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Population Genetic Status of the Western Indian Ocean: What do we Know?

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Abstract—Population genetics offers a useful technique for studying the population structure of marine organisms and has relevance to both systematics and the conservation of biodiversity. The Western Indian Ocean (WIO) is faced with increasing evidence of degradation and effective management initiatives are needed to curtail the environmental decline. The management of the WIO region can therefore benefit from the information that population genetics can provide. Extensive literature searches revealed only 31 genetic references for the WIO region. From a biogeographic point of view, the WIO shows little genetic exchange with the rest of the Indo-Pacific, but from a regional perspective, the limited information that exists points towards widespread genetic structuring in the reefs off tropical Africa and the Indian Ocean islands, and greater connectivity amongst southeast African reefs. However, much more information is needed in the region before the true strength of population genetic data can be used as a primary tool for management.

INTRODUCTION

Tropical marine systems are amongst the most biologically diverse ecosystems, representing critical resources to millions of people worldwide (e.g. tourism, fisheries, coastal protection). Despite their importance, tropical marine environments have been and continue to be challenged by an ever increasing number of both global and anthropogenic influences. For example, recent measures indicate that the abundance of healthy coral reefs worldwide is in decline, with as much as 37% of healthy coral reefs already lost and an expected 30% more to be lost over the next 10 to 30 years (Wilkinson, 2000). Whatever the system, whether coral reefs, sea grasses or mangroves, the general consensus appears to be that tropical marine systems are in decline (Jackson, 2001).

The Western Indian Ocean (WIO) forms a coherent subdivision of the tropical Indo-Pacific (Sheppard, 2000), and thus represents an important biogeographic region of tropical seas. In spite of this, Kenya, Mozambique, Somalia, South Africa, Tanzania, Comores, Madagascar, Mauritius, Reunion, and the Seychelles have shown major obvious signs of environmental degradation, as well as declines in natural resources and biodiversity (Berg *et al.*, 2002). According to Berg *et al.* (2002), poverty combined with rapid population growth and a poor understanding and management of coastal resources has resulted in a number of resource use problems in the WIO. These include habitat destruction, overexploitation of fisheries, human induced erosion, and pollution.

Successfully managing the impacts facing the WIO and tropical marine systems in general will therefore depend in part on gaining a better understanding of the factors and processes involved in shifting between healthy and degraded states. Information on the population dynamics of tropical marine organisms therefore seems crucial to this understanding. Most marine species

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have life histories that include at least one widely dispersive phase and populations of marine organisms are therefore typically perceived to be much more open than their terrestrial counterparts (Roberts, 1997). This assumption is based on the generalization that marine species with long larval phases are thought to disperse further, have higher gene flow, larger geographic ranges, and lower levels of genetic differentiation among populations (Féral, 2002). However, recent genetic research appears to challenge this long-held view of 'openness' in marine systems because genetic pools of widely distributed species are rarely homogenous from one end of their distribution to the other (Reeb and Avise, 1990; Hilbish, 1996; Ayre and Hughes, 2004). For example, Ayre and Hughes (2004) showed that, by studying five species of scleractinian corals, the reefs at Lord Howe Island are genetically isolated from those 700 km to the north on Australia's Great Barrier Reef, despite the southward flowing direction of the East Australian current.

The new found challenge of the 'openness' of marine populations may be due to several nonrandom factors, and genetic adaptation in the marine environment may therefore occur through ecological and geographic limitations such as dispersal capability, niche partioning and/or local adaptation (Hedgecock, 1986; Féral, 2002). Whatever the reason, population genetics offers a useful advance in the understanding and management of marine systems as the relationship between the dispersive ability of organisms and the genetic differentiation of populations not only provides a fundamental link between ecology and evolution (Ayre and Hughes 2000), but measures of genetic relatedness also represent a proxy to the extent of recruitment that is occurring between two areas.

