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Multiple scales of genetic connectivity in a brooding coral on isolated reefs following catastrophic bleaching

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Abstract

Understanding the pattern of connectivity among populations is crucial for the development of realistic and spatially explicit population models in marine systems. Here we analysed variation at eight microsatellite loci to assess the genetic structure and to infer patterns of larval dispersal for a brooding coral, *Seriatopora hystrix*, at an isolated system of reefs in northern Western Australia. Spatial autocorrelation analyses show that populations are locally subdivided, and that the majority of larvae recruit to within 100 m of their natal colony. Further, a combination of *F*- and *R*- statistics showed significant differentiation at larger spatial scales (2–60 km) between sites, and this pattern was clearly not associated with distance. However, Bayesian analysis demonstrated that recruitment has been supplemented by less frequent but recent input of larvae from outside the local area; 2–6% of colonies were excluded from the site at which they were sampled. Individual assignments of these migrants to the most likely populations suggest that the majority of migrants were produced at the only site that was not decimated by a recent and catastrophic coral bleaching event. Furthermore, the only site that recovered to prebleaching levels received most of these immigrants. We conclude that the genetic structure of this brooding coral reflects its highly opportunistic life history, in which prolific, philopatric recruitment is occasionally supplemented by exogenously produced larvae.

Keywords: dispersal, disturbance, recruitment, resilience, Scott Reef, *Seriatopora hystrix*

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Introduction

For marine organisms whose life histories include a pelagic larval phase, the spatial scale and pattern of demographic connection among populations have profound ramifications for their survival, regeneration and evolution (Hellberg *et al*. 2002; Gaines *et al*. 2003; Ayre & Hughes 2004). For example, the resilience of populations to severe disturbances depends on the supply of larvae from outside the disturbed area. If local production contributes to the majority of recruitment, that population will be slow to recover when the impacts occur throughout that local scale. Consequently, the development of realistic models of population connectivity is crucial for the effective management of threatened marine systems (Palumbi 2003). More specifically, marine reserve networks need to facilitate the recovery of populations by protecting sources of larvae, whether they are local or external (Roberts 1997; Cowen *et al*. 2006). This requires a spatially explicit understanding, not only of the patterns and dynamics of larval movements, but also of the scale and severity of disturbances.

Due to anthropogenic impacts that include overharvesting, pollution, disease and climate change, coral reefs are under serious threat around the world (Wilkinson 2002; Hughes *et al*. 2003; Bellwood *et al*. 2004). As a result, models of population connectivity are urgently needed for the conservation of these systems (Baums *et al*. 2005b). The Scott Reef system in northern Western Australia, provides a unique opportunity to investigate the influence of larval dispersal on recovery of corals after disturbance. In 1998, elevated sea-water temperatures and reduced water circulation caused a catastrophic mass-bleaching (Smith *et al*.

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2006). Although the extent of the bleaching varied somewhat across sites, the percentage cover of dominant coral taxa decreased by over 85% at all locations studied, and recovery has been slow. It is not known whether recent recruits in severely disturbed sites were produced by the few survivors in the local area, or from those sites within Scott Reef that were less severely damaged by the bleaching.

Indeed, our understanding of the degree to which local production results in recruitment to other populations in marine systems is generally deficient (Hellberg *et al*. 2002; Palumbi 2003; Cowen *et al*. 2006). Investigations have been limited by the considerable difficulties involved in tracking small propagules through the expansive oceans. Because of the resultant lack of direct, empirical data detailing patterns of larval dispersal or retention, researchers have had to draw on a wide range of indirect, interpretative and aggregative studies (Thorrold *et al*. 2002; Largier 2003). Analysis of the spatial distribution of genetic variation is one such method. Because gene flow reduces genetic divergence, population models are used to partition the genetic variation of a species among different geographical locations, and consequently assess the spatial scales over which they are reproductively closed. However, estimating recent patterns of migration from these models requires several simplified and often unrealistic assumptions (Whitlock & McCauley 1999). Alternatively, when highly variable DNA markers such as microsatellites are utilized, the units of analysis can be shifted from populations to individuals, allowing more detailed and direct estimates of gene flow at ecologically relevant scales (Estoup & Angers 1998). In particular, several tests are now available that can assign individuals to their population of origin, from which present day migration patterns can be inferred (Waser & Strobeck 1998). Although the development of high resolution DNA markers in scleractinian corals has been difficult (Marquez *et al*. 2002), recent progress has been made (Magalon *et al*. 2003; Miller & Howard 2004; Baums *et al*. 2005a; Underwood *et al*. 2006). Here, we present biological data utilizing the microsatellites developed by Underwood *et al*. (2006) to investigate the pattern of genetic connectivity among populations of the brooding pocilloporid *Seriatopora hystrix* within the Scott Reef system in northern Western Australia.

The life history characteristics and genetic structure of *S. hystrix* suggest that the majority of dispersal is local. Larvae are produced sexually through internal fertilization of the eggs, are brooded within the polyp, and then released into the water column at an advanced developmental stage. Laboratory studies have demonstrated that larvae are competent to settle within hours and that most will settle within one or two days of release, provided suitable substrata are available (Harrison & Wallace 1990). In addition, it is unlikely that sperm survive for more than 10 h (Wallace & Willis 1994). Consequently, the potential for long distance dispersal over tens of kilometres or more of sperm or larvae via ocean currents seems limited.

Data from allozymes of *S. hystrix* on the Great Barrier Reef (GBR) support this conclusion (Ayre & Dufty 1994; Ayre & Hughes 2000). Levels of genetic differentiation are extraordinarily high (F_{ST} = 0.43 in both studies), and inbreeding and localized recruitment appear to be central features of these populations. The authors concluded that individual reefs depend primarily upon self-seeding for maintenance of populations, and that longer distance dispersal is rare over ecological time. Further, data from three microsatellite loci on *S. hystrix* from the Red Sea also indicated high levels of localized subdivision and spatially restricted dispersal over scales less than 20 km (Maier *et al*. 2005). However, because distances between individual *S. hystrix* colonies within sampling sites were not recorded in these studies, the finest scale of genetic subdivision and recruitment (i.e. metres to hundreds of metres) could not be determined.

While it is clear from these laboratory experiments and genetic studies that brooded larvae of corals routinely disperse over short distances, other information suggests that larvae may be capable of periodically dispersing over much larger distances. Because *S. hystrix* planulae are relatively large when released into the water column (Atoda 1951) and contain maternal zooxanthellae (Harrison & Wallace 1990), they may be well provisioned for a long maximum competency period (Richmond 1987; Isomura & Nishihira 2001), and are capable of settling after many weeks when deprived of substrata in the laboratory (Richmond 1987; Harii *et al*. 2002; Nishikawa *et al*. 2003). Due to the limitations of the indirect models used to assess gene flow in the genetic studies conducted thus far for *S. hystrix* and many other coral reef organisms, researchers have not been able to clearly separate recent gene flow from historical patterns (Niegel 1997; Benzie 1999). Therefore, further research is required to detail the prevalence and significance of recent, longer-distance migration of coral larvae between reefs.

