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Panmixia in East African Populations of *Platygyra daedalea* (Scleractinia: Faviidae)

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Abstract—Very little is known about coral population connectivity and dynamics at regional scales, particularly in the western Indian Ocean. *Platygyra daedalea* was collected from Indian Ocean coral reefs, mainly from the east African coast between Mombasa Marine Park (Kenya) in the north and Maputaland (South Africa) in the South. Simple-sequence repeats from five independent loci in the nuclear genome were used to measure differentiation between populations of *P. daedalea*. Of 350 specimens successfully amplified for one or more simple-sequence repeats, 231 amplified at three or more loci; the remaining specimens comprised a data set that included null alleles. Overall heterozygosity was high, He = 0.8, and the mean number of alleles across loci, per population, was 4.31. The large numbers of null alleles encountered across loci may be attributed to possible parapatric divergence of the nuclear genome in this genus. Ten populations of the nineteen sampled in this study showed signs of heterozygote excesses and deviation from expectations of Hardy-Weinberg equilibrium. The populations studied thus conformed closely to expectations of a panmictic metapopulation with fine-scale structure amongst sub populations (F_{ST} = 0.049), although admixture was evident.

INTRODUCTION

The level of genetic connectivity between coral reefs determines the extent to which they may rely on each other for the maintenance of genetic diversity. Genetic diversity, in turn, serves as a buffer to environmental and extraneous perturbations that may otherwise threaten reef coral health. The connectivity of reef coral populations downstream of each other relative to oceanic current flow is of particular interest to southern African coral reef ecologists.

Reef systems influenced by unidirectional current systems may be connected to one another in a stepwise fashion. Reef corals on

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the east African coast, from southern Tanzania to South Africa, are subject to predominantly south-moving currents and gyres (in the Mozambique Channel, Fig. 1) (Lutjeharms, 2006). Within this context, reef-building corals range from species-rich, accretive systems in the north to hard coral communities with lower species complements in the south (Riegl, 1996; Veron, 2000).

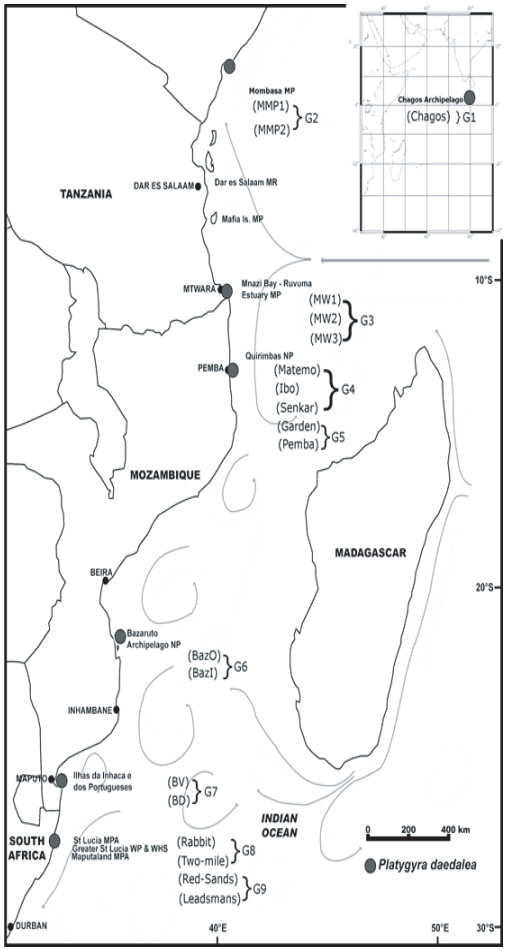

Figure 1. *Platygyra daedalea* sampling sites in the western Indian Ocean and population groups used for AMOVAs. Groups tested for variance were: G1= Chagos Archipelago, G2 = Mombasa Marine Park, G3 = Mnazi Bay, G4 = Quirimbas Archipelago, G5 = Pemba Bay, G6 = Bazaruto Archipelago, G7 = Inhaca Island, G8 = Rabbit Rock Reef and Two-mile Reef and G9 = Red Sands Reef and Leadsman Shoal. Grey lines indicate predominant oceanic currents in the region.

Reef corals have a pelagic larval stage and thus the potential to disperse over large distances and maintain open populations (Avise, 1998). However, there is mounting evidence that most reef-building corals recruit locally (Miller & Mundy, 2003a), making it likely that corals have spread from regions of origin to the boundaries of their distribution in a stepwise fashion. The "stepping-stone model" (Nei, 1972) would appear to best describe regional coral dispersal in coastal waters, where populations adjacent to one another are connected by occasional migrants along a current-mediated passage. This becomes increasingly relevant approaching temperate zones where suitable habitat becomes increasingly less common, as do species of reef-building coral (Bellwood & Hughes, 2001).

