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Historical and contemporary factors shape the population genetic structure of the broadcast spawning coral, *Acropora millepora*, on the Great Barrier Reef

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Abstract

Effective management of reef corals requires knowledge of the extent to which populations are open or closed and the scales over which genetic exchange occurs, information which is commonly derived from population genetic data. Such data are sparse for Great Barrier Reef (GBR) corals and other organisms, with the studies that are available being mostly based on a small number of sampling locations spanning only part of the GBR. Using 11 microsatellite loci, we genotyped 947 colonies of the reef-building coral *Acropora millepora* from 20 sites spanning almost the full length of the GBR (~12° of latitude and ~1550 km). The results show a major divide between the southernmost central to southern offshore populations and all other sampled populations. We interpret this divide as a signature of allopatric divergence in northern and southern refugia during the Pleistocene glaciations, from which the GBR was subsequently recolonized. Superimposed on this pattern is a cross-shelf genetic division, as well as a separation of inshore populations south of the Cape Clifton Front at ~21.5–22°S. Most inshore populations north of this, as well as mid-shelf populations in the northern and far northern GBR, are open, exchanging recruits frequently. In contrast, inshore populations south of the Cape Clifton Front and offshore populations in the central and southern GBR are largely self-seeding, at least within the spatial resolution that was achieved given our sampling intensity. Populations that have been impacted by recent disturbance events causing extensive coral mortality show no evidence of reduced genetic diversity.

Keywords: dispersal, gene flow, microsatellites, Pleistocene glaciations, Scleractinia, stochastic recruitment

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Introduction

Reproductive connectivity is the dispersal of individuals among (sub)populations that survive to reproduce (Cowen *et al.* 2007). Knowledge of the extent to which reef coral populations are connected and the spatial scale over which gene flow occurs is extremely valuable for the effective management of coral reefs, as it will help to delineate the boundaries between and determine the size of marine protected areas (MPAs) (Almany *et al.* 2009). By identifying key sites likely to survive major disturbances and incorporating patterns of connectivity and replenishment into MPA design, risk of catastrophic events can be spread, thus increasing the likelihood of reef survival (Green *et al.* 2007). These principles were applied by Mumby *et al.* (2011) in the Bahamas where Sea Surface Temperature data were used in conjunction with connectivity models to develop and test reserve designs with a view to maximize resilience of reefs into the future. Australia's Great Barrier Reef (GBR) is a world heritage area; it is also the world's largest reef system with a surface area of ~350 000 km^2, of which ~21 000 km^2 consists of coral

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reef and comprises ~2900 separate reefs (Wachenfeld *et al.* 2007). More than 33% of the GBR is located in no-take areas (Fernandes *et al.* 2005). Despite this, surprisingly few data on the connectivity of GBR species are available with adequate sampling intensity to assess the connectivity at the scale of whole of the GBR (Williams & Benzie 1993; Benzie 1994; Burnett *et al.* 1995; Uthicke *et al.* 1999; Bastidas *et al.* 2001, 2002; Uthicke & Benzie 2001; Bergenius *et al.* 2006; Gerlach *et al.* 2007; Bay *et al.* 2008; Howells *et al.* 2009; Jones *et al.* 2009, 2009; Yasuda *et al.* 2009; Evans *et al.* 2010; Farnsworth *et al.* 2010). Data are particularly sparse for corals, including reef-building scleractinian corals.

Scleractinian corals are benthic and mostly attached to the substratum in the adult life stage. While coral colony fragments can sometimes re-establish (Smith & Hughes 1999), dispersal predominantly occurs through the larval stage. The oceanic transport of pelagic coral larvae is extremely difficult to quantify from direct observations, because coral larvae are small and lack structures for physical or chemical tagging. Some visual observations exist for larvae of brooding coral species, which are relatively large compared to those of broadcast spawning species and settle close to the maternal colony (Best & Resing 1987; Carlon & Olson 1993), but visual tracking of larvae of broadcast spawning coral species is not feasible. A radar drogue study of coral spawning slicks suggests that positively buoyant coral larvae of broadcast spawning species have the potential to disperse over 10 s of km (Oliver & Willis 1987; Willis & Oliver 1990) within their typical 2–5 day pre-competency period (e.g. Babcock & Heyward 1986; Miller & Mundy 2003). While good hydrodynamic models could predict the potential dispersal distances and routes for coral larvae, a more common and direct approach for assessing reproductive connectivity among coral populations is its inference from genetic data.

In addition to information on connectivity, population genetic data can provide insights into how disturbance (storms, coral bleaching, etc.) and vicariant (changes in sea level resulting in land barriers, ocean currents forming dispersal barriers, etc.; Veron 1995) events have impacted on coral population structure. This includes the relative importance of sexual vs. asexual reproduction, the potential loss of genetic diversity and genetic signatures of past allopatric divergence. Vicariance and dispersal often operate at the same time, with vicariance usually having occurred at certain points in the geological past, while dispersal takes place over all timescales. Extreme disturbance events causing extensive coral mortality, such as mass bleaching or crown-of-thorns starfish outbreak events (Sweatman *et al.* 2011), may represent a bottleneck (a temporary but significant reduction in population size) for coral populations, and this can lead to a loss of genetic diversity (Allendorf & Luikart 2006). Loss of genetic diversity is detrimental to the population in terms of its ability to cope with environmental fluctuations as well as to adapt to environmental change.

Here, we use 11 previously developed microsatellite loci (van Oppen *et al.* 2007; Wang *et al.* 2009) to assess reproductive connectivity, diversity and population structure in the broadcast spawning coral, *Acropora millepora* (Cnidaria; Scleractinia; Acroporidae), along almost the full length of the GBR and including several cross-shelf comparisons. *A. millepora* is a broadcast spawning coral that is common on the GBR, particularly on inshore reefs. It is a comparatively well-studied species (a Web of Science search on the key word '*Acropora millepora*' revealed 139 hits between 1991 and July 29th 2011); its phenology and environmental stress responses have been extensively studied, and excellent genomic resources are available (Kortschak *et al.* 2003), including its complete genome sequence (the genome assembly can be accessed from Coral Base: http://coralbase.org/). The results of this study reveal the signatures of both past and contemporary events and may contribute to future revisions of the zoning of the GBR, especially when combined with similar data for other coral reef species.

Material and methods

Coral sampling

At each of 20 locations (Fig. 1; Table S1, Supporting information), spanning almost the full length of the GBR (~12° of latitude and ~1550 km), one branch was snapped off from each of ~50 colonies using a diving knife. Collections were made between 1 and 11 m depth (Table S1, Supporting information) over an area of approximately 300 × 300 m at each site. Coral branches were fixed in absolute ethanol for downstream DNA analysis. The GBR Marine Park is divided into four management areas: the far northern, the Cairns/Cooktown, the Townsville/Whitsunday and the Mackay/Capricorn management area (Fig. 1, the red dotted lines indicate the boundaries between the management areas). For ease of reading, we refer to those hereafter as the far northern, northern, central and southern GBR.

