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Population genetic structure of the *Pocillopora damicornis* morphospecies along Ningaloo Reef, Western Australia

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ABSTRACT: The effective management of a coral reef system relies on a detailed understanding of the population structure of dominant habitat-forming species. For some corals, however, high levels of phenotypic plasticity have made species delineation based on morphological characteristics alone unreliable, suggesting that previous studies of population genetic structure may have been influenced by the inclusion of multiple genetic lineages in the analyses. We examined the population structure of the *Pocillopora damicornis* morphospecies along the World Heritage Ningaloo Coast, Western Australia, and recovered 2 mitochondrial haplotypes from sympatrically occurring colonies possessing morphological characteristics consistent with taxonomic classification of *P. damicornis.* Despite a high degree of genetic differentiation between these lineages, we detected low levels of unidirectional admixture between them, suggesting that reproductive barriers are not fully developed. We found dual modes of reproduction for both lineages with considerable variation in the contribution of sexual reproduction among sample sites. Lastly, we identified a high dispersal potential of sexually produced propagules in the most common lineage with positive spatial autocorrelation detected over distances up to 60 km. Based on these results, it appears that populations of *P. damicornis* have a high capacity to recover from environmental perturbations as long as the effects of disturbances are patchy across Ningaloo Reef.

KEY WORDS: Ningaloo Reef · *Pocillopora damicornis* · Dispersal · Resilience

INTRODUCTION

Fundamental to the resilience of coral reefs is the rate of recovery of populations following environmental perturbations (Nyström et al. 2000), which has been strongly linked to the level of connectivity between adjacent reefs (West & Salm 2003, Hastings & Botsford 2006). In situations where the effects of a disturbance are patchy, the recovery of an impacted reef is often reliant on the supply of recruits from adjacent areas that avoided the disturbance. As a result, populations with high levels of connectivity are likely to be more resilient than isolated populations. Effective management of a coral reef system therefore requires a comprehensive understanding of the population structure of habitat-forming species.

In contrast to the detailed knowledge of population genetics and connectivity of corals that underpins the

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science and management of the Great Barrier Reef (GBR, e.g. Ayre & Dufty 1994, Ayre et al. 1997, Ayre & Hughes 2000, Smith-Keune & van Oppen 2006, Miller & Ayre 2008, Souter et al. 2010), little is known about the levels of connectivity among coral populations in the eastern Indian Ocean (but see Underwood et al. 2007, 2009, Underwood 2009). Ningaloo Reef is situated along the northwest coast of Western Australia between 21° 47′ and 23° 38′ S, and is the only fringing reef system on the western coast of a continent. It harbours 217 hermatypic coral and 460 fish species (Veron & Marsh 1988) and is currently managed as a multiple-use marine park. The reef stretches continuously for approximately 250 km, providing an excellent opportunity to explore connectivity across a region uninterrupted by oceanographic barriers.

The common Indo-Pacific coral *Pocillopora damicornis* (L.) is a dominant habitat-forming coral throughout Australia, and one of the most extensively studied scleractinian coral species, partly due to its wide geographic distribution (Veron 2000). In Western Australia, *P. damicornis* is found from the far north of the Kimberley region to the temperate waters of the southwest (Veron & Marsh 1988). *P. damicornis* is hermaphroditic and exhibits mixed modes of reproduction by brooding of asexual planulae, as well as broadcast spawning of gametes (Ward 1992). While the majority of populations along the GBR exhibit little evidence of asexual recruitment (Benzie et al. 1995, Ayre & Hughes 2000, Miller & Ayre 2004, Sherman et al. 2006, Torda et al. 2013), populations in Western Australia appear to be dominated by clonal recruits (Stoddart 1984, Whitaker 2006).

Previous assessments of *P. damicornis* population structure in the region identified strong levels of genetic subdivision and restricted gene flow (Whitaker 2006); however, recent evidence has shown that high levels of phenotypic plasticity within *Pocillopora* make species delineation based on morphological characteristics alone unreliable (Schmidt-Roach et al. 2014). This has led to widespread inconsistencies in the taxonomic classification of individuals within this genus and suggests that earlier population genetic studies may have been biased by the inclusion of multiple gene pools into analyses.