This study utilizes high resolution genetic markers in combination with a detailed sampling design to explore the fine-scale processes influencing the local genetic structure and assess present day migration patterns over larger scales for *S. hystrix* at the Scott Reef system. In addition, we explore the influence of larval dispersal and adult abundances on the rates of recruitment and recovery of this abundant species following a catastrophic disturbance in a system that is isolated from others in the region, and from mainland and associated anthropogenic influences. Specifically, we present data on variation of microsatellite markers and changes in coral cover at different sites at Scott Reef, to address the following questions. First, at which sites was *S. hystrix* worst affected by the bleaching? Second, what is the scale of genetic subdivision

of *S. hystrix* at Scott Reef five years after the bleaching, and how far have the majority of larvae dispersed within this system (i.e. metres to tens of kilometres)? Third, have the new recruits at the most severely affected sites been produced locally from a few remaining colonies, from other sites on the same reef, or from other reefs within the Scott Reef system that were less affected by the bleaching?

Materials and methods

Study site and percentage cover of coral

Scott Reef is one of three isolated coral systems that lie on the edge of the continental shelf of northern Western Australia. It is located 270 km from the mainland, 250 km southwest of the Ashmore Reef system, and 400 km northeast of the Rowley Shoals system (Fig. 1a). We present data describing changes in percentage cover of *Seriatopora hystrix* from six sites in the Scott Reef system, which includes Seringapatam Reef (Fig. 1b). All sites consisted of five permanent 50 m transects separated by 10 m on the reef slope at approximately 9 m depth. Transects were filmed six months before the bleaching in October 1997, six months after the bleaching in October 1998, and approximately five years after the bleaching in November 2003. The percentage cover along each transect was estimated using a point intercept method (Smith *et al*. 2006). Percentage cover at each site in each year was calculated from the mean percent cover over the five, 50 m transects.

Genetic sampling

In total, 287 samples from individual colonies of *S. hystrix* were collected from six sites within the Scott system in January 2004, including three sites from south Scott (SL1, SL2 and SS1), one from north Scott (SL4), one from the Sandy Islet Reef (SL5), and one from Seringapatam Reef (SS3) (Fig. 1b). All of these sites were identical to the sites that were videoed for coral cover estimates, with the exception of SL5, where genetic samples were collected a few hundred metres from the videoed site. Using self-contained underwater breathing apparatus (scuba), approximately 1.5 cm of branch tips of individual colonies were snapped off by hand and placed in individually labelled bags underwater. At each site, the exact location of each sampled colony along a permanent 300 m transect was recorded, along with the global positioning system (GPS) coordinates at the beginning of each transect. This allowed the development of an x- and y-coordinate map of the entire sampling area. Between 45 and 50 colonies were sampled at regular intervals along each transect. Because we were interested in the connectivity of populations via the transport of sexually produced larvae, care was taken not to collect samples that were likely to have been produced from a nearby colony through vegetative fragmentation. Samples were taken at distances of at least 2 m apart, and not from loose fragments of colonies or colonies directly down-slope from another colony. Distances between sites varied from 2 to 60 km. Coral samples were preserved in 100% ethanol, pending DNA extraction.

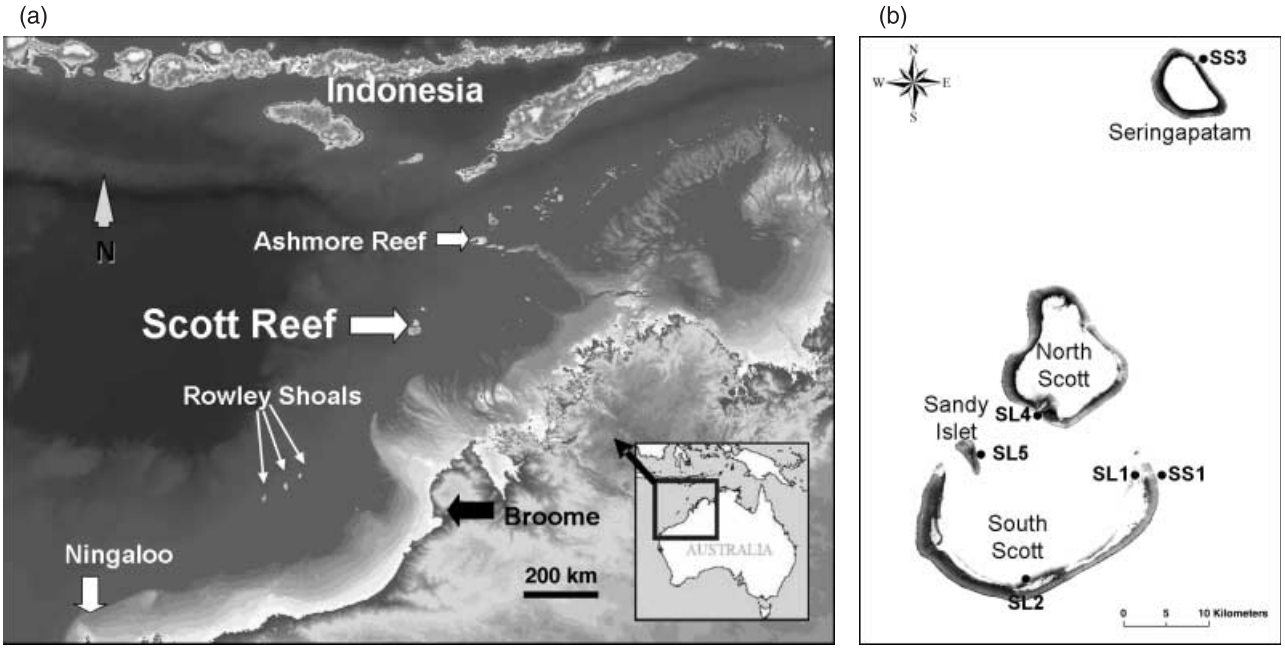

Fig. 1 Maps of (a) the major coral reefs of northern Western Australia and (b) the sites where genetic samples of *Seriatopora hystrix* were collected and where coral cover of *Seriatopora* was assessed at Scott Reef.

Genotyping

Details of genotyping procedure are described in Underwood *et al*. (2006). Briefly, after DNA extraction, two multiplex polymerase chain reactions (PCRs) were performed per individual, using fluorescently-labelled primers to assay nine loci containing a mixture of dimer, trimer and tetramer repeats. PCR products were analysed on a MegaBACE 1000 capillary sequencer (Amersham Biosciences), and the resulting electropherograms were scored using the program MEGABACE GENETIC PROFILER 2.2 (Amersham Biosciences). To minimize genotyping errors, all automated scorings of alleles were checked manually, and uncertainties were cleared by re-amplification and comparison. Alleles were scored as PCR product size in base pairs and converted to repeat size by subtracting the flanking region.

Of the 287 individuals genotyped, only two pairs of individuals shared the same diploid multilocus genotype. The probability that two unrelated individuals drawn from the same population had the same multilocus genotype by chance (P_{ID}) was very low; the biased probability of identity, P_{ID}, was 2.4×10^{-6}, and the unbiased P_{ID} was 2.1×10^{-6}, as calculated in GIMLET v133 (Valière 2002). Hence, because these pairs were sampled from the same site, they were considered to be clone mates, and one individual from each pair was removed from subsequent analyses so that each unique genotype was represented only once.