Regionally, three important research directions for population genetics have been outlined, albeit for southern Africa (Grant, 1993). These include: (1) the measurement of population genetic structure; (2) the study of the influence of historical biogeographical events on present day populations; and (3) the use of more realistic models to understand the genetics of natural populations (Grant, 1993). Given these research objectives, and the applicability of population genetics to management in both marine and terrestrial realms, it was decided to search the scientific literature to determine the level of population genetic information that is available for the WIO region. This paper therefore provides a synopsis of what population genetic information is currently available in the forefront scientific literature for the WIO, and whether there is sufficient information to start challenging current regional management paradigms.

MATERIALS AND METHODS

Literature searches were performed using *ISI Web of Science* (1990 to March 2004) and Cambridge Scientific Abstracts: Biological Sciences Collection (1981 - March 2004) databases using electronic library resources from the library facilities at the University of Queensland, Australia. Both these databases provide access to current and retrospective multidisciplinary information from greater than 6 000 of the most high impact research journals in the world. Three search parameters were tested: (1) "Western Indian Ocean"; (2) "Western Indian Ocean" and "genetics"; (3) "Indian Ocean" and "genetics". In addition, *Marine Biology* (1993 to March 2004), *Coral Reefs* (1993 to March 2004), *Evolution* (1995 to 1999), *Molecular Ecology* (1996 to March 2004), *Ambio* (2000 to March 2004), the *South African Journal of Marine Science* (2000 to 2003), and the *Western Indian Ocean Journal of Marine Science* (all issues up to March 2004) were searched using electronic library resources from the library facilities at the University of Queensland. These journals are known to be the major resources of marine genetic and / or regional information and were therefore included for completeness. Due to the common difficulty of accessing 'grey literature', only the primary scientific literature was utilized in this study.

RESULTS AND DISCUSSION

A total of 31 references were identified by the search criteria (Table 1), however 11 of these were deemed not relevant to the purposes of this study (references 21 to 31 listed in Table 1). Of the

Table 1. Population genetic references to species in the West Indian Ocean

Content	Phylum	Family	Species	Common name	Reference
Western Indian Ocean population genetics only	Cnidaria	Pocilloporidae	Pocillopora verrucosa	Wart coral	1. Ridgway *et al.* (2001)
	Mollusca	Mytilidae	Perna perna	Brown mussel	2. Grant *et al.* (1992)
	Mollusca	Patellidae	Patella granularis	Granular limpet	3. Ridgway *et al.* (1998)
	Arthropoda	Penaeidae	Penaeus monodon	Black tiger prawn	4. Forbes *et al.* (1999)
	Arthropoda	Portunidae	Scylla serrata	Mud crab	5. Fratini and Vaninni (2002)
Biogeography	Alveolata	Symbiodiniaceae	Symbiodinium spp.	Zooxanthellae	6. Burnett (2002)
	Rhodophyta	Ceramiaceae	Spyridia filamentosa	Red benthic algae	7. Zuccarello *et al.* (2002)
	Echinodermata	Holothuridae	Holothuria nobilis	Sea cucumber	8. Uthicke and Benzie (2003)
	Echinodermata	Holothuridae	Holothuria atra	Sea cucumber	9. Uthicke *et al.* (2001)
			Stichopus chloronotus		
	Echinodermata	Ophidiasteridae	Linckia laevigata	Blue starfish	10. Williams and Benzie (1998)
	Echinodermata	Acanthasteridae	Acanthaster planci	Crown-of-thorns starfish	11. Benzie (1999)
	Arthropoda	Penaeidae	Penaeus monodon	Black tiger prawn	12. Benzie *et al.* (2002)
	Arthropoda	Penaeidae	Penaeus monodon	Black tiger prawn	13. Duda and Palumbi (1999)
	Arthropoda	Portunidae	Scylla serrata	Mud crab	14. Gopurenko *et al.* (1999)
	Arthropoda	Gerridae	Halobates spp.	Oceanic insect	15. Andersen *et al.* (2000)
	Chordata	Mugilidae	Mugil cephalus	Striped mullet	16. Rossi *et al.* (1998)
	Chordata	Scaridae	Chlorurus sordidus	Bullethead parrotfish	17. Bay *et al.* (2004)
	Chordata	Scombridae	Thunnus obesus	Bigeye tuna	18. Alvarado Bremer *et al.* (1998)
	Chordata	Scombridae	Thunnus obesus	Bigeye tuna	19. Appleyard *et al.* (2002)
	Chordata	Xiphiidae	Xiphias gladias	Swordfish	20. Chow *et al.* (1997)
Phylogeography and evolution	Streptophyta	Acanthaceae	Avicennia spp.	Black mangrove	21. Duke *et al.* (1998)
	Echinodermata	Diadematidae	Diadema spp.	Long-spined urchin	22. Lessios *et al.* (2001)
	Echinodermata	Toxopneustidae	Tripneustes spp.	Urchin	23. Lessios *et al.* (2003)
	Chordata	Mullidae	Mulloidichthys spp.	Goatfish	24. Stepien *et al.* (1994)
	Chordata	Clupeidae	Sardinops spp.	Pilchard	25. Bowen and Grant (1997)
	Chordata	Aulostomidae	Aulostomus spp.	Trumpetfish	26. Bowen *et al.* (2001)
	Chordata	Cheloniidae	Caretta caretta	Loggerhead sea turtle	27. Bowen *et al.* (1994)
Eastern Indian Ocean only	Streptophyta	Rhizophoraceae	Kandelia candel	Mangrove	28. Chiang *et al.* (2001)
	Arthropoda	Coenobitidae	Birgus latro	Coconut crab	29. Lavery *et al.* (1996)
	Chordata	Scombridae	Thunnus obesus	Bigeye tuna	30. Chow *et al.* (2000)
	Chordata	Clupeidae	Tenualosa ilisha	Hilsa shad	31. Salini *et al.* (2004)