This study examined the population structure of *P. damicornis* along Ningaloo Reef using a panel of polymorphic microsatellite markers (Starger et al. 2008) and a single hyper-variable region of the mitochondrial genome (open reading frame, ORF; Flot & Tillier 2007) that is useful for interspecific delineation of *Pocillopora*. The aims of this study were to document the number of genetic lineages associated with coral colonies having morphological characteristics consistent with traditional classification of *P. damicornis* and to then examine the population genetic structure across the reef within a single lineage.

MATERIALS AND METHODS

Sample collection and DNA extraction

Samples from 303 colonies of *Pocillopora damicornis* (as described in Veron 2000) were collected from 8 sites along Ningaloo Reef and from 2 sites at the Muiron Islands in December 2012, spanning the entire length of Ningaloo Marine Park and Muiron Islands Management Area (hereafter referred to collectively as Ningaloo Reef; see Fig. 1). Distances between sample sites ranged from 4 to 250 km, and samples were collected along a 150 m transect at depths less than 5 m. Small fragments were taken from colonies separated by a minimum of 2 m to reduce the chance of sampling individuals that were formed via fragmentation. Samples were preserved in 99% analytical reagent grade ethanol until DNA extraction. Genomic DNA was extracted using a modified silica-based method as described in Ivanova et al. (2006).

DNA sequencing and analysis

To determine the number of discrete genetic lineages in our sample set, the mitochondrial ORF was amplified using primers FATP6.1 (5′-TTT GGG SAT TCG TTT AGC AG-3′) and RORF (5′-SCC AAT ATG TTA AAC ASC ATG TCA-3′; Flot & Tillier 2007) following thermal cycling conditions in Souter et al. (2010). ORF regions were amplified in 25 µl containing 12.5 µl of MyTax Mix (Bioline®), 0.5 µl BSA (10 mg ml^{-1}), 0.5 µl of each primer (10 µM), 20 ng of DNA template and water to volume. Amplicons were purified and sequenced in both directions on an AB3730 *xl* platform (Australian Genome Research Facility, Perth Node). Sequence chromatograms were edited and analysed in Geneious Pro v.5.4 (Drummond et al. 2011). Sequences were aligned using a gap-opening penalty of 12 and a gap extension penalty of 3. Network v.4.5.1.6 (www.fluxus-technology.com) was used to construct phylogenies using the median joining-algorithm (Bandelt et al. 1999).

Microsatellite genotyping and analysis

Microsatellite markers (Table 1) were amplified in 10 µl reactions following thermal cycling conditions in Starger et al. (2008). Size fragment analysis was performed with fluorescent-labelled primers in GENEMARKER v.1.90 (SoftGenetics) using automated scoring of alleles with manually prepared bins. All scores were checked manually to minimise genotyping errors. Tests for significant heterozygote deficiencies were conducted in GENEPOP v.4.2 (Raymond & Rousset 1995) and for any evidence of linkage disequilibrium in ARLEQUIN v.3.5 (Excoffier et al. 2005). The microsatellite dataset was uploaded to the Dryad data repository (doi:10.5061/dryad.h4n48).

Admixture between lineages

All of the following analyses were conducted on the data set with replicate multi-locus genotypes (MLG) at each site removed. To determine the proportion of genetic variation that could be attributed to differences among lineages, analysis of molecular variance (AMOVA) was performed in GENALEX v.6.3. A STRUCTURE (Pritchard et al. 2000) analysis was then performed to test for evidence of hybridization between the lineages under the admixture model that assumed correlated allele frequencies with a location prior and a burn-in value of 100 000 and 1 000 000 Markov chain Monte Carlo (MCMC) iterations. The appropriate K value was determined by plotting the log probability, L(K), and ΔK across K values ranging from 1 to 10 (Evanno et al. 2005) as implemented in STRUCTURE HARVESTER (Earl & vonHoldt 2012) based on 10 independent runs for each K value. Results were averaged using CLUMPP (Jakobsson & Rosenberg 2007) before graphics were generated. NEWHYBRIDS v.1.1 (Anderson & Thompson 2002) was used to identify admixed individuals as potential hybrid colonies, using a MCMC procedure to identify individuals as either pure, hybrids or backcrosses. Results were averaged across 5 independent runs using uninformed (Jeffreys) priors with no individual-specific assumptions and based on a burn-in value of 100 000 and 1 000 000 sweeps. A posterior probability value of 0.50 was used as a threshold for hybrid assignment (Vähä & Primmer 2006).