Microsatellite genotyping of coral colonies

DNA was extracted following a slightly modified method used for the black tiger shrimp (Wilson *et al.* 2002). PCR primers for the 11 microsatellite loci are described in van Oppen *et al.* (2007) and Wang *et al.* (2009). The 11 loci were combined into 4 multiplexes

(Table S2, Supporting information), and PCR for each was carried out in 10 μL volumes. Cycling conditions were as follows: 95 °C for 15 min, followed by 28 cycles of 95 °C for 30 s, 60 °C for 90 s and 72 °C for 30 s. This was followed by 30 min at 60°. Following amplification, PCR products were diluted 1/45 and separated on the Beckman CEQ8800 Genetic analysis system. An internal size standard (Genome Lab 400 bp, Beckman Coulter) was run in every sample. Fragment sizes (alleles) were determined from the microsatellite traces using the fragment analysis module of the CEQ8800 system software (version 10). All automatic scoring was checked manually, and samples that yielded ambiguous or no signal were re-amplified and rerun.

Genetic data analyses

The probabilities of identity by random sexual mating (Waits *et al.* 2001) were calculated using an AMOVA approach (Excoffier *et al.* 1992) in GenAlEx v6 (Peakall & Smouse 2006). Individuals sharing the same multilocus genotype (MLG) were inferred to be clone mates if probabilities of identity by random sexual mating were low. For this reason, all but one individual with this MLG were removed prior to further data analysis. Genotypic linkage disequilibrium (LD) and conformance to Hardy–Weinberg Equilibrium (HWE) were assessed in GENEPOP (web version 4.0.10) by estimation of exact *P*-values by the Markov chain method (Raymond & Rousset 1995) using default settings. The frequency of null alleles was estimated under the assumption of HWE using the software package FreeNA (Chapuis & Estoup 2007). This method suggested a considerable null allele frequency for some loci in some populations (in some instances >20%, even in populations without any null homozygotes; data not shown). However, only 39 null allele homozygotes were observed in the total data set of 10 142 single-locus genotypes (0.4%, Table S3, Supporting information), indicating that biological rather than methodological factors are mostly responsible for heterozygote deficits. Further, *F*-statistics and STRUCTURE analyses of the seven loci without null homozygotes reveal the same major patterns as analyses of the full data set (11 loci). All further analyses were therefore conducted on the full data set uncorrected for null alleles. Genetic differentiation between sites was

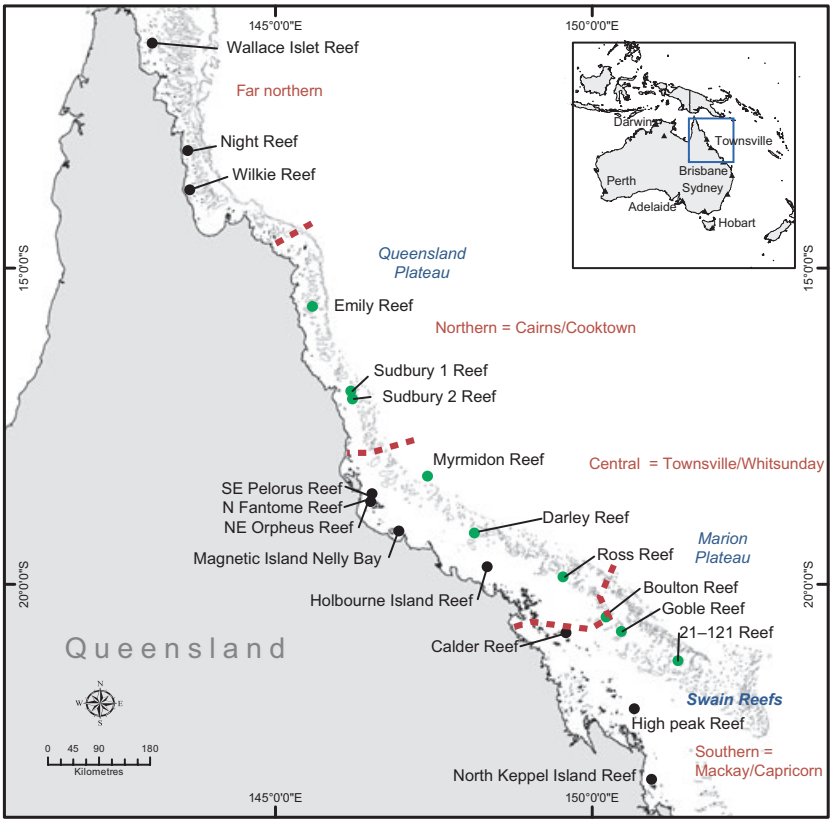

Fig. 1 Map showing the 20 sampling locations on the Great Barrier Reef, the four management areas (red dotted lines indicate the boundaries between the management areas), the location of the Queensland and Marion Plateaus, and the Swain Reefs. Inshore reef locations are indicated by black symbols, and offshore reef locations, by green symbols.

estimated in the following ways: (i) F_{ST} values were calculated using an AMOVA approach (Excoffier *et al.* 1992) in GenAlEx v6. (ii) In addition, standardized Φ_{ST} values (Φ'_{ST}; Meirmans 2006) were calculated in GenoDive 2.0b18 (Meirmans & Van Tienderen 2004). The standardized statistic is calculated by dividing the Φ_{ST} value by the maximum value possible given the within-population variance (Hedrick 2005). To assess the significance of differentiation between sites, we applied a Fisher exact test (Goudet 1995) using Genepop v4.0 with the default Markov chain parameters. This test is well suited to unbalanced sample sizes. Statistical significance for all pairwise tests was adjusted for multiple comparisons by the B-Y false discovery rate (FDR) method (Narum 2006). (iii) Jost's (Jost 2008) actual measure of differentiation (D_{est}) was computed in SMOGD version 1.2.5 (Crawford 2010). To visualize the genetic relationships among populations, the genetic distance measures between pairs of populations listed earlier were plotted using a principal coordinates analysis (PCoA) with GenAlEx v6. Mantel tests were run in GenAlEx v6 using F_{ST} and Φ'_{ST} against linear distance between sampling locations.