remaining 20 studies, all have appeared in the literature in the past six years, and examined variation in allozymes, mitochondrial DNA, or intron variability in nuclear DNA.

The starfish *Linckia laevigata* showed that a single Western Indian Ocean (WIO) population from South Africa was distinct from populations off Western Australia (Eastern Indian Ocean, EIO) (Williams and Benzie 1998), providing an early suggestion of a divide in the Indian Ocean. This tentative genetic break was further substantiated by the crown-of-thorns starfish (*Acanthaster planci*), which showed similar patterns to *L. laevigata*, however the genetic differentiation among populations in the WIO was higher than those in the Pacific, indicating that the populations in the Pacific appear more connected (Benzie, 1999). The WIO-Pacific divide was also loosely substantiated by the holothurians *Stichopus chloronotus, Holothuria atra* and *H. nobilis* (Uthicke *et al.*, 2001; Uthicke and Benzie, 2003), but unlike *A. planci*, the genetic variability of *S. chloronotus* at Reunion was low.

However, the most comprehensive species specific genetic information that is currently available for the WIO comes from the black tiger prawn, *Penaeus monodon.* Duda and Palumbi (1999) looked at intron variability at multiple Indo-Pacific sites that included Madagascar, Mauritius and Tanzania, whereas Benzie *et al.* (2002) also looked at multiple sites in the Indo-Pacific (including South Africa, Mozambique and Madagascar) but used mitochondrial DNA. Interestingly both studies, using different regions of DNA, independently showed that the WIO populations were genetically distinct from their EIO and Pacific counterparts. However, the genetic diversity of southeast African populations was the lowest of all populations studied (results mirrored by Forbes *et al.*, (1999)), which is in direct contrast to the WIO populations of *L. laevigata* (Williams and Benzie, 1998) and *A. planci* (Benzie 1999).