Table 1. Standard diversity statistics for each open reading frame (ORF) lineage recovered from samples along Ningaloo Reef. N: Number of samples; N_A: number of alleles per locus; N_E: effective number of alleles per locus; H_o: observed, H_e: expected; F_{IS}: inbreeding coefficients. Numbers in **bold** indicate significant deviations (heterozygote deficiencies) from Hardy-Weinberg Equilibrium (HWE)

ORF Locus	N	N_A	N_E	H_o	H_e	F_{IS}
Type α						
Pd3-005	162	10	3.443	0.580	0.710	**0.182**
Pd3-009	162	6	3.879	0.753	0.742	−0.015
Pd3-004	162	3	2.269	0.630	0.559	−0.126
Pd3-008	162	5	1.999	0.556	0.500	−0.111
Pd2-001	162	2	1.124	0.117	0.110	−0.062
Pd2-007	162	5	1.756	0.327	0.430	**0.240**
Type β						
Pd3-005	141	12	3.960	0.915	0.747	−0.224
Pd3-009	141	8	4.627	0.908	0.784	−0.158
Pd3-004	141	4	2.091	0.454	0.522	**0.130**
Pd3-008	141	6	2.238	0.681	0.533	−0.231
Pd2-001	141	4	1.538	0.319	0.350	0.087
Pd2-007	141	11	3.554	0.950	0.719	−0.323

Patterns of clonality

The probability of 2 independent samples having identical MLGs was calculated in GENEALEX v.6.3 (Peakall & Smouse 2006). This value provides an estimate of the exclusion power of the loci used in the analysis to accurately distinguish between different individuals. The extent of asexual reproduction was assessed within each lineage using genotypic richness, R (Dorken & Eckert 2001), and genotypic diversity, D (Nei 1987), which was calculated in GENODIVE (Meirmans & van Tienderen 2004) and provides an estimate of how evenly the genotypes are divided over a population. These indices were only calculated when more than 10 colonies were sampled at a particular site.

Population structure

Population structure was assessed for each lineage separately using Bayesian clustering analysis in STRUCTURE and spatial autocorrelation (SA) analysis in GENEALEX v.6.3. The STRUCTURE analyses were based on the same parameters as above. SA analysis was implemented to determine the genetic neighbourhood size of each lineage. SA uses pairwise matrices of genetic distance and geographic distance between sample sites to generate a plot of genetic similarity over increasing distance classes. We calculated the SA coefficient (r) for a range of dis-

tance classes up to 200 km for each lineage. The location where *r* crosses the *x*-intercept and no longer differs significantly from 0 provides an estimate for the extent of detectable spatial genetic structure. For each distance class, 95% confidence intervals were generated based on 10 000 permutations and 10 000 bootstrap replicates.

RESULTS

Discrete mitochondrial DNA lineages

Two ORF haplotypes (GenBank accession nos. KJ690905 and KJ690906) were recovered from 303 colonies across Ningaloo Reef (Fig. 1). Network analysis revealed that these haplotypes formed 2 genetically distinct lineages, separated by 6 evolutionary steps and corresponding to Types α and β in Schmidt-Roach et al. (2013) and Types 4 and 5 in Pinzón et al. (2013) (Fig. 2). The ORF haplotypes recovered in this study, hereafter referred to as Type α and Type β, were found at all sampling locations.