The Φ'_{ST} values were transformed into networks using tools created with the igraph package (Csardi & Nepusz 2006) within the R environment (http://cran.r-project.org). Each sample site is represented by vertices that are connected by lines denoting genetic interaction. The probabilities provided by the population and regional pairwise genetic differentiation (Φ'_{ST}) are taken to indicate the strength of interaction between sample populations. Low Φ'_{ST} values indicate a high level of interaction between populations, noting that negative Φ'_{ST} values were reassigned to zero value. Each line then has the attributes of connection strength but not the direction of flow. Initially, the network is complete, with each sample population connected to the remaining 19 populations with lines of varying strength, but this restricts scrutiny of the metapopulation structure. To reveal the backbone (Serrano *et al.* 2009) of the *A. millepora* population genetic structure, it is necessary to remove the weakly connected lines. The Φ'_{ST} statistical method considers the proportion of variance among populations relative to the total variance so we can select a global threshold to exclude the lines between dissimilar populations. This threshold is derived from the optimum formation of clusters (Kininmonth *et al.* 2010) based on a modularity measure (Newman 2006). Clusters are the regions of densely connected vertices within a network; however, selecting the membership of each cluster is not trivial. The modularity measure seeks to compare the cluster structure against a randomized variant of the network and thus provides a qualitative measure of membership selection. We use the leading eigenvector algorithm by Newman (2006) to select the cluster membership within the igraph environment in R (Csardi & Nepusz 2006). The flow of genetic information across the network means that sample populations will be exposed to differing intensity of colonization as a function of the network distance to all the other populations. To evaluate this distance, we calculated the closeness centrality index which is the sum of the minimum path lengths connecting the focal vertex to all other vertices (Freeman 1978; Dorogovtsev 2010).

The fully Bayesian model-based clustering method implemented in STRUCTURE v2.3.3 (Pritchard *et al.* 2000) was used as an alternative approach to examine spatial genetic structure. The program was run without population information under the admixture model (individuals may have mixed ancestry) and independent allele frequencies. Length of the burn-in was 100 000, and the number of MCMC replications after the burn-in was 1 000 000. Five independent chains were run for each K from $K = 1$ to $K = 20$. The method of Evanno *et al.* (2005) was used to find the most likely value of K by plotting the log probability (L(K)) and ΔK of the data over multiple runs and as implemented in STRUCTURE HARVESTER (Earl 2009).

Populations that have experienced a recent reduction in their effective population size exhibit a reduction in the allele numbers and a transient heterozygosity (H_O) excess at polymorphic loci compared to that under HWE (H_E) (Cornuet & Luikart 1996). If HWE is assumed (i.e. no bottleneck), there is an equal probability of getting a positive or a negative difference between the observed and the expected heterozygosities. In contrast, following a recent bottleneck, a heterozygosity excess is expected to occur more often than a heterozygosity deficit. Therefore, if the number of loci for which there is a heterozygosity excess is significantly larger than that for which there is a heterozygosity deficit, a recent bottleneck can be inferred (Luikart *et al.* 1998). Bottlenecks are also expected to change the allele frequency distribution (Cornuet & Luikart 1996). To assess whether recent disturbance events have impacted on the genetic characteristics of *A. millepora* populations, we analysed the microsatellite data in the following ways: (i) allelic richness was calculated for each locus using rarefaction in the software package FSTAT 2.9.3 (Goudet 1995). A Mann–Whitney U test was used to compare allelic richness in populations that have experienced a recent major disturbance with that in populations that are unaffected by major recent disturbance events. (ii) The heterozygosity distribution under the assumption of HWE equilibrium and the infinite allele mutation model was calculated for each population and for each locus in the software package Bottleneck 1.2.02 (Cornuet & Luikart

1996). The method established for each locus whether there was a heterozygosity excess (as expected under a recent bottleneck scenario). Further, the allele frequency distribution was established to see whether it was approximately L-shaped (as expected under HWE) or not (recent bottlenecks provoke a mode shift).

Results

Genetic diversity

In total, 947 *Acropora millepora* colonies from 20 sites along the GBR were genotyped at 11 microsatellite loci. Within those, 23 MLGs are repeated. Repeated MLGs occur at Emily (1 MLG occurs twice), Magnetic Is (1 MLG occurs twice), Darley (1 MLG occurs twice), Goble (1 MLG occurs twice), Ross (3 MLGs occur twice), Calder (1 MLG occurs twice, and 1 MLG occurs 3 times), High Peak (1 MLG occurs twice, 1 MLG three times, 1 MLG four times and 1 MLG 5 times) and North Keppel Is (3 MLGs occur twice). The probabilities that these MLGs have been produced through sexual reproduction are small (1.13×10^{-14} to 7.3×10^{-7}), suggesting that they are the result of asexual reproduction (fragmentation). All but one of each repeated MLG were removed prior to data analysis.

The 11 loci screened are polymorphic in all populations sampled. Numbers of alleles per locus (A) range from 2 to 21, and expected heterozygosity (H_E) ranges from 0.29 to 0.88 (Table S4, Supporting information). Allelic richness is the same in populations having experienced a recent major disturbance (SE Pelorus, NE Orpheus, N Fantome, High Peak, N Keppel Is; see Discussion) vs. those that have not (all other populations; $P = 0.604$). The bottleneck analyses showed that all populations have a normal L-shaped allele frequency distribution, consistent with mutation–drift equilibrium. All but one of the populations exhibit no significant heterozygote excesses (Wilcoxon sign-rank one-tailed test, $0.139 < P < 0.860$), also consistent with mutation–drift equilibrium. The one population showing a significant heterozygote excess (Darley Rf, $P = 0.042$) is not known to have been impacted by recent disturbance events.

Genetic structure

Significant LD is present in 64 of 1100 comparisons (5.8%), 21 of which occur in the southernmost central and southern offshore reefs, Darley Rf, 21–121 Rf, Goble Rf, Ross Rf and Boulton Rf, and 26 of which occur at High Peak Rf. These six reefs are the most genetically divergent compared to the other 14 reefs sampled (Tables 1 and 2). AMOVA shows that 4% of the total genetic variation observed is partitioned among populations ($P = 0.001$). Of the 190 pairwise F_{ST} values, 141 (74%) are statistically significant (Table 1). Statistically significant F_{ST} values are more abundant in comparison with and within the southern GBR as opposed to the central, northern and far northern GBR. The southern GBR populations at 21–121, High Peak and North Keppel Is reefs are significantly distinct from all other sampled populations, and those from Goble, Boulton and Darley (Darley is located in the southern central GBR) reefs are distinct from all but one of the other populations. The highest standardized values of genetic differentiation are found in comparisons involving Boulton, Goble and 21–121 Rf (almost all values >0.1; Table 2). Most comparisons in the central, northern and far northern GBR show F_{ST} values not significantly different from zero; only those with the offshore reefs Myrmidon, Darley Reef and Ross Reef and NE Orpheus in the Palm Island group are mostly statistically significant. For example, the far northern GBR reefs, Wilkie, Wallace Is and Night, are mostly not genetically different from Emily, Sudbury 1 and 2, SE Pelorus, N Fantome, Magnetic Is, Holbourne Is and Calder reefs, but show significant F_{ST} values with reefs to the south of those as well as with the offshore reefs (Table 1). Further, the Magnetic Is population shows significant genetic differentiation from its geographically nearest populations at Myrmidon, NE Orpheus and SE Pelorus Is (but not with the N Fantome Is population). Along the inshore reefs, no significant genetic differentiation was observed over a linear distance of up to ~1270 km (Wallace Is to Calder). Isolation by distance (IBD) was not observed in the total data set ($P = 0.226$), nor for the inshore populations ($P = 0.322$), but was significant among the offshore populations ($P = 0.001$, Fig. 2). An IBD analysis of the central and southern GBR populations only (inshore and offshore locations combined), where both inshore and offshore populations were sampled, is statistically significant ($P = 0.028$, $R^2 = 0.0685$; not shown). This IBD is largely driven by the offshore population, because pairwise F_{ST} values are not significantly different from zero in most inshore pairwise comparisons (except for the two southernmost populations, High Peak and N Keppel Is).