Although there is evidence for stochastic long-distance larval dispersal in the Scleractinia, which might mask signals of local structure, the general consensus is that these events rarely take place (Underwood *et al*., 2009). The most abundant reef-building corals on low-latitude reefs appear to have adopted a broadcast-spawning strategy whereby they release gametes into the water column in a single mass-synchronised event (Babcock *et al*., 1994). Recruitment studies indicate that, although local South African hard coral communities (on high-latitude reefs) do not spawn en masse as described above, they employ a similar strategy (Mangubhai & Harrison, 2006) and undergo subsequent periods of high-intensity recruitment (Glassom *et al*., 2006). Simulations of the dispersal of the pelagic propagules of reef corals indicate that most are retained on natal reefs for periods that ensure they are likely to recruit locally (Black *et al*., 1990).

Although spawning events in the south-west Indian Ocean are not as clearly punctuated as those in the Pacific or Caribbean, they appear nonetheless to be stochastic. Difficulties associated with monitoring the dispersal of propagules make it necessary to use a proxy, such as molecular markers, to gauge the relatedness of corals.

Initial studies of reef coral connectivity made use of allozyme frequencies and tested fixation and differentiation within and between reef coral populations at varied scales of separation using Wright's F-statistics (Ayre & Hughes, 2000; Hellberg, 1994). Recent studies of reef coral connectivity have used simple-tandem repeats (STRs or microsatellites) in different genera and at different scales as they show sufficient variation in allele frequency to distinguish fine-scale differences between reef coral populations (Baums *et al*., 2005; Starger *et al*., 2007). Baums *et al*. (2005) found that meta-populations of Caribbean reef corals were regionally-isolated from one another and thus warranted management as separate resources. They used microsatellites to measure genetic diversity (and Wright's F-statistics) within and between reef complexes of *Pocillopora verrucosa* from Bazaruto Island (Mozambique), Kosi Bay, Sodwana Bay and southern Maputaland (South Africa) and found fine-scale differentiation between Mozambican and South African populations.

Platygyra daedalea was chosen as a suitable study organism owing to the availability of effective markers, which were developed for use on Great Barrier Reef (GBR) corals (Miller & Howard, 2004) and used to study east African species (Souter & Grahn, 2008). Recruitment studies have recently shown that *Platygyra daedalea* settles relatively quickly (60–66 h after planulae become viable), which makes local recruitment likely (Miller & Mundy, 2003b). Local populations are therefore likely to be self-seeding; however with occasional migrants, levels of differentiation between populations may be expected to be low. It is plausible that reef populations situated in either naturally-protected areas (deeper reefs or otherwise-inaccessible habitats) or marine protected areas would seed adjacent populations subject to anthropogenic stressors, contributing to local diversity. This hypothesis is tested in this study for populations in the WIO.

The aim of this study was to quantify the partitioning of genetic diversity in extant Indian Ocean populations of *P. daedalea* on the east African coast and reefs in the Chagos Archipelago (Fig. 1), within both legislated marine protected areas and areas under no official management (Wells & Ngusaru, 2004). The diversity and level of connectivity between these populations will serve as an indicator of the resilience of local *P. daedalea* populations, both within and adjacent to marine protected areas (MPAs). We hypothesized that populations of *P. daedalea* are isolated from one another (over ecological scales of connectivity) at scales relevant to their management.

MATERIALS and METHODS

This study complied with the convention on international trade in endangered species of wild fauna and flora (CITES permit no. 075861). Corals were sampled from sites along the east African coast, using SCUBA and snorkel diving (Fig 1). Care was taken to avoid the collection of clone-mates by sampling colonies separated by at least 5m. Samples were immediately stored in either a dimethyl sulfoxide salt buffer (0.25M EDTA; 20% (v/v) DMSO, saturated with NaCl) or 70% ethanol. All DNA was isolated using a Fermentas Life Sciences™ genomic DNA purification kit according to the instructions of the manufacturer. All samples were amplified according to the method of Miller and Howard (2004) in their publication on simple tandem repeat (STR) primer pairs. PCR amplification of specimen DNA was carried out using 3% bovine serum albumin as an adjuvant and at a variety of DNA dilutions to account for the inhibiting effects of contaminants. Primer pairs were then labelled with fluorescent dyes and successful PCRs were repeated with labelled oligonucleotides.

Genotyping

STRs, labelled with recommended dyes (5' 6-FAM, 5' CAL Fluor Orange 560™), were genotyped on an ABI 3750XL automated sequencer and scored manually using STRand v. 2.2.30 (Locke *et al*., 2000).