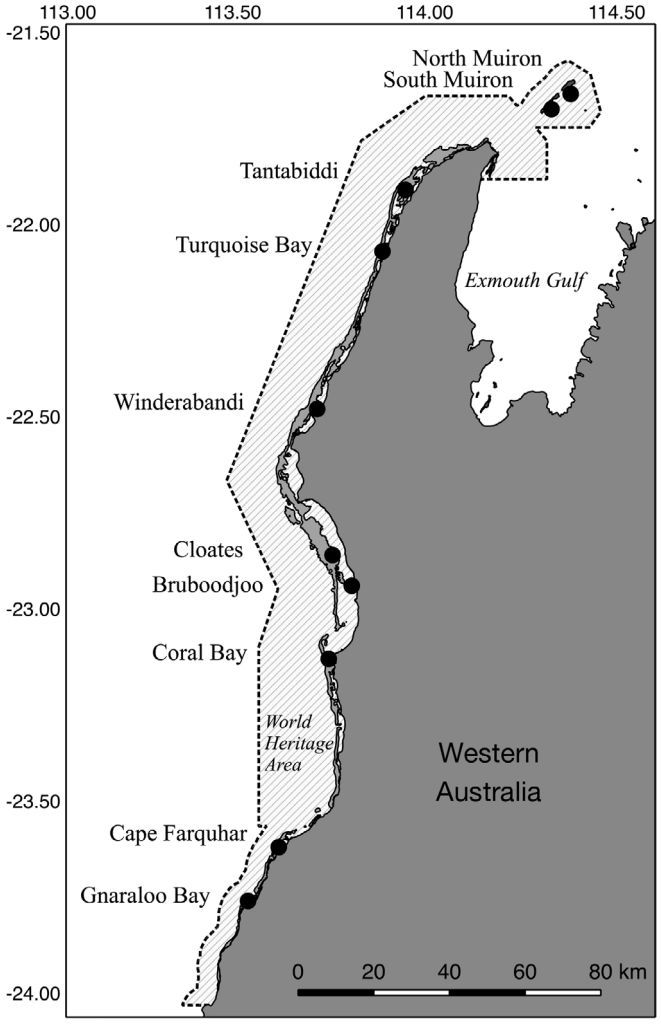

Fig. 1. Sample sites along Ningaloo Reef and Muiron Islands Management Area

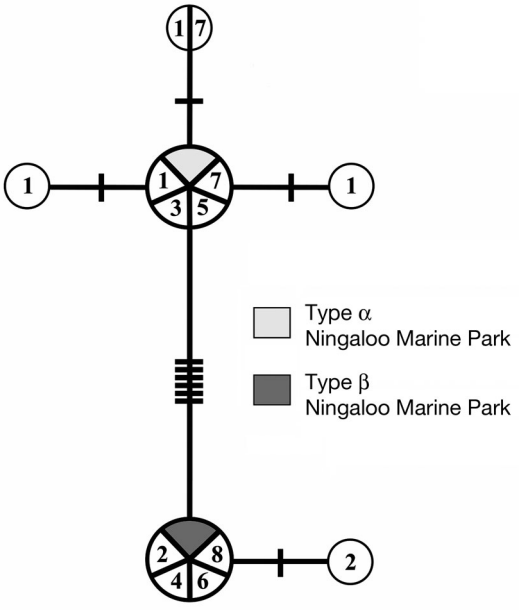

Fig. 2. Maximum parsimony tree adopted from Schmidt-Roach et al. (2013) and redrawn to include Type α and Type β haplotypes recovered from this study. Numbers inside the figure correspond to the following: 1 = Great Barrier Reef (GBR) (Type α; Schmidt Roach et al. 2013); 2 = GBR (Type β; Schmidt-Roach et al. 2013); 3 = Hawaii (Type a; Flot et al. 2008); 4 = Hawaii (Type b; Flot et al. 2008); 5 = Taiwan (Chen et al. 2008); 6 = East Africa (Type F; Souter 2010); 7 = Type 4 (Pinzón et al. 2013); 8 = Type 5 (Pinzón et al. 2013)