The patterns of pairwise genetic differentiation are visualized in a PCoA plot of pairwise F_{ST} (Fig. 3). PCoA plots of Φ'_{ST} and D_{est} values are similar to those of F_{ST} (Fig. S1A,B, Supporting information). A second visualization of genetic relationships among populations we present is the network of Φ'_{ST} (Fig. 4). The network created from the Φ'_{ST} statistics contains 20 vertices and 189 connecting lines. By increasing the global threshold from 0.001 to 0.400 (Fig. 4A), we determined the optimum threshold to be 0.061, so that connecting lines with a Φ'_{ST} value greater than this value were deleted (leaving 102 lines). The leading eigenvector algorithm detects three

Table 1 Pairwise F_{ST} values below diagonal, *P*-values above diagonal. Statistically significant values have shaded background, and *P*-values smaller than adjusted α are printed in italic font (adjusted α = 0.009)

	Wallace Is	Night	Wilkie	Emily	Sudbury 1	Sudbury 2	SE Pelorus	NE Orpheus	N Fantome	Magnetic Is	Myrmidon	Holbourne Is	Darley	Ross	Calder	Boulton	Goble	21–121	High Peak	N Keppel Is
Wallace Is		0.070	0.054	0.614	0.019	*0.005*	0.013	*<0.001*	0.014	0.031	*0.001*	0.052	*<0.001*	0.010	0.021	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
Night	0.000		0.360	0.067	0.080	0.138	0.010	*<0.001*	*0.004*	0.054	*<0.001*	0.147	*<0.001*	*<0.001*	0.010	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
Wilkie	0.003	0.000		0.017	0.036	0.427	0.033	*<0.001*	0.016	0.152	*0.001*	0.115	*<0.001*	*<0.001*	0.012	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
Emily	0.000	0.006	0.008		*0.007*	0.025	0.019	*<0.001*	0.037	*0.003*	*0.001*	0.480	*<0.001*	0.012	0.048	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
Sudbury 1	0.004	0.000	0.005	0.016		0.205	0.051	*<0.001*	0.316	0.080	*0.004*	*0.002*	*<0.001*	*0.001*	0.219	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
Sudbury 2	0.009	0.003	0.005	0.009	0.007		*0.006*	*<0.001*	0.009	*<0.001*	*<0.001*	*0.001*	*<0.001*	*<0.001*	0.023	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
SE Pelorus	0.008	0.003	0.004	0.013	0.002	0.019		*<0.001*	0.320	*0.006*	0.045	0.058	*<0.001*	0.049	0.122	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
NE Orpheus	0.047	0.052	0.042	0.060	0.039	0.062	0.025		0.038	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
N Fantome	0.005	0.007	0.008	0.012	0.000	0.018	0.000	0.014		0.029	*0.008*	*0.001*	*<0.001*	*<0.001*	0.140	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
Magnetic Is	0.001	0.003	0.000	0.014	0.000	0.022	0.002	0.041	0.004		*<0.001*	0.143	*<0.001*	*<0.001*	*0.005*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
Myrmidon	0.010	0.006	0.005	0.018	0.005	0.014	0.009	0.032	0.008	0.014		*0.001*	*<0.001*	*0.003*	*0.005*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
Holbourne Is	0.000	0.000	0.000	0.000	0.004	0.006	0.000	0.040	0.007	0.006	0.004		*<0.001*	*0.080*	*0.009*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
Darley	0.026	0.039	0.038	0.041	0.035	0.056	0.035	0.060	0.038	0.036	0.027	0.031		0.049	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
Ross	0.007	0.015	0.018	0.022	0.009	0.027	0.010	0.048	0.016	0.009	0.012	0.009	0.006		*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
Calder	0.004	0.005	0.004	0.009	0.001	0.011	0.003	0.036	0.005	0.010	0.001	0.001	0.028	0.022		*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
Boulton	0.054	0.068	0.066	0.071	0.059	0.081	0.066	0.105	0.073	0.056	0.062	0.064	0.017	0.016	0.071		0.329	*<0.001*	*<0.001*	*<0.001*
Goble	0.059	0.079	0.078	0.078	0.066	0.091	0.075	0.105	0.077	0.058	0.072	0.075	0.028	0.025	0.081	0.000		*<0.001*	*<0.001*	*<0.001*
21–121	0.146	0.176	0.173	0.170	0.162	0.182	0.173	0.209	0.179	0.152	0.161	0.166	0.087	0.096	0.173	0.031	0.032		*<0.001*	*<0.001*
High Peak	0.045	0.039	0.040	0.043	0.033	0.047	0.041	0.089	0.040	0.049	0.035	0.038	0.071	0.070	0.024	0.103	0.118	0.220		*<0.001*
N Keppel Is	0.025	0.019	0.022	0.027	0.023	0.039	0.015	0.040	0.011	0.019	0.025	0.021	0.050	0.035	0.018	0.086	0.097	0.204	0.048	

Table 2 Pairwise standardized Φ_{ST} values (Φ'_{ST}) among the 20 population studied. Negative values were converted to zero