Data quality and null alleles

The data were checked for null alleles and errors in scoring with Micro-checker (van Oosterhout *et al*., 2004). Null allele frequencies were calculated and adjusted with FreeNA and F_{ST} values were calculated, restricting calculations to observed allele sizes (excluding null alleles, ENA; Chapuis & Estoup, 2007; Weir, 1996). A distance matrix and a neighbour-joining tree were calculated from this (Saitou & Nei, 1987).

Genetic diversity and Hardy-Weinberg equilibrium

Data were explored using GenAlex 6 (Peakall & Smouse, 2006). Microsatellite analyser (Dieringer & Schlötterer, 2003) and Genepop (Raymond & Rousset, 1995) were used to ascertain levels of genetic diversity and deviations from Hardy-Weinberg equilibrium amongst populations and loci. F-Stat was used to measure linkage disequilibrium amongst populations (Goudet, 1995). The rarefaction approach, implemented in Adze (Szpiech *et al*., 2008), was used to calculate allele richness values to adjust for unequal sample sizes.

The final data set comprised 231 individuals collected from 19 localities in the western Indian Ocean. Levels of heterozygosity were calculated, as well as both expected (He) and observed (Ho), mean (Na) and effective (Ne) number of alleles per population, and the Shannon-information index (I) (Table 1). Large numbers of loci failed to amplify across all populations and we calculated adjusted F_{ST} values and population distances to adjust for the large numbers of null alleles (Table 2).

Table 1. Genetic diversity indices for *Platygyra daedalea* in the western Indian Ocean based on five simple-tandem repeat (STR) loci.

Pop	N	Null	Na	SE(±)	Ne	SE(±)	I	SE(±)	Ho	SE(±)	He	SE(±)
Chagos Archipelago	5	0.1	2.2	0.37	1.87	0.26	0.63	0.17	0.7	0.2	0.41	0.11
Mombasa MP1	18	0.24	5.4	0.87	3.41	0.38	1.35	0.14	0.8	0.08	0.69	0.04
Mombasa MP2	26	0.26	6.2	0.37	3.48	0.35	1.4	0.09	0.91	0.05	0.7	0.03
Mtwara 1	10	0.27	5.2	0.8	3.67	0.37	1.41	0.13	0.88	0.07	0.72	0.03
Mtwara 2	7	0.36	4	0.55	3.22	0.47	1.21	0.16	0.95	0.05	0.66	0.05
Mtwara 3	1	0	1.2	0.49	1.2	0.49	0.42	0.17	0.6	0.25	0.3	0.12
Matemo Island	6	0.14	3.4	0.51	3.07	0.49	1.11	0.16	0.82	0.09	0.64	0.05
Ibo Island	2	0.2	2.2	0.2	2.13	0.13	0.76	0.07	1	0	0.53	0.03
Sencar Island	4	0.06	4	0	3.3	0.25	1.27	0.05	0.6	0.1	0.69	0.03
Garden of Eden	18	0.18	5.2	0.66	3.67	0.55	1.37	0.15	0.85	0.06	0.7	0.05
Pemba	12	0.26	4	0.45	2.87	0.38	1.15	0.13	0.78	0.15	0.63	0.05
Bazaruto Archipelago	22	0.29	5.6	1.08	3.24	0.33	1.32	0.12	0.75	0.1	0.68	0.04
Bazaruto Island	6	0.11	4	0.45	3.36	0.28	1.27	0.1	0.81	0.08	0.69	0.03
Bareira Vermelha	7	0.28	2.8	0.37	1.98	0.27	0.77	0.13	0.63	0.19	0.46	0.07
Baixo Danae	6	0.19	2.4	0.4	1.99	0.33	0.69	0.19	0.67	0.19	0.43	0.12
Rabbit Rock	15	0.08	4.8	1.07	3.23	0.47	1.25	0.19	0.86	0.05	0.66	0.06
Two-mile Reef	18	0.12	7	1.3	4.1	0.65	1.53	0.18	0.91	0.02	0.73	0.04
Red Sands Reef	12	0.1	4.8	0.8	3.5	0.5	1.33	0.16	0.81	0.07	0.69	0.05
Leadsman Shoal	36	0.19	7.4	1.21	4	0.55	1.51	0.17	0.78	0.06	0.72	0.06
Grand Mean and SE over Loci and Pops												
Average	**10**	**0.18**	**4.31**	**0.23**	**3.01**	**0.12**	**1.14**	**0.04**	**0.8**	**0.03**	**0.62**	**0.02**

N = sample size, Null = null allele frequency, Na = allelic richness, Ne = effective number of alleles, I = Shannon diversity index, Ho = observed heterozygosity and He = expected heterozygosity.

Table 2. Fixation indices calculated for *Platygyra daedalea* in the western Indian Ocean based on analysis of five STR loci.