Further evidence for this WIO-EIO divide is provided by studies on various species of fish. Allozyme studies of the striped mullet (*Mugil cephalus*) showed that the WIO sites in Egypt and South Africa were genetically separated from those off the coast of West Australia (Rossi *et al.* 1998). Using mtDNA, Alvarado Bremer *et al.* (1998) showed Atlantic stocks of bigeye tuna (*Thunnus obesus*) to be distinct from those in the Indo-Pacific. However, only a single collection from Reunion was considered representative of the Indian Ocean. Including additional samples from Madagascar and the Seychelles and using microsatellites in addition to mtDNA, Appleyard *et al.* (2002) found some evidence for a WIO-EIO divide in *T. obesus*, further dividing up the worldwide stocks. A similar pattern was found in another fish group, the reef fish species *Chlororus sordidus* (Bay *et al.*, 2004). In *C. sordidus*, populations from Amirante and the Seychelles have no shared mitochondrial DNA haplotypes with the EIO and the rest of the Pacific (Bay *et al.*, 2004). Furthermore, even red algae (*Spyridia filamentosa*) and oceanic insects (*Halobates* spp.) from WIO sites show limited gene flow with the Pacific (Andersen *et al.*, 2000; Zuccarello *et al.*, 2002).

Thus, the limited number of population genetic studies of species in the Indian Ocean typically shows little genetic exchange between the WIO and the EIO. In contrast, there was no significant difference between mitochondrial DNA sequences from swordfish (*Xiphius gladius*) populations from the Indian Ocean and the South Atlantic and Pacific (Chow *et al.* 1997). However, the Indian Ocean contained only a single location in Sri Lanka and therefore the pattern is not really representative of the WIO region as a whole. Additionally, mud crab (*Scylla serrata*) populations from the Red Sea, Mauritius and South Africa showed no genetic separation from Pacific Ocean populations, leading Gopurenko *et al.* (1999) to hypothesize that unlike other Indian Ocean populations, radiation of *S. serratta* in the Indo-West Pacific occurred as a single rapid wave of expansion, possibly originating from a west Pacific origin during the late Pleistocene. However, due to the small sample sizes of the WIO populations in Gopurenko *et al.* (1999), Fratini and Vannini (2002) express caution with this finding of low differentiation, because using the same DNA marker they found significant genetic structuring in *S. serrata* populations sampled from Kenya and Tanzania, highlighting the importance of ecologically meaningful sample sizes in marine population genetic studies.

An interesting regional case is the study of Burnett (2002), who assessed latitudinal variation in algal symbionts (*Symbiodinium* spp.) from the Indian Ocean zoanthid *Palythoa caesia*. Surprisingly, whilst some *Symbiodinium* genotypes are geographically widespread, populations of WIO *P. caesia* have different algal complements from their EIO relatives. All WIO samples (Mauritius, Rodrigues, Zanzibar, Seychelles) contained only clade C genotypes, whereas EIO populations contained a combination of clade C and clade D genotypes (Burnett, 2002). As *P. caesia* acquires its symbionts directly from the environment, the failure to observe clade D in the WIO may reflect either an ecological difference from the EIO, or perhaps a reduced environmental availability of this clade relative to clade C (Burnett, 2002). Interestingly, samples from the Maldives had a mixture of both clades and therefore superficially appear more similar to the EIO. However, as light is considered to be the major contributing factor to determining *Symbiodinium* clade in a host, the fact that the Maldives samples were collected from greater depths than the other WIO samples, may explain the occurrence of clade D (supposed EIO clade), as this clade is known to favor lower light conditions (Burnett, 2002).

Nevertheless, based on the published literature, which includes population samples from South Africa, Mozambique, Tanzania, Kenya, Madagascar, Amirante, the Seychelles, the Maldives, Reunion, and the Red Sea (Figure 1), there appears to be limited gene flow between the WIO and the rest of the Indo-Pacific. This is interesting in that based on currently available population genetic information, further support is added to Sheppard's (2000) justification (based on the biogeographic patterns of corals) that the WIO is a distinct subdivision of the tropical Indo-Pacific. Given the patterns uncovered and the uniqueness of the WIO as a genetic sub-region of the Indo-Pacific, regional population genetic studies therefore are all the more important and key to management initiatives in the WIO region.