	Wallace Is	Night	Wilkie	Emily	Sudbury 1	Sudbury 2	SE Pelorus	NE Orpheus	N Fantome	Magnetic Is	Myrmidon	Holbourne Is	Darley	Ross	Calder	Boulton	Goble	21–121	High Peak
Night	0.000																		
Wilkie	0.005	0.000																	
Emily	0.000	0.011	0.015																
Sudbury 1	0.007	0.000	0.009	0.031															
Sudbury 2	0.018	0.006	0.008	0.016	0.013														
SE Pelorus	0.016	0.006	0.007	0.025	0.005	0.036													
NE Orpheus	0.092	0.100	0.084	0.117	0.075	0.124	0.049												
N Fantome	0.008	0.012	0.017	0.022	0.000	0.034	0.000	0.025											
Magnetic Is	0.002	0.006	0.000	0.026	0.000	0.041	0.004	0.081	0.008										
Myrmidon	0.016	0.008	0.006	0.029	0.006	0.026	0.014	0.066	0.012	0.027									
Holbourne Is	0.000	0.000	0.000	0.000	0.008	0.012	0.000	0.080	0.013	0.010	0.003								
Darley	0.052	0.077	0.081	0.082	0.070	0.118	0.070	0.126	0.076	0.073	0.058	0.065							
Ross	0.012	0.027	0.034	0.041	0.017	0.053	0.019	0.095	0.030	0.016	0.022	0.016	0.010						
Calder	0.007	0.009	0.007	0.015	0.001	0.023	0.006	0.074	0.010	0.019	0.000	0.000	0.060	0.043					
Boulton	0.115	0.141	0.142	0.148	0.124	0.174	0.137	0.225	0.151	0.115	0.134	0.137	0.036	0.031	0.154				
Goble	0.116	0.154	0.157	0.151	0.129	0.185	0.147	0.214	0.151	0.107	0.149	0.152	0.058	0.048	0.167	0.000			
21–121	0.275	0.327	0.332	0.318	0.303	0.350	0.325	0.404	0.336	0.279	0.317	0.319	0.170	0.175	0.337	0.060	0.058		
High Peak	0.087	0.073	0.078	0.082	0.062	0.092	0.077	0.175	0.074	0.091	0.064	0.074	0.148	0.135	0.046	0.224	0.243	0.420	
N Keppel Is	0.042	0.030	0.037	0.043	0.037	0.068	0.024	0.075	0.018	0.033	0.045	0.036	0.097	0.063	0.033	0.167	0.180	0.366	0.082

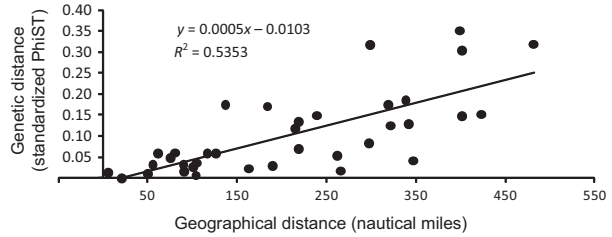

Fig. 2 Relationship between geographic and genetic (Φ'_{ST}) distances among the offshore *Acropora millepora* populations.

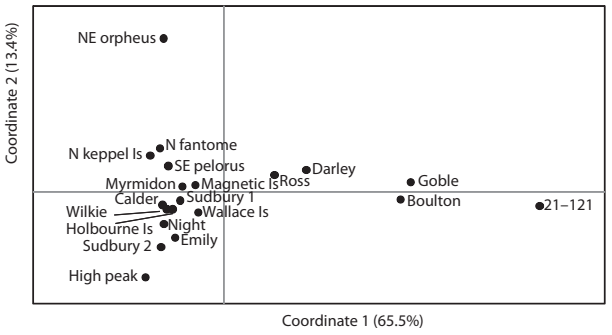

Fig. 3 Principal coordinates analysis of pairwise F_{ST} values among the 20 sampled *Acropora millepora* populations.

distinct clusters as shown by the vertices' grey shade in Fig. 4B: (i) Darley, Ross, Boulton, Goble and 21–121 reefs; (ii) High Peak Reef; and (iii) a well-mixed and central group with some peripheral reefs loosely connected; this group comprises all other reefs. While not forming distinct clusters, NE Orpheus and N Keppel Is show a relatively low closeness to the centre of the network (the size of the vertices in Fig. 4B represents the closeness centrality index (Table S5, Supporting information) and highlights how each sample population is connected to the main cluster). The N Keppel Is population has many connections, but all are weak. Ross Reef and to a lesser extent Darley Reef serve to connect Boulton, Goble and 21–121 Reefs to the main group.

The optimal number of genetic clusters (K) estimated using the Bayesian model-based clustering method is equivocal, as there is no clear peak in the ΔK values (data not shown). However, L(K) starts to approach an asymptote at approximately $K = 5$. We therefore present the cluster assignment plots for $K = 2$ to $K = 5$ (Fig. 5), which confirm the genetic distinction of the southern-most central and southern offshore reefs, as well as NE Orpheus. These results further illustrate that both SE Pelorus and N Fantome are genetically intermediate between NE Orpheus and other central, far northern, northern and inshore southern populations.

The estimated frequency of null alleles under the assumption of HWE was considerable for some loci in some populations (data not shown). However, only 39 null allele homozygotes were observed in the total data set of 10 142 single-locus genotypes (0.4%, Table S3, Supporting information), and these occurred only in four loci (Am2_006, Am2_008, WGS_189 and WGS_196). While the low frequency of null homozygotes indicates that biological rather than methodological factors are mostly responsible for heterozygote deficits, we re-analysed the data with these four loci excluded

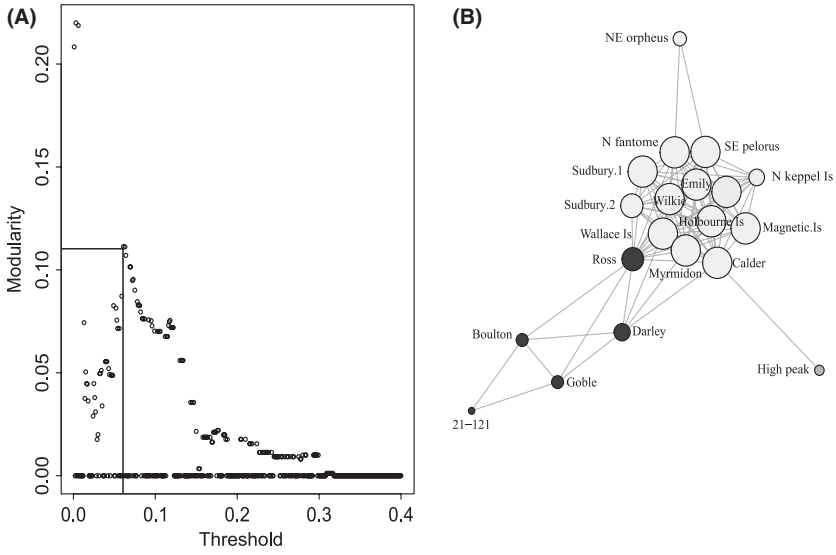

Fig. 4 (A) Plot of the changes in modularity as the global threshold is increased with lines highlighting the optimal threshold value. (B) Network of *Acropora millepora* with lines with strength <0.061 Φ'_{ST} remaining. The clusters are displayed with vertices in grey scale, while the size represents the closeness index value (Table S5, Supporting information).