Microsatellite genotyping results

All loci analysed were polymorphic for both lineages. The number of alleles for Type α ranged from 2 (Pd2-001) to 10 (Pd3-005), and for Type β from 4 (Pd2-001/Pd3-004) to 12 (Pd3-005). When estimated for all populations, 2 loci for Type α (Pd3-005 and Pd2-007) and 1 locus for Type β (Pd3-004) showed significant signs of heterozygote deficiencies (Table 1). No loci deviated significantly from Hardy-Weinberg Equilibrium (HWE) across all sample locations (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m513p111_supp.pdf). While significant ($p < 0.001$) linkage disequilibrium was detected in a number of cases, no two loci were linked in all locations following standard Bonferroni corrections.

Admixture between lineages

AMOVA revealed that a substantial proportion of the total variation (30%, $p < 0.001$) could be attributed to differences between genetic lineages. Bayesian clustering analysis including Types α and β revealed $K = 2$ as the most likely number of clusters according to plots of L(K) and ΔK across different K values (Fig. S1). The clustering results showed that an individual's membership to a genetic cluster was consistent with the lineage designations based on mitochondrial ORF data (Fig. 3). Low levels of unidirectional admixture were also identified (n = 13, 11% of MLGs) from Type α into Type β. All of the admixed individuals were identified as F_1 hybrids except for one at Site CLO, which was a backcross to a Type β parent (Fig. S2). Hybrids were recovered from Sites NM (n = 6), SM (n = 4) and CLO (n = 3); two of the F_1 hybrids shared the same MLG and were recovered from different sites (CLO and SM).

Patterns of clonality

A total of 118 MLGs were identified from the 303 samples analysed, 40% of which were shared between at least 2 colonies. The combined probability of identity for the panel of microsatellite markers was 2.6×10^{-4} and 3.3×10^{-5} for Types α and β, respectively, and indicated it was unlikely that the samples with shared MLGs were different sexually-produced individuals. Both lineages exhibited signs of mixed modes of reproduction with high levels of spatial variation in clonality (Table 2). Genotypic richness for Type α ranged from 0.15 to 0.87 and for Type β from 0.07 to 0.77. When samples were pooled, Type α exhibited much higher levels of genotypic richness (R = 0.52) than Type β (R = 0.24). Genotypic diversity was also higher for Type α (D = 0.98) than Type β (D = 0.85). The maximum number of colonies associated with a single Type α MLG was 13 from Site GB. The maximum number of colonies associating with a single Type β MLG was 50 and was shared across 3 sites (FQ, CB and BBJ). There were 4 instances where a Type α MLG was shared between sites (TRQ/NM, SM/NM, SM/FQ, GNB/FQ/CB) and 7 instances where a Type β MLG was shared between sites (SM/CLO, WNB/BBJ, CB/BBJ, FQ/CB/BBJ, TBD/CB, WNB/NM, SM/NM). Distances between sites that shared an MLG ranged from 6 to 240 km.

Population structure

Because high levels of clonality reduced MLG sample sizes, population-level analyses such as F-statistics were avoided, and only individual-level genetic analyses were performed. The following analyses were only conducted on Type α, as sample sizes for Type β were too small to provide meaningful results.