	F_{IS}	F_{IT}	F_{ST}	F_{ST} (ENA)	Nm
Pd29-2	-0.192	-0.046	0.122	0.053	1.793
Pd31	**-0.297**	-0.191	0.081	0.022	2.832
Pd48	-0.293	-0.149	0.111	0.057	2.002
Pd61	**-0.289**	-0.168	0.094	0.035	2.406
Pd62	-0.298	-0.125	0.134	0.08	1.622
Overall	-0.274	-0.136	0.108	0.049 $_{(0.032- 0.064)}$	2.131

Bold values indicate significant differences from assumptions of HW equilibrium. 95% confidence limits are indicated for overall F_{ST}.

Population genetic structure

Meta-population structure was inferred from the data using Structure v2.2.4 according to the prescribed method, by applying the default settings without specifying populations to which specimens belonged (Pritchard *et al*., 2000). Five runs, each consisting of 100 000 burn-in iterations and 100 000 iterations, were computed for each value of k (the number of populations) from 2 to 22. The distribution of variance among and within these populations was assessed using AMOVA in Arlequin 3.1.1 (Excoffier *et al*., 2005) and compared to other population structures which might be expected on the basis of geographic and physiological parameters (life strategy, larval competency and settlement patterns; Table 3). Missing data were ignored when generating distance matrices for AMOVA analysis in Arlequin.

Table 3. Components of variance from AMOVA of five STR loci in *Platygyra daedalea* in the western Indian Ocean.

Source of variation	F_{ST}	Component variance in %	$p < 0.05$
(1) Populations in nine geographic groups (Fig. 4.1)	0.12		
Among groupings		6.32	*
Among populations within groupings		5.73	*
Within populations		87.96	*
(2) Populations grouped according to country	0.12		
Among groupings		3.21	*
Among populations within groupings		8.73	*
Within populations		88.06	
(3) Populations in two geographic groupings (North and South)	0.13		
Among groupings		2.58	*
Among populations within groupings		9.94	*
Within populations		87.48	*
(4) Populations in groups designated by Structure	2.2.4	0.18	
Among groups		17.59	*
Within groups		82.41	*

These are based on different potential population structures: 1) geographic groups (Fig. 1), 2) geopolitical (country) groups, 3) north/ south groups and 4) groups designated by Structure 2.2.4 (Pritchard et al. 2000).

RESULTS

Specimens for which there was too little information were assumed to have damaged template material and were removed from the data-set. Some populations contained very low numbers of individuals, as colonies of *Platygyra daedalea* were sometimes difficult to locate where they occurred in low abundance (such as in the Sencar Channel and at Ibo Island). Specimens from low-density populations were included in analyses where appropriate, e.g. as individuals in composite populations.

Data quality

Although considerable data were missing due to non-amplification, they did not conform to expectations of null alleles or large allele dropout. The data were checked for the presence of clonemates and Ng:N was calculated; levels of sexual reproduction were inferred from this. None of the loci were found to be in linkage disequilibrium after standard Bonferroni correction. Considering the large amounts of missing data, all specimens with a minimum of three successfully-amplified loci were considered as containing null alleles at loci that did not amplify (Table 1). Specimens with data missing for more than two loci were considered to have damaged templates and were discarded. Of necessity, specimens were preserved in different media (alcohol, DMSO) during the fieldwork for this study, and the relative quality of the template may have been variable amongst samples.

Genetic diversity

Some indices of genetic diversity in *P. daedalea* (Table 1) varied widely, for example allelic richness (Na = 7.4 – 1.2, SE = 0.23) and the effective number of alleles (Ne = 3.67 – 1.2, SE = 0.12); others showed less variability, for example Shannon's index of diversity (I = 1.53 – 0.42, SE = 0.04). The expected heterozygosity of STR loci (He = 0.62, SE = 0.02) was lower than that observed (Ho = 0.8, SE = 0.3). Large numbers of null alleles were found in the sub-set of samples (this data-set) considered to be of high enough quality for effective data-analysis (Null = 0.18).