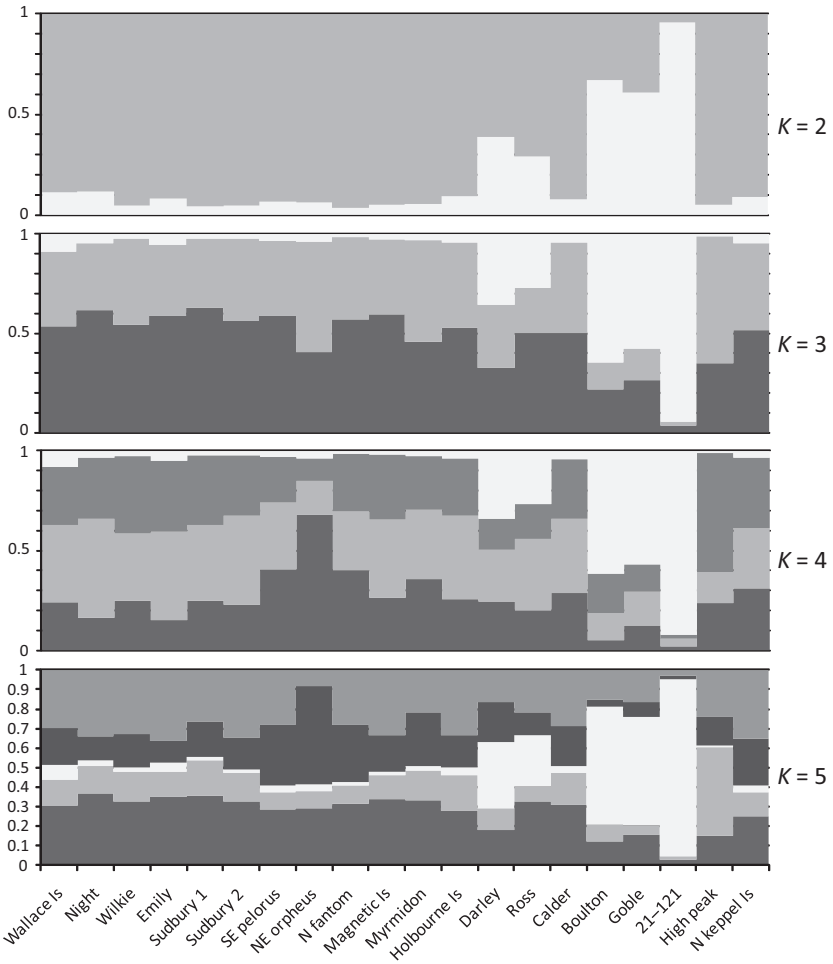

Fig. 5 Results of a Bayesian model-based cluster analysis $K = 2$ to $K = 5$ of the 20 *Acropora millepora* populations from the Great Barrier Reef. Each population is represented by a vertical bar, and the grey scale indicates the relative membership proportion to each genetic cluster of the population. Sampling location is given along the *x*-axis.

to assess their impact on the genetic patterns observed. In this re-analysis (data not shown), the southernmost central and southern offshore populations at Darley, Ross, Boulton, Goble and 21–121 reefs remain separated from all other populations based on pairwise F_{ST} values as well as the STRUCTURE analysis. The High Peak and N Keppel Is populations are also distinct. However, the genetic distinctiveness of the Orpheus Is population is no longer as strong using only seven loci (i.e. there were only three significant pairwise F_{ST} values).

Discussion

Indices of pairwise genetic differentiation (Figs 3 and 4) and the Bayesian cluster analysis (Fig. 5) distinguish five main genetic groups based on the data from 11 microsatellite loci in the *Acropora millepora* samples collected from 20 populations spanning ~12° of latitude: (i) the southernmost central and southern offshore populations at Darley, Ross, Boulton, Goble and 21–121 reefs, (ii) the southernmost inshore population of North Keppel Is reef, (iii) the High Peak reef population just north of the Keppel Islands, (iv) the NE Orpheus Is population and (v) all other populations. We argue that these patterns of genetic structure are the result of both historical and contemporary events, including allopatric divergence during the Pleistocene glaciations, major disturbance events in the more recent past as well as contemporary sea surface circulation.

Recolonization of the GBR from a northern and southern refuge following the Pleistocene glaciations

The Bayesian cluster analysis (Fig. 5, this division is already evident at $K = 2$), the network analysis (Fig. 4)

as well as the pairwise values of genetic differentiation (Tables 1 and 2, Fig. 3) indicate that the greatest genetic split exists between the southernmost populations of the central GBR at Darley and Ross reefs and the southern offshore populations at Boulton, Goble and 21–121 reefs vs. all other sampled populations. This pattern probably reflects post-glacial recolonization of the GBR by *A. millepora* from two refugia, possibly the Queensland Plateau in the north and the Marion Plateau in the south (Davies 1994) (see Fig. 1). The Queensland Plateau is a large submarine plateau located between approximately 13.5°S and 18°S (Betzler *et al.* 1995). The Marion Plateau is located between 18°S and 23°S on the northeastern Australian continental margin. This plateau is the most southerly of the northeast Australian marginal plateaus, forming a deeper extension of the Queensland continental shelf. At the height of the last Pleistocene glaciation (~18 000 yr ago), sea levels were 130–175 m lower than today (Hopley & Thom 1983); hence, coral reefs could not persist on the shallow continental shelf on which the GBR is currently located. Instead, the Queensland Plateau is believed to have been a main refuge for shallow water GBR organisms, while reef corals have likely also persisted on the Marion Plateau (Davies 1994). Alternatively, inshore coral reefs occur as far south as Moreton Bay (~27.5°S), and a glacial refugium may have existed there during the Pleistocene (van Herwerden & Doherty 2006). When sea levels rose, the GBR re-established at ~10 000 years ago (Carter & Johnson 1986). Genetic patterns very similar to those observed here for *A. millepora* have been described for the shallow water calcareous sponge, *Leucetta 'chagosensis'* (Wörheide *et al.* 2002), and independent recolonization events from the Queensland and Marion Plateau refugia onto the GBR were inferred. Further, significant genetic separation of populations in the Swain Reefs in the southern GBR (see Fig. 1) from those at other GBR locations has been detected in a range of other species, including the olive sea snake, *Aipysurus laevis* (Lukoschek *et al.* 2007), the giant clams, *Tridacna derasa* (Macaranas *et al.* 1992; Benzie 1994) and *T. maxima* (Benzie 1994), the crown-of-thorn-starfish, *Acanthaster planci* (Benzie 1994), and the reef fishes, *Acanthochromis polyacanthus*, *Amphiprion melanopus*, *Pomacentrus molucensis*, *Chromis atripectoralis* and *Stegastes nigricans* (Doherty *et al.* 1995), supporting the existence of a northern and southern refuge during past low-level sea stands from which the GBR was subsequently recolonized.