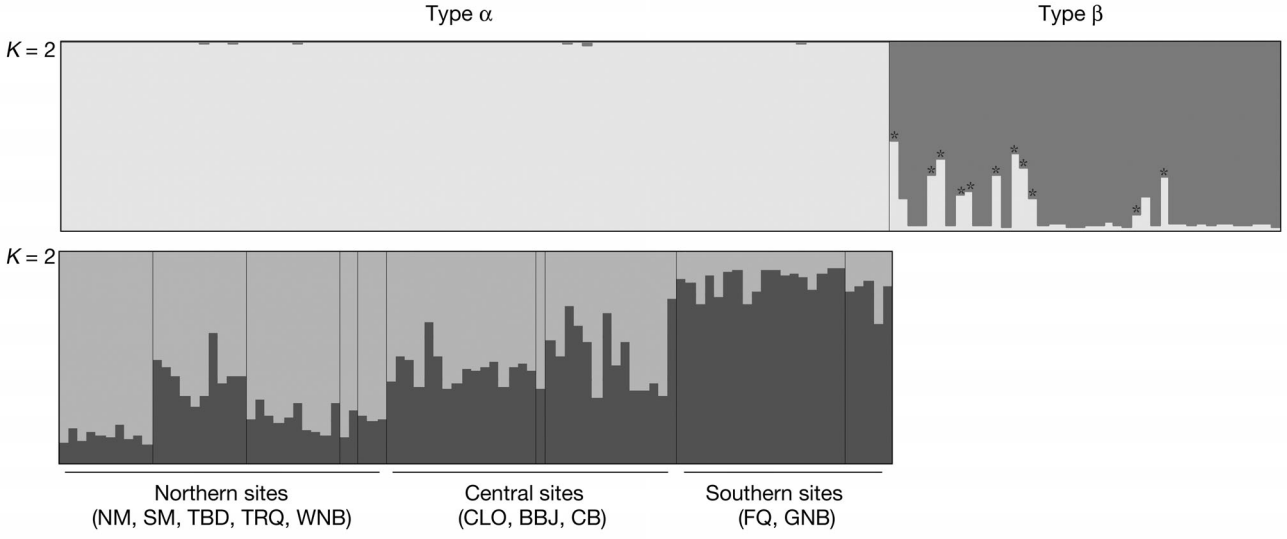

Fig. 3. Bar plots from the Bayesian clustering analysis in STRUCTURE testing for admixture between lineages (above) and structure within Type α across sample sites (below). For the above figure, individuals were grouped according to open reading frame (ORF) lineage (K = 2). See Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m513p111_supp.pdf for plots of log probability L(K) and ΔK across different K values. Individuals identified as hybrid colonies using NEWHYBRIDS are indicated by asterisks. For the below figure, sample sites are grouped as northern (NM, SM, TBD, TRQ, WNB), central (CLO, BBJ, CB) and southern (FQ, GNB) sites. See Fig. S3 for plots of L(K) and ΔK across different K values for Type α analysis

Investigating population structure of Type α in STRUCTURE revealed $K = 2$ as the likely number of genetic populations (Figs. 3 & S3). Under the $K = 2$ model, proportional membership for each sampling location showed a gradual transition from Cluster 1 in the far north (0.907) to Cluster 2 in the far south (0.801). For SA analyses, we plotted *r* over even distance classes (20 km), which left no bins empty and a minimum of 194 pairwise comparisons per bin. Significant positive *r*-values were found for the first 3 distance classes (up to 60 km), after which *r* decreased and became significantly negative at 120 km and beyond (Fig. 4). The multiple distance class analysis revealed positive genetic structure over distances up to 200 km.

Table 2. Indices of genotypic richness (*R*) and genotypic diversity (*D*) for each open reading frame (ORF) lineage. Abbreviations are provided along with sample size (N) and number of unique multilocus genotypes (N_G)

Sampling sites	Abbrev.	N	N_G	*R*	*D*
Type α					
North Muiron	NM	16	10	0.60	0.94
South Muiron	SM	13	10	0.75	0.95
Tantabiddi	TBD	22	10	0.43	0.90
Turquoise Bay	TRQ	3	2	–	–
Winderabandi	WNB	6	3	–	–
Cloates	CLO	27	16	0.58	0.94
Bruboodjoo	BBJ	1	1	–	–
Coral Bay	CB	16	14	0.87	0.98
Cape Farquhar	FQ	30	18	0.59	0.96
Gnarraloo Bay	GNB	28	5	0.15	0.73
Sites pooled		162	84	0.52	0.98
Type β					
North Muiron	NM	14	11	0.77	0.96
South Muiron	SM	16	5	0.27	0.75
Tantabiddi	TBD	2	2	–	–
Turquoise Bay	TRQ	2	2	–	–
Winderabandi	WNB	35	6	0.15	0.77
Cloates	CLO	4	4	–	–
Bruboodjoo	BBJ	46	4	0.07	0.27
Coral Bay	CB	12	3	0.18	0.62
Cape Farquhar	FQ	9	4	0.38	0.58
Gnarraloo Bay	GNB	1	1	–	–
Sites pooled		141	34	0.24	0.85

