic structuring and demographic changes of lobster species in the region. Even though lobsters have extended planktonic dispersal phases, some genetic structuring between sampling areas was recovered for the Tristan rock lobster, *Jasus tristani*,[72] and for the Natal deep-sea lobster, *Palinurus delagoae*, which exhibits shallow but significant structuring between Mozambican and South African populations.[34] In the most important commercially exploited crustacean in South Africa, the west-coast rock lobster, *Jasus lalandii*, genetic diversity is highest on the south-west coast and decreases towards the edge of the species' distribution.[73] In contrast, the south-coast rock lobster, *Palinurus gilchristi*, shows no population genetic structuring along its range.[74]

Southern Africa and beyond

Indo-West Pacific phylogeography

Many marine organisms with high dispersal potential have long been considered to have distributions incorporating the entire Indian Ocean whereas the presence of temperate low-dispersal species in southern Africa and Australasia has traditionally been attributed to morphological stasis in Gondwanan relics that diverged as a result of the break-up of the ancient supercontinent. Both paradigms have been challenged by genetic studies. Large-scale phylogeographic studies have indicated that the populations of many marine organisms can be divided into lineages that are confined to the western Indian Ocean and lineages that are associated with the eastern Indian Ocean and/or the West Pacific.[75,76] A

recent study on fish species that occur both in southern Africa and in Australia indicated that, although there is little genetic structure in pelagic species, many inshore species are highly divergent between the regions. This study suggests that a third of the nearly 1000 fish species that occur in both regions may include cryptic species.[77] Molecular dating further indicates that many of the low-dispersal species thought to be Gondwanan relics diverged long after the break-up of the supercontinent, and post-Gondwanan transoceanic dispersal is considered to be a more appropriate hypothesis explaining the observed sister-taxon relationships.[78] Colonisation of Australia from southern Africa via the west wind drift has been proposed for low dispersal species,[78] but colonisation patterns of highly dispersed taxa are not yet fully understood.[79]

Coastal phylogeography in the western Indian Ocean

Despite the importance of the western Indian Ocean as a biodiversity hotspot and several major research initiatives, the region's phylogeography remains poorly explored. The majority of phylogeographic studies dealing with marine species from the western Indian Ocean have included samples from South Africa only.[28,80] Studies that included samples from other western Indian Ocean countries have mostly compared large-scale genetic structure between the western and eastern Indian Ocean, or throughout the Indo-West Pacific.[75,81] Very few studies have focused on genetic structure and gene flow along the East African coast, or between the African mainland and the region's islands. In those that have, low sample sizes and the inclusion of just a handful of sampling sites have made inferences about the location of phylogeographic breaks and levels of gene flow throughout the region problematic,[82,83] a notable exception being a recent study of the fiddler crab, *Uca annulipes*.[84] An earlier attempt at summarising what few data there are suggested that genetic structure in the western Indian Ocean exists mostly at tropical locations, whereas south-eastern African marine populations lacked genetic structure,[85] a trend that was rejected by several more recent studies.[34,35] To date, most of the phylogeographic studies that have employed a fine-scale sampling approach, and that have not dealt exclusively with South African fauna, involved extensive sampling in South Africa plus some additional Mozambican sites.[33,35] Even these studies have suffered from the problem of large gaps between the South African and Mozambican sites. To study the phylogeography of the western Indian Ocean more comprehensively requires that the level of sampling that has proven so useful to detect genetic structure in temperate and subtropical South Africa be extended to the tropical regions to the north-east. However, the size of this region, and the logistical difficulties involved in reaching sampling sites, will require not only substantial funding, but also a strengthening of collaborations amongst researchers from different western Indian Ocean countries.