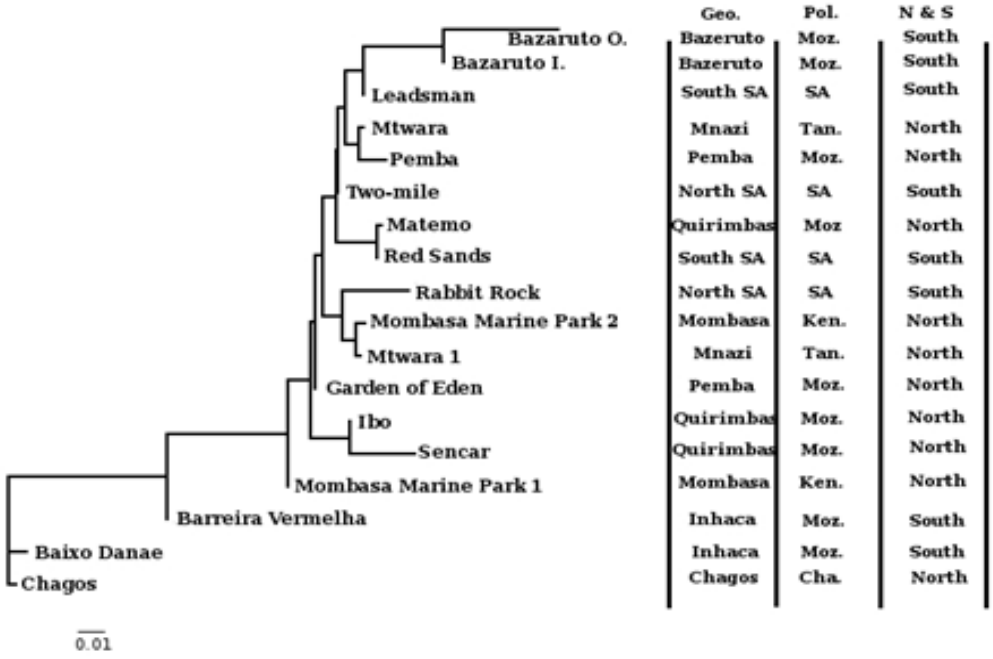

Figure 2. Neighbour-joining tree of population distances for *Platygyra daedalea* in the western Indian Ocean, calculated from the allele frequencies of microsatellite markers. Columns indicate population membership to geographic group of origin (Geo.), country of origin (Pol.) and northern or southern region (N & S).

Distance-based analyses

In the neighbour-joining analysis, populations grouped with those immediately adjacent to one another at scales of less than 100 km (Fig. 2). There was no obvious grouping that followed geo-political boundaries or arbitrary assignment to either southern or northern population groups (as in the AMOVA, Table 3).

Heterozygosity and Hardy-Weinberg equilibrium

With the exception of the Sencar channel population from northern Mozambique, which manifested a heterozygote deficiency, all populations had negative inbreeding coefficient (F_{IS}) values indicative of an excess of heterozygotes. Overall, 17 of the 95 loci (five loci per population) deviated significantly from proportions expected under Hardy-Weinberg (HW) equilibrium conditions; 13 due to heterozygote excesses and four due to heterozygote deficits (Table 1). In all, ten populations deviated significantly ($p < 0.05$) from proportions expected under HW equilibrium. Populations from the central and southern reef complexes in South Africa showed no overall significant deviations from HW equilibria, although they were all characterized by negative F_{IS} values with the exception of the northernmost of the South African populations (Rabbit Rock).

Northern populations (eight sites north of the Bazaruto Archipelago) were found to differ from proportions expected under HW equilibrium; seven displayed heterozygote excesses and one a heterozygote deficit. Among-population comparison of allele frequencies at the five STR loci indicated significant heterozygote excesses, and two loci, Pd 31 and Pd 61, deviated significantly from expected HW proportions of hetero- and homozygotes (Table 2). Both loci were found to harbour an excess of heterozygotes in a global test of adherence to HW equilibrium. The mean overall Ng (214):N (231) value was 0.93, an indication that most genotypes in this dataset were unique. In fact, only four samples in population MMP2 were likely to be clonal and their genotype probability was relatively high ($p = 0.018$).

DISCUSSION

Genetic diversity

Levels of genetic diversity in this study on *Platygyra daedalea* were higher than those found in previous regional studies. Higher levels of heterozygosity at all loci, compared