Allelic frequencies, allelic patterns and expected heterozygosities under Hardy–Weinberg equilibrium, and the number of private alleles were calculated in GENALEX v6 (Peakall & Smouse 2006) (Table 1). Tests for Hardy–Weinberg and linkage disequilibrium were conducted using FSTAT v2.9.3 (Goudet 1995), and significance levels where adjusted with sequential Bonferroni correction for multiple tests when $P < 0.05$. The Hardy–Weinberg test was based on 1000 permutations of alleles among individuals within localities using the inbreeding coefficient F_{IS} (Table 1). While heterozygote deficits were present in at least one population at seven of the nine loci, consistent heterozygote deficits were detected across all populations only for locus Sh4–010. This suggested the presence of null alleles at this locus and consequently it was excluded from all subsequent analyses.

Spatial autocorrelation analysis

Because earlier research suggested that most *S. hystrix* larvae disperse locally (Ayre & Dufty 1994), our first investigation of the genetic structure of *S. hystrix* at Scott Reef was at the finest scale possible. Thus, a spatial autocorrelation analysis was applied within each site. We used the method in GENALEX v6 (Peakall & Smouse 2006) that uses a pairwise genetic and pairwise geographical distance matrix to generate an autocorrelation coefficient (r) for a given distance class. The pairwise genetic distance matrix was calculated from all loci, and an associated linear pairwise geographical distance matrix was calculated from the x- and y-coordinates of the location of each colony.

Specifically, we performed two complimentary analyses. First, r was plotted for a range of distance classes, and this overall plot, or correlogram, illustrated the relative genetic similarity between pairs of individuals whose geographical separation fell within a specified distance class. Under restricted gene flow, and in the absence of selection, spatial genetic autocorrelation will be positive at short distance classes, subsequently declining through zero and becoming negative (Sokal & Wartenberg 1983; Epperson & Li 1996; Smouse & Peakall 1999; Peakall *et al*. 2003; Double *et al*. 2005). The distance where r first crosses the x-intercept provides an estimate of the extent of the positive genetic structure. This is the point where the random effects of genetic drift, not gene flow, are the primary determinants of genetic composition. When neutral loci are utilized, a single correlogram depicts the interplay between the relative influences of gene flow and stochastic forces on the genetic relatedness among individuals separated by different distances. Here, because we are interested in local scale dispersal processes that are likely to be common to all sites, we computed r over all sites to give the combined correlation coefficient *rc* (*Multiple pop* suboption in GENALEX). It is important to note that *rc* is calculated relative to the genetic variation within each site, ignoring among site genetic differences.

Second, because the capacity to detect spatial genetic structure from a single correlogram depends on the interaction between the true (but unknown) extent of genetic structure, as well as the distance class sizes chosen and the associated number of samples per distance class, we also conducted a multiple distance class analysis (*Multiple Dclass* suboption in GENALEX). In this analysis, the combined correlation coefficient *rc* was calculated for increasing, inclusive distance classes, ranging from the minimum distance between samples to the maximum distance of sampling. When significant positive structure is present, the estimated value of *rc* will decrease with increasing size of the distance class. The distance class size at which the estimate of *rc* is no longer significant provides another approximation of the extent of detectable positive spatial genetic structure (Peakall *et al*. 2003).

The statistical significance of r at each distance class, for both the single correlogram and the multiple distance class analysis, was tested in two ways. First, under the assumption of no spatial structure, the autocorrelation coefficient (*rp*) was calculated by the random shuffling of all individuals among the geographical locations. From 1000 random permutations, the upper and lower bounds of

Locus		Sampling site SL1	SL2	SL4	SL5	SS1	SS3	All	Mean
	N	48	49	46	49	46	46	284	
Sh4–001	***A***	6	7	4	4	2	6	9	6
	H_O	0.42	0.50	0.27	0.37	0.09	0.43		
	H_E	0.40	0.51	0.51	0.35	0.08	0.53		
	F_{IS}	–0.032	0.035	**0.485**	–0.04	–0.035	0.198		
Sh2–002	***A***	13	20	12	15	11	16	24	19
	H_O	0.72	0.75	0.73	0.82	0.62	0.85		
	H_E	0.86	0.85	0.88	0.87	0.71	0.89		
	F_{IS}	**0.174**	0.127	**0.173**	0.067	0.131	0.062		
Sh3–003	***A***	2	1	2	2	1	1	3	2
	H_O	0.04	0.00	0.02	0.02	0.00	0.00		
	H_E	0.04	0.00	0.02	0.02	0.00	0.00		
	F_{IS}	–0.011	NA	0	0	NA	NA		
Sh3–004	***A***	7	7	7	6	4	5	8	7
	H_O	0.65	0.76	0.54	0.55	0.56	0.63		
	H_E	0.65	0.74	0.68	0.51	0.57	0.51		
	F_{IS}	0.016	–0.005	**0.216**	–0.06	0.031	–0.222		
Sh2–006	***A***	11	10	8	8	3	6	20	11
	H_O	0.60	0.45	0.31	0.47	0.17	0.13		
	H_E	0.70	0.74	0.32	0.57	0.20	0.22		
	F_{IS}	0.158	**0.399**	0.031	0.192	0.123	0.411		
Sh3–007	***A***	3	3	6	3	4	4	7	5
	H_O	0.11	0.12	0.28	0.02	0.24	0.18		
	H_E	0.10	0.12	0.47	0.10	0.37	0.37		
	F_{IS}	–0.036	–0.04	**0.433**	**0.795**	0.355	**0.527**		
Sh3–008	***A***	2	4	3	3	1	2	5	3
	H_O	0.02	0.14	0.17	0.14	0.00	0.00		
	H_E	0.14	0.40	0.16	0.19	0.00	0.04		
	F_{IS}	**0.849**	**0.647**	– 0.073	0.238	NA	1		
Sh3–009	***A***	5	6	4	4	4	5	9	6
	H_O	0.66	0.47	0.35	0.57	0.26	0.31		
	H_E	0.63	0.58	0.36	0.60	0.24	0.28		
	F_{IS}	–0.032	0.194	0.035	0.053	–0.094	–0.111		
Sh4–010	***A***	4	7	7	5	5	7	8	7
	H_O	0.19	0.31	0.35	0.29	0.33	0.31		
	H_E	0.39	0.59	0.76	0.74	0.56	0.66		
	F_{IS}	**0.514**	**0.485**	**0.572**	**0.619**	**0.431**	**0.534**		
N_A		5.9	7.2	5.9	5.6	3.9	5.8		
P_{VA}		7	10	3	1	1	4		
F_{IS} **All**		**0.141**	**0.236**	**0.288**	**0.186**	**0.178**	**0.2**		

Table 1 Characteristics of the nine *Seriatopora hystrix* microsatellite markers from the six sites at Scott Reef. Given are, the number of unique multilocus genotypes (*N*), the number of alleles (*A*), the proportion of observed (H_O) and expected (H_E) heterozygotes per locus and site, and the F_{IS} calculated for each locus and each site (F_{IS} All); numbers in bold indicate significant deviations from Hardy–Weinberg equilibrium because of heterozygote deficits at the 0.05 level after sequential Bonferroni corrections. Also given are average number of alleles per locus (N_A) and the number of private alleles (P_{VA}) at each site, and the total number and the arithmetic mean of alleles per locus across sites

the 95% confidence interval were defined, and when the calculated *r*-value fell outside this confidence belt, significant spatial genetic structure was inferred. Second, an estimate of the 95% confidence interval about *r* was generated via 1000 bootstrap trials, and when this interval did not straddle $r = 0$, significant spatial genetic structure was inferred. While providing an alternative statistical test, this bootstrap test is less powerful than permutational tests, and thus to a greater extent favours the null hypothesis of no spatial structure (Double *et al*. 2005).