Antitropical distributions in the eastern Atlantic Ocean

Several temperate southern African marine animals have sister-taxon relationships with species in the temperate north-eastern Atlantic. Examples include hake (*Merluccius* spp.),[86] anchovies (*Engraulis* spp.),[87] krill (*Nyctiphanes* spp.),[88] *Octopus vulgaris*,[89] spiny lobsters (*Palinurus* spp.)[90] and intertidal ascidians (*Pyura herdmani*).[91] Although it is possible that some of these disjunct distributions are the result of recent human-mediated transport from one region to the other, molecular dating indicates that most divergence events considerably predate the historical period. This suggests that migrants must have crossed the highly significant dispersal barrier represented by warm equatorial waters to establish themselves successfully. The findings to date indicate that the dispersal direction may differ amongst taxa. Whereas dispersal in *Nyctiphanes* spp. and *P. herdmani* was most likely from southern Africa to the north-eastern Atlantic, *Merluccius* spp., *Engraulis* spp. and *Palinurus* spp. most likely originated in the Northern Hemisphere.

Genetic markers used in marine phylogeography

Mirroring a global trend in phylogeographic research,[10] the majority of studies on southern African marine organisms have used mtDNA sequence data, with the *cytochrome oxidase c* subunit I gene being particularly popular. The reason for this is obvious – the primers for this marker are 'universal' and can be used for a wide variety of taxa. However, there are numerous disadvantages to using mtDNA exclusively, including that with a few exceptions, it is only inherited in the female line and is thus unsuitable for the study of hybridisation or reproductive isolation amongst different genetic lineages, and that molecular dating based on a single marker is less accurate than dating based on multilocus data.[92]

Several recent studies have used nuclear sequence data such as nuclear genes, introns or ribosomal RNAs in conjunction with mtDNA, and congruent genetic patterns were recovered for the two types of genetic markers.[24,33] These studies have so far rejected the notion that in species with low dispersal potential, haphazard genetic structure can readily arise in the absence of any underlying environmental factors.[93] To researchers who have exclusively used mtDNA sequence data until now, introns are likely to become the nuclear marker of choice. Not only are similar skills required in terms of data generation and interpretation, but the information content of introns is similar to that of mtDNA. Recent software developments for phasing the two sequences superimposed onto each other in trace files generated from heterozygous individuals[94,95] have rendered tedious cloning unnecessary, and a number of universal[96] and taxon-specific[33,97,98] primer sets have been developed. In non-model organisms for which no suitable primers are available for amplifying introns, the development of anonymous nuclear markers[99] may be a suitable alternative.

Whilst DNA sequence data from mtDNA or nuclear markers have proven suitable for detecting phylogeographic breaks and identifying cryptic speciation, they are of limited use in the study of very recently evolved genetic patterns, such as

those that formed during or after the Last Glacial Maximum, or those that formed during historical times. Microsatellites (also known as short tandem repeats) are excellent markers for the study of such recent evolutionary events because of their high mutation rate. Even though a number of microsatellite libraries have been developed specifically for South African marine organisms, particularly for teleosts,[100,101,102,103] we are aware of only four research papers that have actually used these markers to study marine phylogeography in southern Africa.[25,35,37,104]

Other types of genetic markers with considerable potential for the elucidation of marine phylogeography have yet to be used in southern Africa. For example, amplified fragment length polymorphism (AFLP) is now firmly established as a genetic marker for terrestrial plants,[105] but we are not aware of any studies on southern African algae, seagrasses or mangroves that have used them, and their use in animals is so far limited to aquaculture.[106]

Where to from here?

Although there are substantial data on some aspects of marine phylogeography in southern Africa, other aspects require further attention. Firstly, despite considerable insight into marine phylogeographic breaks gained during the past decade, two regions have not received sufficient attention. In the tropical north-east, phylogeographic breaks in species with low dispersal potential were identified near St Lucia,[21,33] and several planktonic dispersers have phylogeographic breaks in southern Mozambique.[34,35] Because of logistical difficulties in accessing sites, there were large gaps between sampling sites in all studies focusing on this region, and it is possible that there is in fact more than one phylogeographic break. Even less research has focused on the west coast, and more intensive sampling, which also includes sites in Namibia and Angola, is needed to better understand genetic structuring in this region.[19]

In terms of the nearshore biota studied, most research has so far focused on rocky shore or estuarine species, and only two studies have been on sandy shore organisms.[13,16] As sandy beaches make up about 42% of the South African shoreline and are a dominant feature particularly on the east coast,[107] more research efforts should be concentrated on understanding the genetic structuring of sandy shore organisms.