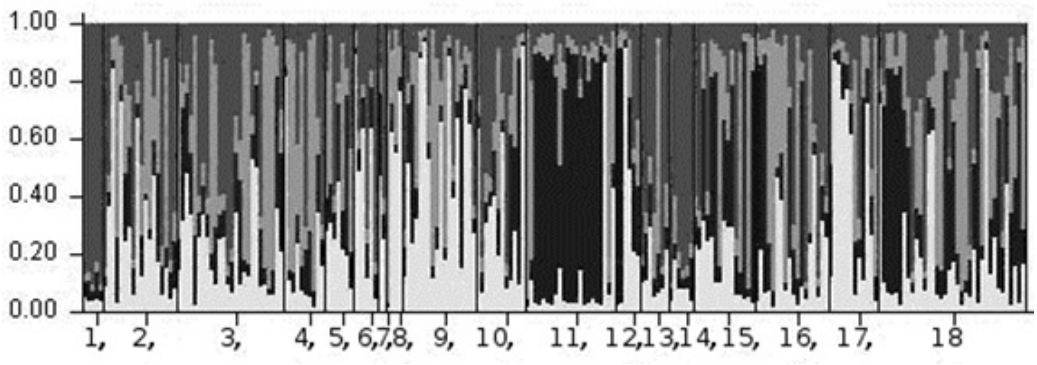

Figure 3. Structure plot of western Indian Ocean populations of *Platygyra daedalea*, showing the likelihood (Y-axis) that specimens at sampling locations (X-axis) belong to each of four meta-populations defined by Hardy-Weinberg equilibria. The numbers 1-18 represent populations of corals arranged from north to south: 1 = Chagos Archipelago; 2 = Mombasa Marine Park 1; 3 = Mombasa Marine Park 2; 4 = Mtwara 1; 5 = Mtwara 2; 6 = Matemo; 7 = Ibo Island; 8 = Senkar Island; 9 = Garden of Eden Reef; 10 = Pemba Bay; 11 = Bazaruto Island 1; 12 = Bazaruto Island 2; 13 = Barreira Vermelha Inhaca Island; 14 = Baixo Danae Inhaca Island; 15 = Rabbit Rock; 16 = Two- mile Reef; 17 = Red Sands Reef; 18 = Leadsman Shoal.

to indices reported in the publication on the markers (Miller & Howard, 2004), belie the fact that the STR primers used in this study were developed from specimens collected on the Great Barrier Reef. However, except for locus Pd29-2, all other loci conformed more closely to originally-published levels of heterozygosity (Miller & Howard, 2004) than to those reported in a more northern study in the western Indian Ocean (Souter & Grahn, 2008). Interestingly, these elevated values for heterozygosity concur with findings on zooxanthellar clade diversity in the SWIO (Macdonald *et al*., 2008; Starzak, 2008).

Tests on Hardy-Weinberg (HW) equilibria indicated that loci in 10 of 19 populations of *Platygyra daedalea* deviated from allele frequencies expected in natural populations and are therefore likely to have been subjected to evolutionary forces: selection, non-random mating, genetic drift or mutation. Most loci that were not in HW equilibrium deviated due to heterozygote excesses. F_{IS} values (inbreeding coefficients) were negative at most localities in this study, indicating either high levels of exchange between localised populations or saturation of allelic differences (Hellberg *et al*., 2002). Souter and Grahn (2008) obtained comparable results for lagoonal populations of *Platygyra daedalea*, and accounted for this by invoking the increased stress to which these populations are subjected. Plausible scenarios that could lead to the levels of heterozygosity observed in this study include small effective population sizes, self-incompatibility (SI) in sexual reproduction, or significant asexual contributions to the gene pool (Stoeckel *et al*., 2006; Balloux *et al*., 2003b).

Miller and Babcock (1997) worked extensively on potential reproductive barriers in Platygyra and concluded that there was limited incompatibility between species, let alone within a species, thus SI was not considered a plausible reason for the observed negative F_{IS} values. It is plausible that asexual reproduction could lead to the estimation of smaller effective population sizes from a given data-set. Balloux *et al*. (2003a) reported that variance of F_{IS} (the major component of variance involved in this study) amongst loci is an indication of the level of asexual reproduction. Hard corals are known to reproduce asexually and this data may be interpreted as stemming from a certain level of clonal propagation amongst the populations sampled. However, this conflicts with the overall Ng:N ratio of 0.93, this being roughly the minimum sexual contribution for the measured genotypic diversity. The proportion of asexual reproduction within a population that is also sexually reproducing is difficult to discern, thus caution should be exercised in making inferences on this parameter (Balloux *et al*., 2003a). It should be noted that no evidence for asexual reproduction in *P. daedalea* was observed in this study.

Small effective population sizes may contribute to heterozygote excesses, as described by Potts (1984), since hard corals are organisms that may have extremely long generation times. Instead of organisms above a certain age making little contribution to a gene pool, old, longer-lived colonies in a region may contribute inordinately to successive generations. "Chronic evolutionary disturbance" and failure to attain genetic equilibrium may have combined to generate high levels of intraspecific variation in scleractinian corals (Potts 1984). Furthermore, Mangubhai and Harrison (2006) found that *P. daedalea* may spawn biannually in Kenya within a relatively narrow time-frame, possibly leading to genetic contributions by even fewer individuals. Census population sizes may potentially be much larger than estimated effective population sizes.