Population subdivision with F- *and* R-*statistics*

Because the spatial autocorrelation analyses measured within-site genetic structure only, to measure the proportion of total genetic variation that is geographically

structured and thus explore the historical genetic connections among sites over a wider scale, we used *F*- and *R*-statistics via analysis of molecular variance (AMOVA) (Excoffier *et al*. 1992). This analysis was performed in GENALEX v6 (Peakall & Smouse 2006) and partitioned the amount of genetic variation within and among sites with respect to different alleles (F_{ST}), and on the sum of squared size differences of the alleles assuming a stepwise model of mutation (R_{ST}). Pairwise comparisons of F_{ST} and R_{ST} between all sites were also calculated. Tests for statistical significance for all estimates were based on 1000 random permutations, and significance levels where adjusted with sequential Bonferroni correction for multiple tests. Lastly, to visualize these genetic relationships among sites, a genetic distance matrix derived from the pairwise F_{ST} and R_{ST} estimates was used to construct a principal coordinates analysis (PCA) graph in GENALEX.

Exclusion/assignment analysis

To infer present day migration patterns and identify individual immigrants, we used the population exclusion method computed in GENECLASS 2 (Piry *et al*. 2004). Although this method assumes Hardy–Weinberg and linkage equilibrium, simulations suggest that small deviations of Hardy–Weinberg equilibrium through heterozygote deficits, similar to those observed here, have little effect on assignment test performance (Cornuet *et al*. 1999). Further, due to the presence of highly localized population structure of *S. hystrix* described here and elsewhere (Ayre & Dufty 1994), and the relatively continuous distribution of many of the reefs within the Scott system, it is highly unlikely that our six sampling sites included all potential source populations of immigrants. Therefore, because this exclusion method does not require that the true population of origin has been sampled, it is likely to be more accurate than other assignment methods under these conditions (Berry *et al*. 2004). This analysis was conducted in two steps.

First, we assessed the probability that each individual colony was produced at the site where it was sampled as follows. The likelihood that an individual belongs to a particular population was computed with a partially Bayesian criterion of Rannala & Mountain (1997). Then, to identify a statistical threshold, beyond which individuals are likely to be excluded from a given reference population, this likelihood was compared to a distribution of likelihoods of 10^4 genotypes simulated from each candidate population with a Monte Carlo algorithm (Paetkau *et al*. 2004). An individual was excluded from its sampling site when the probability of exclusion was greater than 95% (P or $\alpha \leq 0.05$). In an empirical test of these methods on terrestrial skinks, Berry *et al*. (2004) considered this 95% threshold to be stringent and highly accurate. However, because some individuals will appear to be immigrants purely by chance when many tests are performed on large numbers of individuals, this error can be reduced by increasing the stringency (Rannala & Mountain 1997). Further, as noted by Paetkau *et al*. (2004), there is a trade off between power to detect true immigrants and incorrectly identifying residents as immigrants, but analytical procedures to detect true immigrants from individuals excluded by error have yet to be developed. Therefore, we conducted a second exclusion test under the more stringent conditions of P or $\alpha \leq 0.01$. In addition to the empirical work (Berry *et al*. 2004), simulated data indicate that the numbers of loci (8), sample sizes (> 45 individuals per site), and levels of subdivision (mean $F_{ST} = 0.095$, see below) employed here are sufficient for accurate exclusion under these stringencies (Cornuet *et al*. 1999). Therefore, we are confident that these results provide an accurate representation of the numbers of immigrants into each site.

To explore the origins of these immigrants, the second part of this Bayesian analysis utilized the probabilities that the individuals excluded from their sampling site originated from one of the other sites that we sampled. Although simulations show that 100% correct assignment can be achieved with this method with when scoring 10 loci ($H \approx 0.6$) on 30–50 individuals from each of 10 populations when $F_{ST} \approx 0.1$ (Cornuet *et al*. 1999), we sampled from a limited number of populations in a spatially complex system. Therefore, to reduce the chances of assigning an immigrant to a population that we sampled when it actually came from an un-sampled population (e.g. from a genetically differentiated but un-sampled population on the same reef), we introduced a buffer zone between the threshold of exclusion from the sampled site, and the threshold for assignment to another sampled site. Thus, individuals that were excluded from their sampling site when $P \leq 0.05$, were assigned to another site when $P \geq 0.1$. Alternatively, individuals that were excluded from their sampling site in the second more stringent exclusion test when $P \leq 0.01$, were assigned to another site when $P \geq 0.05$. Where the sampling site was excluded, but more than one of the other sites were not excluded, the site with the highest probability was considered the source population. These individuals were classified as putative long-distance migrants, while individuals that were excluded from all sites remained 'unassigned'. To our knowledge, such an approach has not been used in studies utilizing these methods to date, but is warranted here. This highlights the issue that while these methods offer many important advantages, they are yet to be tested in a wide range of biological systems with real data. Consequently, while we interpret these assignments with caution, we present these results as a test of the hypothesis that the numbers of larvae exported out of each site relates to the coral cover and degree of bleaching at each site.

Results

Changes in coral cover

The bleaching caused catastrophic mortality of *S. hystrix* across the Scott Reef system with the exception of site SL4, which did not suffer any detectable mortality following the bleaching (Fig. 2). Of the sites affected by the bleaching, the mean decrease in cover of *S. hystrix* was over 95%; six months after the bleaching cover at SL1, SL2, SL5, SS1 and SS3 was reduced by 100%, 98%, 91%, 95% and 95%, respectively. All of these sites, except SL1, showed signs of recovery five years after the bleaching, but only SL5 had clearly recovered to its prebleaching level.

Within-site genetic structure

Heterozygote deficits were detected at six of the eight loci used in the analyses, but only at a maximum of three of the six populations (Table 1). Of 168 tests, linkage disequilibrium was detected only twice between locus pairs. These two associations both occurred at SL4 between Sh4–001/Sh3–008 and Sh4–001/Sh3–009, and remained significant after Bonferroni correction. We attributed this inconsistent Hardy–Weinberg and rare linkage disequilibrium to genetic subdivision at the local scale, combined with admixture of populations, and concluded that null alleles were not a cause of the heterozygote deficits at these eight loci.

Spatial autocorrelation analysis revealed significant genetic structure within the 300 m transects at each site. We plotted *rc* with respect to even distance classes of 20 m up to 240 m (Fig. 3a). The correlation coefficient was significantly positive for the first distance class (0–20 m), after which *rc* decreased and then levelled off to become nonsignificantly different from zero over the next four distance classes, crossed the *x*-axis at 100 m and then decreased rapidly to become significantly negative at the 100–120 m distance class. At distances greater than 120 m, *rc* tended to oscillate between high and low autocorrelation (although the positive correlations were not significant), indicating a chaotic spatial pattern of genetic relatedness at this scale. Significant genetic structure at the local scale was also detected when *rc* was plotted was plotted with respect to distance classes of increasing sizes from the minimum sampling unit of 20 m to 240 m (Fig. 3b). Genotypes were initially nonrandomly distributed, with the highest *rc* observed in the first distance class of 0–20 m, after which *rc* decreased, but remained significant up to 120 m (if the more conservative bootstrap test is considered), or 220 m (if the more powerful permutation test is considered). This suggests that the scale of sampling and other parameters of our spatial autocorrelation analysis were appropriate for detecting the local scale influence of gene flow on genetic structure of *S. hystrix*.