DISCUSSION

The *Pocillopora damicornis* morphospecies along Ningaloo Reef represents 2 distinct genetic lineages occurring in sympatry throughout the study area. Although large genetic differences were identified between lineages, there was evidence of localized hybridization, suggesting partial pre-zygotic reproductive barriers between them. We found evidence of mixed modes of reproduction within both lineages and a high degree of spatial variation in clonality across the 250 km study site. Finally, large genetic neighbourhoods of the most commonly occurring lineage were identified (up to 60 km), suggesting high levels of connectivity between adjacent reefs across Ningaloo Reef.

Two mitochondrial haplotypes (Type α and Type β) were recovered from sympatrically occurring colonies possessing morphological characteristics consistent

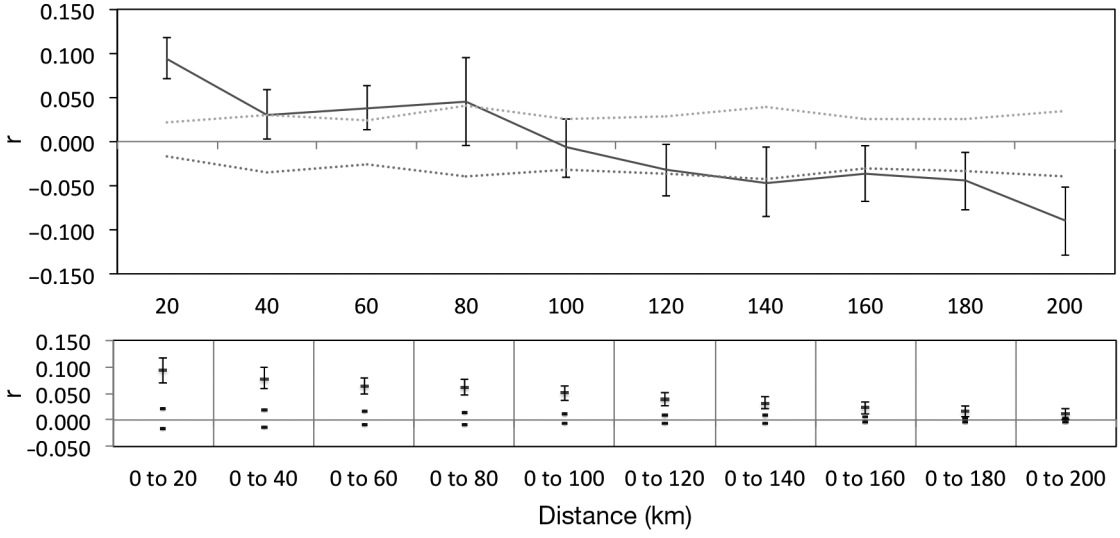

Fig. 4. Spatial autocorrelation analyses of Type α individuals with a single correlogram plot (above) and multiple distance class plot (below); 95% confidence intervals are provided

with *P. damicornis* (as described by Veron 2000). Despite extensive oceanographic barriers between Western Australia's coral reefs and the GBR, there was no endemism in the haplotypes. Both haplotypes have been recovered from colonies in sympatry along the GBR (Schmidt-Roach et al. 2013, Torda et al. 2013), as well as from Hawaii (Flot et al. 2008) and Taiwan (Chen et al. 2008, Pinzón et al. 2013). While Type α appears to be restricted to the Indo-Pacific and East Indian Ocean, Type β has also been recovered off East Africa (Type F; Souter et al. 2009, Souter 2010), the Andaman Sea and the Persian Gulf (Pinzón et al. 2013).