Surprisingly little phylogeographic research has been conducted on commercially important species.[37,67,89,104] Given that commercially exploited coastal teleosts have primarily been used as model taxa to position Marine Protected Areas, more phylogeographic research evaluating the current Marine Protected Areas network is warranted. In addition, the dearth of offshore genetic research demands serious attention. In the light of increased commercial, artisanal and recreational fishing, as well as possible warming of ocean currents in the region,[108] it becomes all the more important not only to understand population structuring, but also the likely evolutionary response of offshore marine species to climatic change.[55] Phylogeographic studies have also inadvertently uncovered cryptic speciation in marine species.[109] With at least 25% of southern African endemic fishes yet to be described,[110] it is likely that biodiversity inventories not only of fishes, but of all marine taxa will greatly benefit from phylogeographic research.

In addition to focusing on neglected taxa and obtaining samples from regions where little research has been conducted, considerably more effort needs to be placed on generating, not only multispecies, but also multilocus genetic data sets. In addition to the increased use of nuclear sequence data and AFLPs, the development of microsatellite libraries needs to be a major focus of southern African marine phylogeography in the coming years. As a result of their high mutation rate, microsatellites will allow researchers to study genetic patterns driven by factors such as fishing pressure and climate change, as well as to obtain more reliable information on gene flow. For example, migration rates estimated using coalescent-based methods such as those implemented in MIGRATE-N[111] or IMa[112] are often interpreted as reflecting contemporary gene flow,[23,24] but they may in fact be strongly influenced by historical events,[111] particularly when they are based on comparatively slowly evolving markers such as mtDNA or introns. Microsatellites would further allow the identification of cryptic species or stocks that have evolved too recently to be detectable using DNA sequence data. Recent advances in sequencing technology (e.g. 454 pyrosequencing) are likely to make the development of microsatellite libraries and single nucleotide polymorphism libraries more accessible to southern African researchers.

Conclusion

The southern African marine realm is an exceptionally interesting environment in which to study evolutionary processes. Because it is located at the transition zone between the Atlantic Ocean and Indo-Pacific biomes, the region's biodiversity is particularly high. Although South Africa has a very active marine biological community and conventional marine research is of a high standard, research addressing fundamental evolutionary concepts is still poorly developed. In the coming years, marine phylogeographic research needs to move from being mostly descriptive to becoming more analytical. For example, most studies have been limited to interpreting phylogeographic patterns on the basis of oceanographic data, but it would be desirable to explore how marine organisms' evolutionary histories have shaped present-day patterns, which should include testing alternative hypotheses of when and how genetic structure evolved.[113,114] Oceanographic research in southern Africa has concentrated on offshore features, with an enormous emphasis on the economically important Benguela upwelling system,[115] and to a lesser degree on the Agulhas Current.[52] Although recent initiatives have begun to address this,[116] we have a relatively poor understanding of the hydrodynamically complex nearshore region that hampers our ability to interpret genetic

data from taxa that live in shallow waters and disperse within the nearshore arena. In addition, the fact that there is strong evidence for adaptive differentiation between recently evolved sister lineages in the region's different marine provinces suggests that a greater focus needs to be placed on studying selection pressure. In addition to conducting physiological studies on evolutionary lineages that have been identified using selectively neutral genetic markers, focusing on markers that are under selection would greatly improve our understanding of the relative importance of dispersal barriers and selection gradients in driving the evolution of new species. We believe that it is time to put southern Africa 'on the map' as one of the world's most interesting regions in which to study marine phylogeography, and help afford it a similar status to that presently occupied by the Cape Floristic Kingdom, the African Great Lakes and the terrestrial fauna of Madagascar.

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