Among-site genetic structure

The high degree of genetic structure detected within sites by spatial autocorrelation analysis was also present over larger spatial scales among sites. Private alleles were observed at all sites, providing one indication of strong subdivision among sites (Table 1). The numbers of private alleles were highest at SL2 (10) and SL1 (7). The AMOVA assigned 9.5% (F_{ST} = 0.095) and 14.6% (R_{ST} = 0.146) of the genetic variation to among-site variation, and both estimates were significantly different from zero ($P < 0.001$). Further, all populations were significantly different from each other according to pairwise comparisons of F_{ST} and R_{ST} estimates, apart from the two pairwise R_{ST} estimates between SL4 and SS3, and between SL2 and SL5 (Table 2).

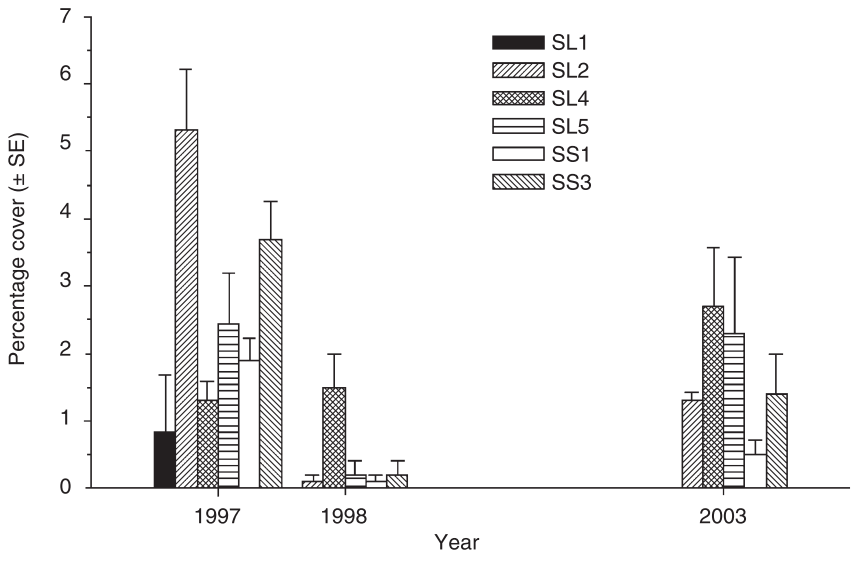

Fig. 2 Changes in percentage cover of *Seriatopora hystrix* (± SE) at each site before (1997), and approximately 6 months (1998) and 5 years (2003) after the mass-bleaching. No *S. hystrix* was observed at site SL1 after the bleaching.

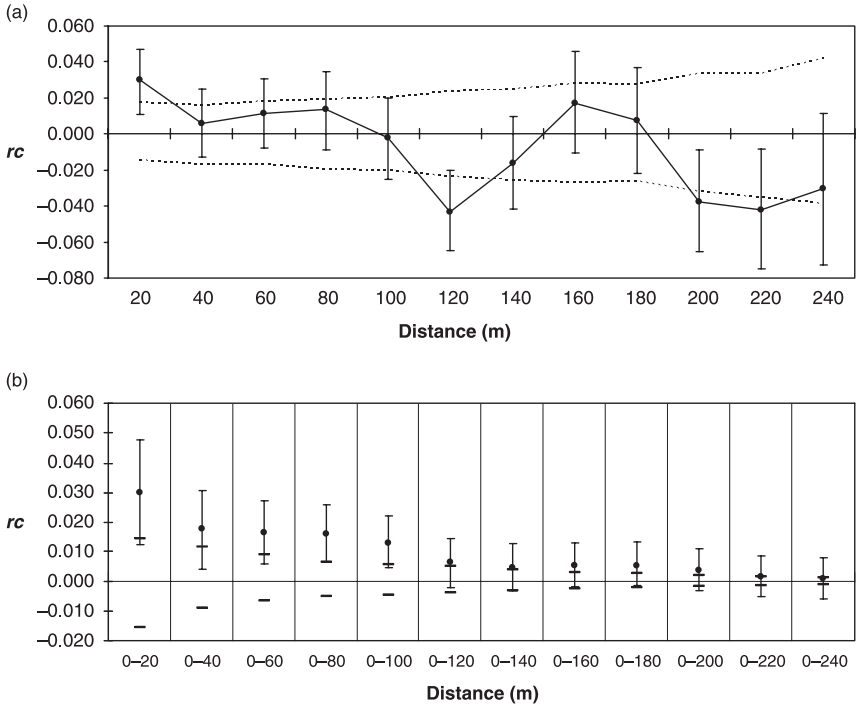

Fig. 3 Spatial autocorrelation analyses of *Seriatopora hystrix* at Scott Reef. The permuted 95% confidence interval (dashed lines) and the bootstrapped 95% confidence error bars are shown. (a) Single correlogram plot of the combined genetic correlation coefficient (*rc*) across all transects as a function of distance. (b) Multiple distance class plot, showing the influence of different distance classes on combined genetic correlation (*rc*) across transects.

Table 2 Pairwise F_{ST} (a) and R_{ST} (b) estimates between sites for *S. hystrix* at Scott Reef below diagonal. Distances between sites in km are shown above diagonal. Estimates in bold indicate significance based on 1000 permutations after sequential Bonferroni correction (P was ≤ 0.001 for all significant comparisons)

(a)

	SL1	SL2	SL4	SL5	SS1	SS3
SL1		20.07	11.21	17.90	3.34	49.67
SL2	**0.045**		19.27	14.45	22.70	65.75
SL4	**0.118**	**0.083**		9.12	14.23	46.49
SL5	**0.064**	**0.065**	**0.077**		21.23	53.53
SS1	**0.187**	**0.163**	**0.068**	**0.106**		49.43
SS3	**0.146**	**0.111**	**0.033**	**0.084**	**0.051**	

(b)

	SL1	SL2	SL4	SL5	SS1	SS3
SL1		20.07	11.21	17.90	3.34	49.67
SL2	**0.082**		19.27	14.45	22.70	65.75
SL4	**0.295**	**0.120**		9.12	14.23	46.49
SL5	**0.129**	0.018	**0.091**		21.23	53.53
SS1	**0.374**	**0.138**	**0.096**	**0.099**		49.43
SS3	**0.327**	**0.147**	0.000	**0.102**	**0.088**	

The PCA of R_{ST} illustrated the close relationships between these two pairs of sites, while the F_{ST} plot supported this genetic similarity between SL4 and SS3, but not SL2 and SL5 (Fig. 4). Importantly, these PCA graphs also show