Localised mating, wherein colonies within a localised area mate with each other but not with colonies from the greater population (or sub-population), may lead to "chaotic patchiness" (Hellberg *et al*., 2002). This scenario is characterised by high migration estimates combined with low estimates of effective population size (Ne) and poorly fitted patterns in genetic structure, such as those observed in the present data (Table 3). This pattern of chaotic patchiness is echoed in studies of marine invertebrate dispersal in other taxa and has been termed 'sweepstakes recruitment success' (Hedgecock, 1994; Flowers *et al*., 2002). However, unless tested amongst generational cohorts, this may not

be confirmed. The high levels of observed heterozygosity and low levels of allelic richness in our samples were tell-tale signs of reproduction by a small number of adult organisms (Hedgecock *et al*., 2007). Island populations (the Chagos Archipelago and Inhaca Island) in this study exhibited low levels of allelic diversity (Fig. 4); this was to be expected in terms of their likely chance of recruitment of discrete 'cohorts' of propagules, relative to other corals in the region. Genetic diversity indices in this study showed that corals in the Chagos Archipelago are genetically more isolated than coral populations along the east African coastline (Table 1; Fig. 4), probably due to their relative geographic isolation. Inhaca Island coral populations may also be expected to be isolated as a result of their location amidst slow-moving current regimes and their distance from habitable substrata for corals in the north (Fig. 1). The present data indicate that the Inhaca Island populations are isolated from nearby reefs, although they may seed South African reefs (south of Inhaca Island) with propagules.

Allelic richness, calculated from the smallest population included in the study (Ibo Island), was comparable throughout most of the study area, with the exception of three island populations (Baixo Danae, Barreira Vermelha, both at Inhaca Island, and the Chagos Archipelago). Use of the rarefaction approach in standardizing sample size made it clear that populations of *Platygyra daedalea* at Inhaca Island and in the Chagos Archipelago have relatively lower levels of allelic richness (Fig. 4). This was corroborated by values of the Shannon-Information Index which mirrored the results of rarefaction in allelic richness (Table 1).

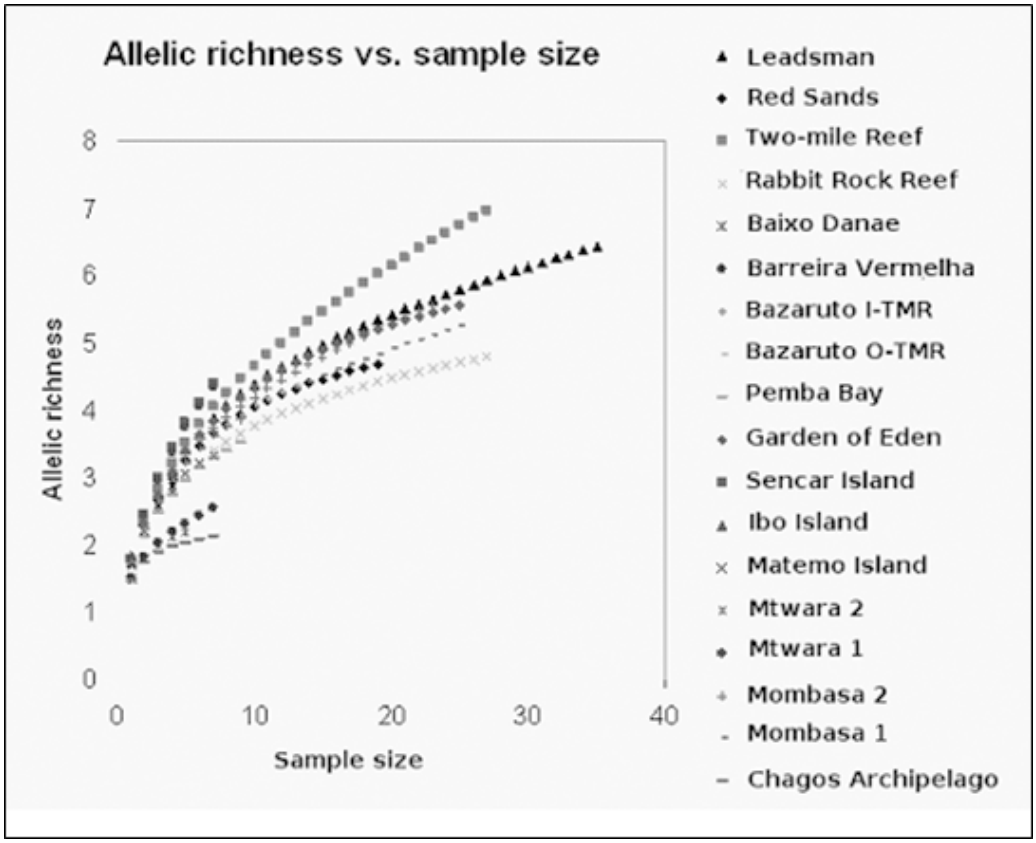

Figure 4 Relationship between allelic richness, calculated using ADZE (Szpiech *et al*., 2008), and sample size in western Indian Ocean populations of *Platygyra daedalea*.