Drifter data (Choukroun *et al.* 2010) and modelled particles (Luick *et al.* 2007) indicate that patterns of ocean surface circulation do not prevent the exchange of larvae between reefs in the northern and central GBR and offshore reefs in the southern GBR. *A. millepora* larvae are competent to metamorphose and settle around 4–5 days post-spawning (Babcock & Heyward 1986), and maximum rates of metamorphosis occur at 8 days post-spawning (Heyward & Negri 1999). Maximum longevity of *Acropora* coral larvae in the water column, however, is much longer (~60–200 days; Nishikawa *et al.* 2003; Graham *et al.* 2008). Modelled particles released on the GBR moved over spatial scales of several 100 s of km in 30 days to up to ~1000 km in 90 days (Luick *et al.* 2007), suggesting that long-distance dispersal of *A. millepora* larvae is feasible. It remains to be confirmed whether this pattern holds for particle release dates timed specifically around the broadcast spawning period of corals. If confirmed, however, a conundrum exists in that dispersal followed by interbreeding (secondary contact) would be expected to have erased the genetic signature of past allopatric divergence (i.e. in a northern and southern refugium during past glaciations). The fact that a genetic signature of past isolation is still detectable suggests that, while larvae may be exchanged between these regions, these are either maladapted to their new environment and selected against (Marshall *et al.* 2010) or show genetic incompatibility with the native population (Bierne *et al.* 2011). A large proportion of cases of non-random associations of alleles (genotypic linkage disequilibrium, LD) were observed in the Darley Rf, 21–121 Rf, Goble Rf, Ross Rf and Boulton Rf populations, suggestive of recent admixture. It is conceivable that pulses of migrants from the north arrive at these sites and establish themselves temporarily. If interbreeding with the native populations occurs, the offspring between the native and migrant colonies may have low fecundity, preventing the northern genotypes from integrating fully with native genotypes and resulting in the signatures of both past isolation (genetic divergence between north and south) and recent admixture (LD in the southern offshore populations). The STRUCTURE plot of individual colonies for $K = 2$ (Fig. S2, Supporting information) shows the sympatric occurrence of individuals with high membership to one or the other genetic cluster, which is also indicative of admixture with assortative mating of the two genetic groups. Evidence for high levels of dispersal followed by post-recruitment mortality exists for the brooding pocilloporid coral, *Stylophora pistillata*, from two regions in the Red Sea ~10 km apart (Zvuloni *et al.* 2008). While genetic characterization of recruits uncovered genetic homogeneity between the two regions, adult populations from the same locations were found to be genetically distinct.

Patterns of pairwise genetic differentiation in A. millepora *on the GBR*

Pairwise population genetic differentiation (Tables 1 and 2) shows a trend of increasing values and statistical significance towards the southern GBR, suggesting that levels of gene flow are lower in the south than in the north. These findings confirm those of Ayre & Hughes (2004), who sampled five species of coral at three locations (northern, central and southern GBR) and also found higher levels of genetic differentiation between Davies Reef in the central GBR and Heron Island in the south on the one hand than between Davies Reef and Lizard Island (northern GBR) on the other. The results are consistent with the ~4-fold faster flow rate of surface waters north of 18° compared to those south of this latitude (Choukroun *et al.* 2010).

Isolation by distance was present among offshore but not inshore reefs. Reefs on the outer to mid-shelf form a more continuous reef matrix compared to inshore reefs, facilitating dispersal and gene flow in a stepping-stone fashion, which is expected to result in IBD. Along the inshore GBR, however, genetic differentiation was absent among most populations separated by a distance of a few to >1000 km, indicative of high levels of gene flow over these spatial scales. The apparent panmixia over such vast distances is quite unexpected, given that the emerging picture is that most recruitment in broadcast spawning corals occurs over 10 s of km, and sometimes over 100 s of km (Treml *et al.* 2008; Jones *et al.* 2009). The Caribbean congener, *Acropora palmata*, however, exhibits similarly high levels of gene flow over large distances and shows F_{ST} values not significantly different from zero over spatial scales of up to 1800 km and 840 km in the western and eastern Caribbean, respectively (Baums *et al.* 2005).

Significant cross-shelf genetic differentiation was observed in all instances (Myrmidon Reef vs. NE Orpheus and N Fantome reefs, Darley vs. Holbourne Is reefs, Calder vs. Boulton and Goble reefs, High Peak vs. 21–121 reefs), except for Myrmidon Reef vs. SE Pelorus Reef. Cross-shelf genetic differentiation is also known from other GBR organisms, including the brooding scleractinian coral, *Seriatopora hystrix* (van Oppen *et al.* 2008), the soft coral, *Clavularia koellikeri* (Bastidas *et al.* 2002), and the algal endosymbiont, *Symbiodinium* sp., harboured by the soft coral *Sinularia flexibilis* (Howells *et al.* 2009), and was observed previously between other *A. millepora* populations on the GBR (Smith-Keune & van Oppen 2006). Further, the GBR exhibits distinct cross-shelf zonation in the community composition of a range of groups of organisms (Done 1982; Russ 1984; Preston & Doherty 1994; Bellwood & Wainwright 2001; Wismer *et al.* 2009). This is generally explained by either environmental gradients or a dispersal barrier across the shelf. The GBR lagoon is a water mass with an average depth of 35 m that separates the inshore from the offshore (mid- and outer shelf) reefs with spatial distances ranging from <15 km in the northern GBR to >150 km in the southern GBR. In combination with the predominantly long-shore movement of sea surface waters on the GBR, the GBR lagoon acts as a strong cross-shelf dispersal barrier (Dight *et al.* 1990; Brinkman *et al.* 2002; Steinberg 2007) to which the observed cross-shelf genetic differentiation can be attributed.

The most divergent population of all is the one at 21–121 reef (Tables 1 and 2). The samples from this location were unambiguously identified as *A. millepora* based on overall colony morphology and have not been confused with the species of similar morphology, *A. spathulata* (Wallace 1999; Souter *et al.* 2010). Whether this genetic divergence is related to its remote location requires additional sampling in the Swain Reef area.

Populations that are characterized by recent disturbance events

The NE Orpheus population within the Palm Is group, a group of small islands with fringing reefs in the central GBR, shows significant genetic differentiation with the two other populations sampled within the Palm Is group (Φ'_{ST} = 0.049 and 0.025 with SE Pelorus and N Fantome, respectively: Table 2), which are separated by a distance as small as ~1 and ~11 km.