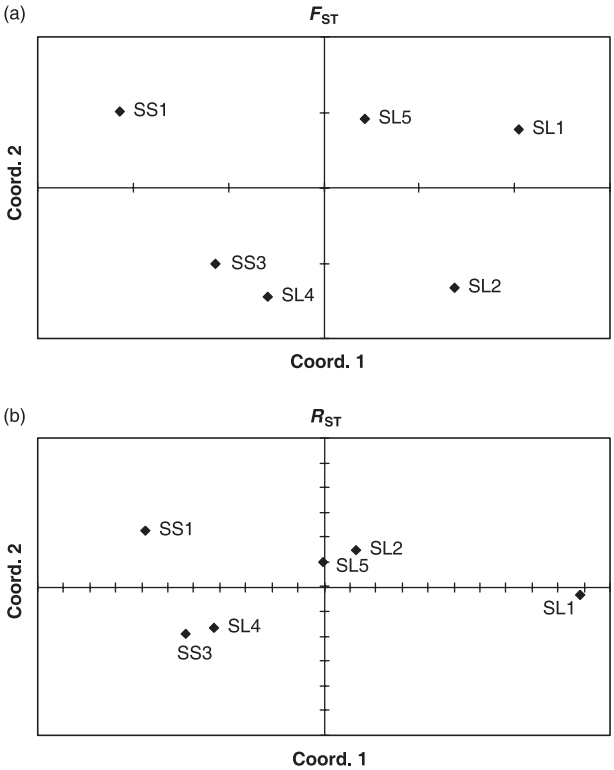

Fig. 4 Plots of principal coordinate analysis calculated in GENALEX from standardized distance matrix of *Seriatopora hystrix* sites at Scott Reef. (a) Pairwise F_{ST} estimates between sites: first two axes explain 95.93% of variation. (b) Pairwise R_{ST} estimates between sites: first two axes explain 98.16% of variation.

clearly that genetic relationships were not related to geographical distances between sites; in particular, sites SL1 and SS1 were the closest but the most genetically divergent of all pairs of sites.

Immigrant and emigrant detection

When we excluded individuals with a probability ≥ 95% ($P \leq 0.05$), 17 of the 285 individuals analysed (6%) were excluded from the site at which they were sampled (Table 3a). Of these, six individuals (2% of total) were assigned to another site that was sampled ($P \geq 0.1$), while 11 (4%) could not be assigned to any site that was sampled. The presumed migration patterns are illustrated in Fig. 5(a), which shows that SL4 produced the most emigrants (three individuals), and SL5 received two-thirds of these (four individuals). In addition, one migrant from SL5 was assigned to SS3 with a probability 0.25.

Although fewer individuals were identified as immigrants in the more stringent test when individuals were excluded from their sampling site with a probability ≥ 99% ($P \leq 0.01$), five immigrants (2%) remained, lending a degree of confidence to these results (Table 3b). Of these, three individuals (1% of total) were assigned to the other sites that we sampled ($P \geq 0.05$). Congruent with the less stringent analysis, of these putative long distance migrants, SL4 produced the majority (two individuals), while SL5 received the majority (two individuals) (Fig. 5b).

Discussion

Microsatellite data from *S. hystrix* corals presented here show strong population structure within the Scott Reef system at all scales that were investigated. We found significant localized structure within the 300 m transects at each site, and significant genetic differences between sites that were separated by 2–60 km. We conclude that the vast majority of larvae recruit to their natal patch of reef. However, we also identified a small proportion of corals that were produced outside this patch, showing that routine local recruitment is occasionally supplemented by successful longer-distance dispersal. Consequently, the genetic structure of this brooding coral reflects multiple processes that influence gene flow and population connectivities over different spatial and temporal scales.

Table 3 Numbers of individual colonies excluded (immigrants) from their sampling sites (sample size in brackets) and their most likely population of origin (assigned population) calculated with GENECLASS 2. Individual colonies were excluded from their sampling site if the likelihood of their genotype occurring in that site was less than 0.05 (a), or 0.01 (b), when compared to a distribution of 10^4 simulated genotypes from that site. Once excluded, the individual was assigned to the site where it had the highest probability of occurring, and if this was below 0.10 (a), or 0.05 (b), then the individual was assumed to have originated from a population that was not sampled (unassigned)

(a)

Sampling site	N immigrants	Assigned site						N immigrants assigned	N immigrants unassigned
		SL1	SL2	SL4	SL5	SS1	SS3		
SL1 (48)	3	0	–	0	0	0	0	0	3
SL2 (49)	3	0	0	–	1	0	0	1	2
SL4 (46)	4	0	0	0	–	0	0	0	4
SL5 (49)	5	0	0	2	1	0	1	4	1
SS1 (47)	1	0	0	1	0	–	0	1	0
SS3 (46)	1	0	0	0	0	0	–	0	1
Total	17	0	0	3	2	0	1	6	11

(b)

Sampling locality	N immigrants	Assigned population						N immigrants assigned	N immigrants unassigned
		SL1	SL2	SL4	SL5	SS1	SS3		
SL1 (48)	0	–	0	0	0	0	0	0	0
SL2 (49)	2	0	–	1	0	0	0	1	1
SL4 (46)	1	0	0	–	0	0	0	0	1
SL5 (49)	2	0	0	1	–	0	1	2	0
SS1 (47)	0	0	0	0	0	–	0	0	0
SS3 (46)	0	0	0	0	0	0	–	0	0
Total	5	0	0	2	0	0	1	3	2