Unfortunately, the numbers of published studies that address purely regional WIO questions are extremely limited. The searches used in this

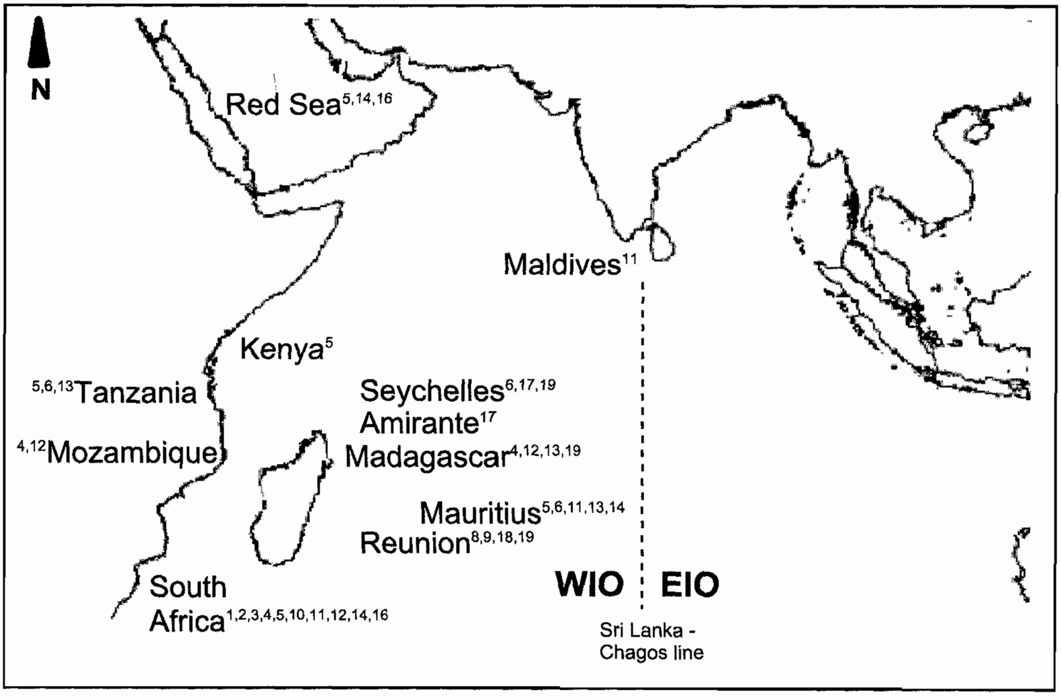

Fig. 1. Map of the Western Indian Ocean showing locations where genetic information is available. The numbers represent the relevant references numerically listed in Table 1

study found only five regional population genetic studies. Of these, Grant *et al.* (1992) and Ridgway *et al.* (1998) focus on biogeography of intertidal invertebrates along the coastlines of Namibia and South Africa, and thus have no applicability to the WIO. Nevertheless, Ridgway *et al.* (2001) did show little genetic structuring in six populations of the coral *Pocillopora verrucosa* from the reefs off South Africa, a result that was mirrored by Forbes *et al.* (1999). Forbes *et al.* (1999) show no genetic differences between *Penaeus monodon* populations from South Africa, Mozambique and Madagascar, which is in agreement with the findings of Duda and Palumbi (1999) and Benzie *et al.* (2002). Fratini and Vaninni (2002) found significant genetic differentiation among five sampled populations of *Scylla serrata*, with the Red Sea populations being completely isolated from those from Mauritius, and both these two populations were in turn almost completely isolated from those from Kenya and Tanzania. Furthermore, the tropical African (Kenya and Tanzania) populations were not homogenous, rather showing population genetic structuring, therefore implying that gene flow may be reduced even between geographically close sites.

While only three useful WIO specific population genetic studies were found in this study, information from WIO populations from the more comprehensive biogeographic studies of Benzie (1999), Uthicke *et al.* (2001), and Williams and Benzie (1998) can be extracted to provide a more comprehensive picture (Table 2 - only studies using the same genetic analyses, i.e. allozyme electrophoresis, are compared). Based on genetic variability within populations and genetic diversity indices, it appears that within the WIO region, southeast African marine populations lack significant population structuring, whereas populations off tropical Africa, the Red Sea and in the more tropical Indian Ocean locations appear to show reduced gene flow and hence more population structuring. However, more information is needed to explore this hypothesis further.