Connectivity

Four populations were defined by the program Structure 2.2.4, irrespective of their geographic origin (Fig. 3). Structure 2.2.4 assumes linkage disequilibrium and Hardy-Weinberg equilibrium to assign colonies to a most probable population on the basis of the individual allele frequencies. The likelihood of four populations, designated by Structure v2.2.4, may in this case correspond to the habitats from which specimens were sampled, namely island-fringing reefs, reef flats (0–1 0m), reef slopes and deep reefs (10–20 m; Bongaerts *et al*., 2010). The evidence of four populations in the data-set may be considered to be the uppermost level of hierarchical structure (Evanno *et al*., 2005). Sub-structures within this hierarchy may be indicative of patterns in topographic- and ocean current-mediated levels of exchange between sub-populations (i.e. the connectivity within a designated population).

Ridgway *et al*. (2001, 2008) studied the regional population genetics of *Pocillopora verrucosa* using allozymes and microsatellites. The allozyme data indicated large-scale panmixia amongst reefal populations in South Africa, whilst STR data indicated that P. verrucosa from the Bazaruto Island Archipelago was only connected to a limited extent to populations in Southern African waters (F_{ST} = 0.054). Local patterns of gene flow in *P. daedalea* showed that discontinuity in connectivity between southern Mozambique and Maputaland may be prevalent in other genera of hard corals with very different life-strategies. The South African populations of *P. daedalea* on Rabbit Rock deviated significantly from expected HW proportions due to an excess of heterozygotes, an indication of an anomalous genetic discontinuity that may be due to their derivation from another source. East Madagascar is under consideration in this regard, the connection being mediated by admixture of waters from the East Madagascar Current into the Agulhas Current which probably first impinges on the African coastline in the vicinity of Rabbit Rock.

Although the Indian Ocean was subject to some of the most severe bleaching episodes experienced globally during 1998, the incidence of bleaching in the SWIO was considerably less severe than that reported further north (Obura, 2000). Lower levels of bleaching may be attributable to a number of factors, including the moderating-effect of the fast-flowing Agulhas Current on temperatures on South African reefs (Lutjeharms, 2006). High levels of heterozygote excess and significant deviations of gene frequencies from HW equilibrium appear to characterise most northern populations of *Platygyra daedalea*, and may indicate selection due to exacerbated stressors in this region.

Comparison of diversity between MPAs, adjacent coral populations and between geo-political regions

Most of the variability within this data-set may be attributed to between-individual differences in allele frequencies, as within-population variances ranged from 87.48% to 88.06% (Table 3). Variation between groupings accounted for between 17.59% and 2.58% of the variance (Table 3). The lowest between-group variance (data not shown) arose from a comparison of protected with open areas; there were no overarching differences between gene frequencies of *P. daedalea* from protected and open areas. However, further sampling of unprotected areas should be undertaken before this can be regarded as conclusive evidence of homogeneity in the protected and unprotected populations.

South African reef systems may be the best-protected on the East African coast in terms of legislation, but some are potentially heavily perturbed through diver damage. Reef systems to the north have recently been declared protected areas, but this may only be in name, with little real protection from anthropogenic extraction of resources or eutrophication (e.g. Bazaruto Archipelago National Park, Quirimbas National Park). The lack of variability between data grouped according to the legislated level of protection (MPAs vs open areas) reflected the lack of discernible genetic signal between these groups. South African

reef populations of *P. daedalea* satisfied Hardy-Weinberg equilibrium measures in general, which may be evidence of their relatively undisturbed habitats. Comparisons of allelic richness and HW equilibria between true accretive reef systems and marginal reefal communities of hard corals would be expected to reveal higher indices of richness in highly diverse, accretive reef systems (Ridgway *et al*., 2008; Souter & Grahn, 2008). The lack of real differences in allelic richness, aside from those between island and coastal communities, could be an indication that the northern reef systems are degraded. This study was conducted over a geographic cline, and thus selection should also not be ruled out as the evolutionary force acting upon these populations.

Geographic structure

The *Platygyra daedalea* population on the south eastern African coast appears to comprise a meta-population that spans the region, manifesting a genetic admixture between populations within the range sampled. On this basis, *P. daedalea* may be expected to recover from localised disturbances. Our hypothesis that populations are separated at ecological time-scales was not supported; even though there was fine-scale structure, it did not appear to be determined by geographic separation of the populations. Furthermore, populations to the south of the study area harboured levels of allelic richness comparable to those in the north. Southern populations of *P. daedalea* also contained as much genetic diversity as their northern congeners and, thus, the ability to adapt to changing environments. This indicates that this species of hard coral may not be at risk over evolutionary time scales at its southernmost limits. However, only one species of hard coral was examined in this study and other species should be included in future studies to obtain a broader picture of genetic connectivity in the region. Finally, the distribution of the genotypes in this study did not appear to be related to geography, which suggests that other factors should be considered that may contribute to genetic partitioning in this species (Bongaerts *et al*,. 2010).

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