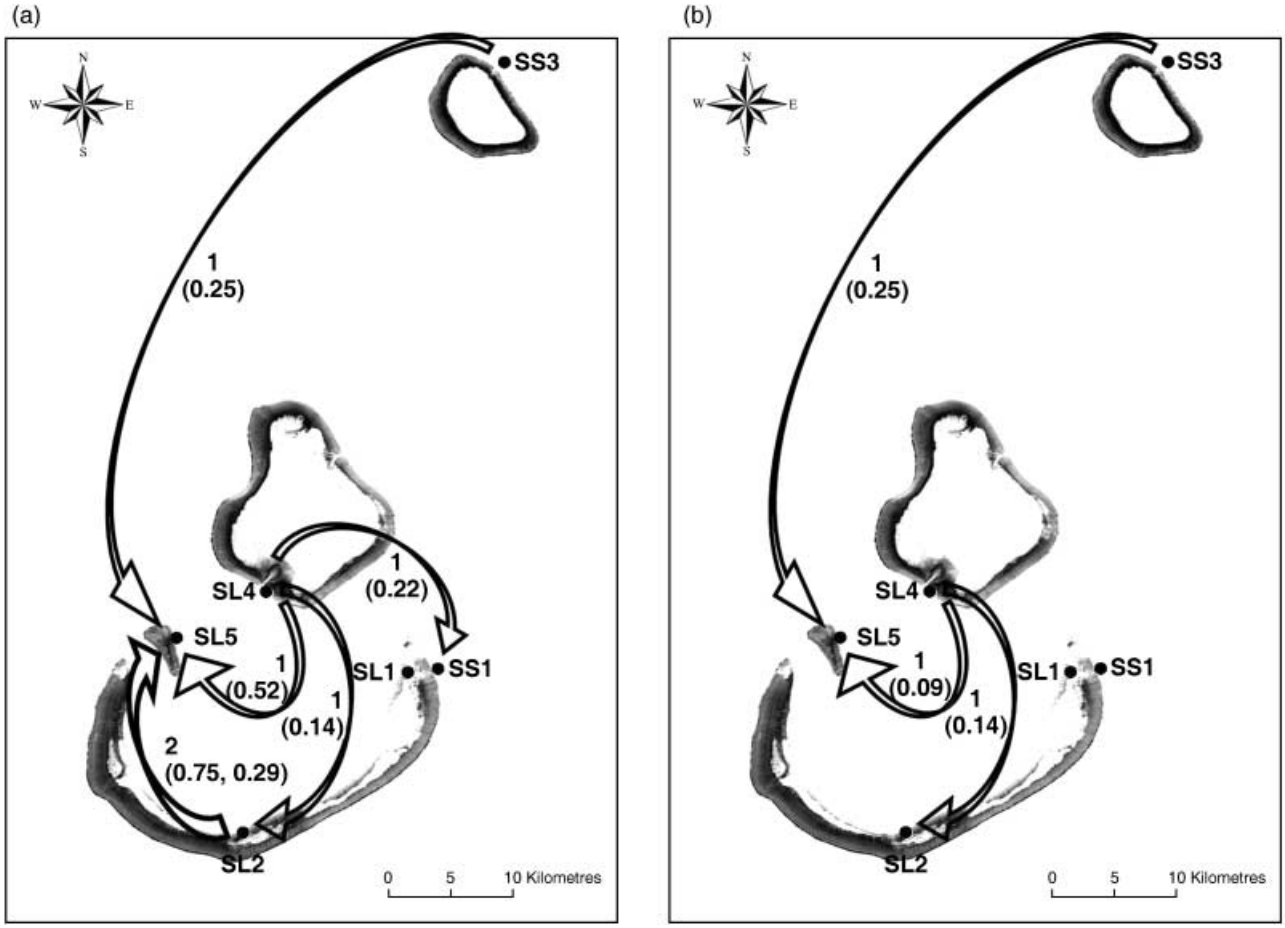

Fig. 5 Migration patterns at Scott Reef as inferred by GENECLASS 2 showing dispersal direction and numbers of immigrants that were excluded from their sampling site at $P \leq 0.05$ (a) or $P \leq 0.01$ (b) but were also assigned to source sites when $P \geq 0.1$ (a) or $P \geq 0.05$. (b) Figures in brackets indicate probability that each individual originated from its assigned site.

Localized recruitment and heterozygote deficits

At the local scale, the spatial autocorrelation analyses demonstrated that proximate corals are more genetically alike than corals that are further apart, indicating that disproportionately more larvae settle within 20 m of their natal colony. Specifically, in both the single correlogram and the multiple distance class analysis, the strongest positive genetic correlation was detected at the smallest distance class of 0–20 m, and this declined to zero as distances between corals increased (Fig. 3). Because these analyses were based on data from the six sites, and genetic distances were computed relative to the variation within sites only, it seems that gene flow over this scale is influenced by processes common throughout the Scott Reef system. This conclusion was supported by the correlograms from individual sites (not shown). While having less statistical power, these correlograms from each site showed similar patterns to the combined correlogram; five of the six sites exhibited maximum positive genetic correlation over the first few distance classes, which then declined to become negative at distance classes greater than 100 m.

The common occurrence of heterozygote deficits observed here further emphasizes the localized nature of recruitment in this species. As shown with allozymes in *S. hystrix* on the GBR (Ayre & Dufty 1994), we observed heterozygote deficits at most sites. Heterozygote deficits are commonly found in brooding and broadcasting hard corals (Ayre & Hughes 2000; Gilmour 2002; Mackenzie *et al*. 2004; Whitaker 2004; Maier *et al*. 2005; Nishikawa & Sakai 2005) and in marine species in general (Tracey *et al*. 1975; Johnson & Black 1982), but it is often not possible to demonstrate the exact mechanism generating these deficits (Zouros & Foltz 1984). Often, processes operating on scales smaller than that sampled are given as explanations; specifically, a Wahlund effect brought about by sampling of individuals that do not originate from a randomly mixed gene pool (Tracey *et al*. 1975; Johnson & Black 1984).

Because we recorded the location of individual colonies, we were able to explore the genetic relationships between individuals, providing direct evidence that heterozygote deficits are caused by mixing of genes from such fine spatial differences among local breeding groups of hard corals. Congruently, the spatial signal in the single correlogram of individual sites (not shown) was strongest for SL4, which was the site that exhibited the highest number of heterozygote deficits. This nonrandom mating within sites appears to be a product of restricted dispersal of both larvae and sperm. However, because we cannot gauge quantitatively whether the fine-scale genetic subdivision accounts for all the observed heterozygote deficits, it is also possible that other factors are involved. First, mixing of genetically distinct cohorts may have contributed to a temporal Wahlund effect (Johnson & Black 1984). Second, self-fertilization has been documented in other corals in the family of Pocilloporidae (Harrison & Wallace 1990) and, if common, may have contributed to the heterozygote deficiencies observed here. Third, because private alleles were common, it is possible that the deficits of heterozygotes at certain sites were produced by null alleles that were absent from the other sites. Lastly, it is also important to note that Ayre & Dufty (1994) showed that genotype frequencies within sheltered lagoon sites on the GBR were typically in Hardy–Weinberg equilibria. This indicates that habitat type may affect mating or dispersal, and the fine scale heterogeneity detected here on the reef slopes need not apply in other populations.

In addition to the prevalence of heterozygote deficits and the within-site spatial autocorrelation, our analysis of spatial genetic variation among sites also indicated that dispersal is predominantly local. All pairs of populations exhibited significant R_{ST} or F_{ST}, even though five of the six sites were separated by less than 30 km, and two of those were separated by only three kilometres. Consequently, our interpretation is that dispersal over the scale of kilometres to tens of kilometres is rare at the Scott Reef system.

Comparisons with Great Barrier Reef populations

Although similar conclusions were drawn from data on *S. hystrix* from the GBR (Ayre & Dufty 1994), the estimates of among-site genetic subdivision (F_{ST} = 0.095) presented here are low compared to those obtained from the GBR (F_{ST} = 0.43). We suggest three possible explanations for this pattern that are not mutually exclusive.

First, although the maximum distance between sites in the two studies was comparable (60 km here compared to 90 km in the GBR study), all corals in this study were collected from the reef slope habitat, whereas the GBR study included a much greater range of habitats and reef types. Ayre & Dufty (1994) analysed samples that were collected from five different habitats on inner-, mid- and outer-shelf reefs; 10% of this among site variation was attributed to habitat, and 10% attributed to across shelf variation. Further, mean F_{ST} among mid-shelf reefs was only 0.15, and this level of subdivision was almost identical to that observed among mid-shelf reefs at a much larger geographical scale (Ayre & Hughes 2000). Therefore, this increased environmental heterogeneity is likely to have contributed to larger among-site genetic differences, compared to our study.

Second, the higher heterozygosities associated with microsatellites compared to allozymes (average heterozygosity of 0.36 here vs. 0.16 in the GBR study) are likely to deflate F_{ST} estimates (Balloux & Lugon-Moulin 2002). When we standardized this measure of genetic differentiation by keeping the number and frequency of alleles within populations the same, but not allowing any populations to share alleles (Hedrick 2005), F_{ST} equalled 0.16, which is equal to the subdivision among mid-shelf reefs on the GBR. Further, F_{ST} estimated from microsatellite data for *S. hystrix* from the Red Sea (0.089) was almost identical to that detected here (Maier *et al*. 2005). Therefore, it seems that different molecular markers with different heterozygosities also account for some of the differences in estimates of subdivision between the GBR and Scott Reef.