While population genetic data has been shown to yield useful information to aid in the conservation and management of most biological systems, the genetic studies of marine populations has made limited progress when compared to their terrestrial counterparts. Nevertheless, the applied aspects of such population genetic research to the marine environment is enormous and spans topics such as stock identification and management, marine aquaculture, creation of marine reserves, conservation of coastal zones, taxonomy, and ultimately the protection of species (Féral, 2002). One of the most important applications of population genetic principles is the understanding

Table 2. Summary of allozyme electrophoretic data from population genetic studies in the Western Indian Ocean. F_{IS} = genetic variation within populations; N/A = not possible to get information from published study

Species	Population	Mean observed heterozygosity	% polymorphic loci	F_{IS}	Reference
Stichopus chloronotus	Reunion	0.198	20	-0.536	Uthicke *et al.* (2001)
Acanthaster planci	South Africa	0.200	66.7	N/A	Benzie (1999)
	Mauritius	0.089	33.3	N/A	
	Maldives	0.106	66.7	N/A	
Linckia laevigata	South Africa	0.375	N/A	N/A	Williams and Benzie (1998)
Pocillopora verrucosa	South Africa	0.145	100	0.026	Ridgway *et al.* (2001)
Penaeus monodon	South Africa	0.102	72.3	0.197*	Forbes *et al.* (1999)
	Mozambique	0.115	77.8	0.197*	
	Madagascar	0.088	66.7	0.197*	

* Data not available for individual populations. Data calculated from pooled populations.

of connectedness among populations of a species. This is particularly important and relevant for regions such as the WIO, which spans numerous different geographical boundaries, and is experiencing rapid environmental degradation that would benefit from urgent large scale management initiatives.

The design of marine reserve systems requires an understanding of larval transport in and out of reserves, whether reserves will be self-seeding, whether they will accumulate recruits from surrounding exploited areas, and whether reserve networks can exchange recruits (Palumbi, 2003). Direct measurements of mean larval dispersal are needed to understand connectivity in a reserve system, but such measurements are difficult due to logistic problems of tracking marine larvae. Genetic patterns of population structure and gene flow have the potential to add to direct measurement of larval dispersal distance and can help set the appropriate geographic scales on which marine reserve systems will function effectively. Ridgway *et al.* (2001) made an initial attempt at gaining such data by looking at the population genetic structure of *Pocillopora verrrucosa* in two already established marine reserve zones in South Africa, and found that all reefs were genetically homogenous. However, it is still too premature to make predictions from such studies and there is therefore a need to gather management directed population genetic data in the WIO if we hope to challenge the current degradation.

In conclusion, we are still far from addressing the research goals outlined by Grant (1993) (measurement of population genetic structure; influence of historical biogeographical events on present day populations; and the use of more realistic models to understand the genetics of natural populations), as very little population genetic information is currently available for the WIO region. The information that is available is not comprehensive enough to address any major management initiatives in the region. However, given the applicability and usefulness of such information to understanding the population structure and exchange of organisms, there should be an imperative to rapidly gain information of this type in the WIO. Further studies will not only build onto the limited picture that is available at present, but more importantly can be used to drive much needed management decisions and implementation in the region. However, stating that more population genetic information is needed in the WIO does need to be put into perspective given that genetic analyses do require certain infrastructural requirements and technical expertise that are mostly underrepresented in the region. Thus, perhaps it is necessary to set up international collaborations, internships and scholarship initiatives in the WIO whereby local researchers and students can undertake management driven research in the region but the laboratory analysis and support can come from overseas and/or the limited number of local laboratories that are established for such analyses. Not only will information be transferred and technical expertise gained, but the much needed population genetic data will also be generated.

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