According to a recent revision of *Pocillopora* taxonomy, which coupled genetics with morphological analyses, Types α and β are separate species (Type α belongs to *P. damicornis* and Type β to its formerly synonymized sister species, *P. acuta*); however, fine-scale morphological features between the 2 types are indistinguishable, and phenotypic plasticity makes differentiation based on gross morphology alone to be unreliable (Schmidt-Roach et al. 2014). In support of these findings, the low incidence of genetic mixing between Types α and β detected in this study, despite their sympatric distributions, suggests there are reproductive barriers between them. However, the admixture that was detected provides evidence that pre-zygotic barriers are not fully developed. The unidirectional nature of the admixture indicates that Type α has mate recognition systems that inhibit interspecific gamete compatibility, while eggs from Type β may be capable of being fertilized by heterospecific sperm. Hybridization has not been well documented in Pocilloporids (but see Miller & Ayre 2004, Combosch et al. 2008), but the morphological overlap and evidence of hybridization between lineages detected in this study brings into question the stability of these *Pocillopora* species over time.

The population structure of Types α and β reflect mixed modes of reproduction along Ningaloo Reef, with substantial variation in the relative contribution of each mode across the study area. The contribution of asexual reproduction to population structure (Type α = 48%, type β = 76%) was greater than elsewhere in Australia (7 to 28%; Ayre & Hughes 2000, Miller & Ayre 2004, Torda et al. 2013) and across the species' range (2 to 6%; Souter et al. 2009, Starger et al. 2010, Combosch & Vollmer 2011). Populations of *P. damicornis* in southwest Australia display highly clonal population structure relative to their GBR counterparts (Stoddart 1984), and this study confirms that asexual brooded larvae of both Types α and β play a major role in local recruitment along Ningaloo Reef.

The majority of asexually brooded larvae along Ningaloo Reef are retained locally, as there were only a few instances where an MLG was shared between sites. Asexual reproduction is generally believed to be an important mechanism for local-scale proliferation, particularly following a disturbance where areas of once-occupied reef become vacant (Roberts 1997, Ayre & Hughes 2004, Provan et al. 2009). There were a few instances, however, where an MLG was shared exclusively between 2 populations separated by more than 120 km, demonstrating that these clonal propagules are also capable of long-distance dispersal. Although pre-competency periods for *P. damicornis* are relatively short (1 to 2 d; Ayre & Hughes 2000), large lipid reserves (Harrison & Wallace 1990) and photosynthetic capabilities (Fransolet et al. 2012) provide the brooded planulae with the ability to survive in the plankton for an extended period of time (up to 103 d; Richmond 1987) if deprived of a suitable substratum (Harii et al. 2002).

While recruitment of asexually brooded larvae predominantly occurs locally along Ningaloo Reef, sexually-derived colonies display high levels of connectivity between adjacent reefs. Although a clear pattern of differentiation was identified between reefs from the northern and southern extents of our sampling, significant shared genetic structure for Type α was observed at distances up to 60 km, with positive spatial structure extending up to 200 km when distance classes were pooled. These results contrast previous assessment of population structure of *P. damicornis* along Ningaloo Reef that did not distinguish Types α and β and identified high levels of genetic subdivision between populations of sexual origin (Whitaker 2006). We propose that that the morphological overlap of Type α and Type β may have confounded interpretations of population structure in Whitaker (2006) and resulted in an overestimation of population subdivisions. Without directly analysing the samples collected by Whitaker (2006), this remains largely speculative.

This study demonstrates that sampling of *P. damicornis* based on gross morphological characteristics can lead to the inclusion of multiple taxonomic units into analyses of population structure. High levels of phenotypic plasticity within the genus *Pocillopora* means that interspecific delineation is difficult based on morphology alone. *P. damicornis* has been the subject of a number of genetic population studies worldwide, yet very few of these have taken steps to ensure that only a single molecular taxonomic unit was included in the analyses (but see Gorospe & Karl

2013, Torda et al. 2013). Re-examining the population structure of this model species may elucidate the inconsistencies in patterns of population genetic structure and reproductive biology reported around the world and provide more ecologically meaningful insight into the capacity of *P. damicornis* to recover from future disturbances.

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