Third, it is possible that a reduction in population sizes (bottlenecks) and founder events associated with the 1998 bleaching at Scott Reef reduced genetic subdivision among sites. While bottlenecks often reduce genetic variation within populations and increase genetic differentiation among populations, under certain circumstances, founder events may also reduce existing genetic structure (McCauley 1993). Here, severely bleached sites may have been re-established by small numbers of larvae produced from genetically distinct sources, which would have increased the genetic mixing and reduced F_{ST}. However, without more detailed investigation of the extent of bleaching at different depths and sites it is difficult to assess this hypothesis. In theory, testing for bottlenecks with genetic data might have shed more light on this issue. However, tests for genetic bottlenecks cannot be applied to the system investigated here because sites probably receive recruits from more than one genetically distinct population, confounding the signals on which these tests rely (numbers of rare alleles, size of allele ranges, or heterozygote excesses within sites (Luikart & Cornuet 1998; Luikart *et al*. 1998; Garza & Williamson 2001). Additional research at other isolated systems that have not undergone recently a major disturbance will help evaluate further whether these populations at Scott Reef experienced bottlenecks in 1998.

Nevertheless, despite these differences between the two studies, our results not only support the finding of high levels of genetic differentiation by Ayre & Dufty (1994), but also extend our understanding of the processes underlying these patterns, by providing direct evidence that populations

are subdivided on a scale of tens of metres. Consequently, the conclusion that the majority of brooded larvae produced by *S. hystrix* settle very close to their natal colony is now well supported in two very different ecological systems, irrespective of local environmental conditions and history.

Disturbance, broader scale dispersal, and source/sink dynamics

Despite this preponderance of local recruitment over scales of tens of metres, we have also presented evidence that *S. hystrix* larvae periodically disperse over much greater distances. The pairwise *F*- and *R*- statistics indicated that some sites separated by relatively large distances were more closely related than those that were nearer to each other. For example, the pairwise R_{ST} comparison between SL4 and SS3 was not significant. Thus, sufficient gene flow over the 40 km of open water between Seringapatam and Scott Reef has prevented genetic differentiation, assuming that the mutation process conforms to the stepwise mutation model. This pattern contrasts dramatically with the strong and significant differentiation of SS1 and SL1, which occur on the same reef and are separated by only three kilometres. In contrast to microsatellite variation of *S. hystrix* in the Red Sea (Maier *et al*. 2005), gene flow over these larger scales does not follow an isolation-by-distance model, and seems to be influenced by a number of forces in this system. Primarily, physical links between sites via water currents are likely to play a crucial role in determining the long distance dispersal trajectories of larvae (Cowen *et al*. 2006), and recent genetic evidence suggests that complex hydrodynamics associated with island/reef systems may disrupt patterns of isolation by distance (Johnson & Black, in press). Additionally, we propose that the 1998 bleaching event may also have had two important influences on these broad scale patterns of genetic differentiation. First, *S. hystrix* at site SL4 was not affected by the bleaching, and had significantly more cover than all the other sites that were decimated. We predicted that these differences in coral survival and reproductive output among sites would translate into differences in numbers of larvae exported. Second, these pairwise estimates of population subdivision may be complicated because populations are unlikely to be in equilibrium due to localized extinction and colonization processes associated with the recent bleaching and other major impacts in the past (e.g. cyclones, predator outbreaks). Therefore, to explore further the fate of those few larvae that are exported off their local reef patch with analyses that do not rely on these assumptions, we employed the Bayesian exclusion/assignment method.

Broadly, the exclusion tests supported the *F*- and *R*-statistics; the vast majority of individuals (between 94% and 98%) were not excluded from their sampling site. This provides further evidence that most recruits are highly philopatric. However, even if we only accept the more stringent test where $P = 0.01$ (where five individuals, or 2%, were excluded), these results also suggest that rare but recent inputs of larvae from outside the local patch have supplemented this local recruitment. Although these excluded individuals may have come from other genetically differentiated populations on the same reef that were not sampled, given that we found no evidence of isolation by distance, we argue that many of the excluded individuals are as likely to have come from the other reefs within the Scott Reef system.

In addition to these exclusion tests, results from the analyses that assigned individuals that were excluded from their sampling site to other sites indicated that this migration was asymmetric, with some sites operating as sources of larvae and some as sinks. We interpret these between-site dispersal patterns in the context of the levels of coral cover present at the different sites after the bleaching. Irrespective of the levels of stringency, the site that was not affected by the bleaching (SL4) produced the most putative long-distance dispersers. Given that *S. hystrix* releases its brooded larvae several times throughout the year (Harrison & Wallace 1990; Tanner 1996), we argue that SL4 would have produced larvae that dispersed throughout a range of environmental conditions (e.g. wind speeds and directions) in years immediately following the bleaching. This is likely to have increased the chances of dispersal from SL4 to different reefs across the system relative to the other sites. In contrast, SL5 was the only site affected by the bleaching that returned to its previous cover by 2003, and received the majority of immigrants assigned to distant reefs. As a result, we suggest that SL5 is exposed to water circulation from a number of sources and represents a sink for dispersing larvae. Conversely, it appears that SL1 is isolated from other sites. No immigrants were identified at SL1 in the exclusion analysis under conditions of high stringency, and the immigrants that were detected at the low stringency were not assigned to any other sites that we sampled on South Scott Reef or other reefs. In addition, SL1 had particularly high pairwise F_{ST} and R_{ST} estimates with most sites, and a high number of private alleles, and no detectable increases in coral cover five years after the bleaching.

Ecological and management implications

Genetic structure of *S. hystrix* populations at Scott Reef is clearly dominated by highly localized recruitment, but also involves occasional longer-distance dispersal of larvae. Local recruitment seems to be governed by restricted dispersal of sperm and the ability of larvae to settle from the plankton quickly, before they are moved off their natal reef patch. Moreover, local recruitment can be prolific given the protracted reproductive period in *S. hystrix* that

can include several cycles of oogenesis (Harrison & Wallace 1990). Thus, populations should recover relatively quickly after disturbance provided a critical mass of adults survive a disturbance. Observations in the field support this prediction, as *S. hystrix* is often the first to re-colonize disturbed areas. The occasional long-distance dispersal requires large numbers of larvae produced in the source population, and that distant sites are connected hydrodynamically. These conclusions have important implications for the recovery and management of *S. hystrix* corals after severe disturbance. If we can predict which reefs are less likely to be damaged by thermal-induced bleaching, and protect them from other anthropogenic disturbances, these reefs could augment localized recruitment on nearby, decimated reefs, and thus, facilitate recovery over a period of several years to a decade. However, the results presented here apply to brooding corals with 'weedy' life histories, that are particularly susceptible to disturbances such as elevated water temperatures, but which also have rapid growth and high reproductive output. Other taxa with less opportunistic life histories are likely to have different patterns of larval dispersal and trajectories of recovery following major disturbances.

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JU is currently conducting a PhD project, investigating genetic connectivity, recruitment and disturbance in two coral species in northern Western Australia. This is a collaborative project between the School of Animal Biology at the University of Western Australia and the Australian Institute of Marine Science (AIMS). LS and JG are AIMS coral ecologists who are primarily researching the impacts of disturbances on coral reefs in Western Australia, and MvO is a Senior Research Scientist at AIMS in Townsville QLD, who utilizes genetics and molecular biology to explore the impacts of environmental change on coral systems.