In an earlier study on *A. millepora* from the Palm Islands, small-scale genetic differentiation was also documented, although not among the same pairs of sites (Souter *et al.* 2010). The earlier study used a different set and only eight microsatellite loci (only four loci were shared between the two studies). Further, a considerable null allele frequency was detected in the previous study, and the data were corrected for null alleles prior to analyses. These two factors may explain some of the differences between these two studies. The NE Orpheus population and to a lesser extent the SE Pelorus and N Fantome populations are more divergent than other populations sampled in the central and far northern GBR (Fig. 5, K = 4 and K = 5). This probably reflects stochastic recruitment pulses caused by the complexity and temporal variability of patterns of water circulation around the reef (Luick *et al.* 2007; Steinberg 2007; Hogan *et al.* 2010), and founder effects following extensive mortality because of the severe bleaching event of 1998 (Marshall & Baird 2000; Berkelmans *et al.* 2004; Souter *et al.* 2010). The fact that the SE Pelorus and N Fantome populations are genetic intermediates with the NE Orpheus and other central to far northern populations suggests that gene flow among the Palm Is

populations is taking place, but that equilibrium between gene flow and drift has not yet been reached.

Of all other populations examined in this study, the High Peak and N Keppel Is populations also suffered considerably from both the 1998 (10–30% bleaching at High Peak, unknown mortality and >60% bleaching, 15.4% mortality at N Keppel, respectively) and 2002 (100% mortality of *Seriatopora hystrix* colonies at High Peak, 99% mortality of staghorn *Acropora* beds at nearby Percy Island and 35% overall decline in coral cover at N Keppel Is) mass bleaching events (Berkelmans *et al.* 2004; R. Berkelmans unpublished data). In addition, the Myrmidon population suffered 11–75% bleaching-related mortality in 1982 (Fisk & Done 1985). In 2002, bleaching-induced mortality at Myrmidon was 70–80% in the lagoon and channels, but lower on the outer slopes (T. Done, personal communication). The High Peak population exhibits the largest number of repeated MLGs (1 MLG occurs twice, 1 MLG three times, 1 MLG four times and 1 MLG 5 times). It is possible that the past bleaching events caused partial colony mortality and/or fragmentation, resulting in multiple colonies of the same genotype. Experimental fragmentation experiments have shown that *A. millepora* fragments are able to survive and re-attach (Smith & Hughes 1999). Other disturbance events, causing extensive coral mortality in the N Keppel Is population, were a major flood event in 1991, which caused total bleaching and/or mortality of all *Acropora* spp. down to 1.3 m below lowest tide (VanWoesik *et al.* 1995), and the 2006 bleaching event that affected inshore, high latitude reefs on the GBR, including the Keppel Islands (Jones *et al.* 2008; Diaz-Pulido *et al.* 2009). These perturbations may have resulted in population bottlenecks and/or founder events and in combination with stochastic recruitment may explain the genetic characteristics of the affected populations. Surprisingly, levels of genetic diversity as estimated by allelic richness are not significantly different in populations that have undergone a recent major disturbance (SE Pelorus, NE Orpheus, N Fantome, High Peak and N Keppel Is) from those that have not suffered extensive recent mortality (all other populations), and no genetic signatures characteristic of a recent drop in effective population sizes is evident from the Bottleneck analyses. This suggests that recovery through remnant tissue regrowth may be important (Diaz-Pulido *et al.* 2009) and/or that recovery through both new recruitment and possibly tissue regrowth has been fast. The genetic distinctiveness of the *A. millepora* populations at North Keppel Is and High Peak reefs may be attributable to stochastic recruitment following recent mortality, but is likely to be also affected by patterns of sea surface circulation in this region, in particular the Cape Clifton Front (Burrage 1993). Water forced northward by the SE trade winds ceases around the Shoalwater Bay area (around 22°S) and is diverted eastward to the Swain reefs and then southward (Burrage 1993; Kleypas & Burrage 1994; Burrage *et al.* 1996; Weeks *et al.* 2010). High Peak Reef is located at the northern edge of this front (Weeks *et al.* 2010), while the Keppel Islands are well south of it.

Conclusions

This study shows that genetic differentiation in a broadcast spawning coral with planktonic larvae can be absent over 100 s of km, while at the same time, it can be present over distances as small as a few to 10 s of km. It supports the existence of a dispersal boundary around Shoalwater Bay for inshore populations of *A. millepora*, known to oceanographers as the Cape Clifton Front. Most inshore populations of *A. millepora* north of the Cape Clifton Front, as well as mid-shelf populations in the northern and far northern GBR, are open, exchanging recruits frequently. In contrast, inshore populations south of the Cape Clifton Front and mid- and outer shelf populations in the central and southern GBR are largely self-seeding, at least within the spatial resolution that was achieved given our sampling intensity. If these results are indicative of coral populations generally, these may be incorporated in future revisions of the zoning of the GBR Marine Park. The patterns of genetic isolation observed here thus require validation from other coral species with similar reproductive biology and larval duration. Further studies of smaller-scale spatial patterns of genetic structure and connectivity are also needed to examine the geographic distances over which southern and offshore populations show most of their recruitment. Other implications for reef managers are that the artificial exchange of genetic material across this natural barrier (e.g. by ship fouling, ballast water release, transplantation or reef restoration initiatives) may be worth actively preventing to avoid potential adverse impacts on the fitness of native populations. For the translocation of sexually reproducing organisms, this means their removal prior to reproduction. Finally, major disturbance events causing extensive coral mortality have resulted in a change in the genetic composition of the affected populations, but not in a loss of genetic diversity.

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M.J.H.v.O.'s research focuses on understanding the potential for adaptation of corals to climate change and the value and impact of certain management actions to enhance reef coral resilience. L.M.P. applies a wide range of molecular methods to study both neutral and functional genetic diversity in corals and other coral reef invertebrates. S.J.K.'s research seeks to understand large scale ecological phenomena using network theory and spatial analysis. This understanding highlights the dependencies that exist between discrete populations and this is fundamental to conservation planning. R.B. is a coral ecologist with an interest in environmental structuring forces on coral reefs and the ability of corals to acclimatise or adapt to climate change.

Data accessibility

Microsatellite data: DRYAD entry: doi:10.5061/dryad.q0834p71

Supporting information

Additional supporting information may be found in the online version of this article.

Table S1 Coordinates of sampling locations, sampling depth and collection date.

Table S2 List of loci that were combined in each of the four multiplex PCR reactions used to genotype the *Acropora millepora* colonies in this study, as well as the dye labels and primer concentrations for each locus.

Table S3 Null allele homozygotes.

Table S4 Descriptive statistics (after removal of all but one of the repeated MLGs) for the 11 loci in the 20 *Acropora millepora* populations studied.

Table S5 Closeness centrality index for the 20 populations examined populations from the GBR.

Fig. S1 Principal Coordinates Analysis of pairwise genetic distances among the 20 sampled *A. millepora* populations.

Fig. S2 Results of a Bayesian model-based cluster analysis for $K = 2$ of the 20 *A. millepora*.

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