Ecologically Relevant Dispersal of Corals on Isolated Reefs: Implications for Managing Resilience

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Ecologically relevant dispersal of corals on isolated reefs: implications for managing resilience

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Abstract. Coral reefs are in decline worldwide, and marine reserve networks have been advocated as a powerful management tool for maximizing the resilience of coral communities to an increasing variety, number, and severity of disturbances. However, the effective design of reserves must account for the spatial scales of larval dispersal that affect the demography of communities over ecological time frames. Ecologically relevant distances of dispersal were inferred from DNA microsatellite data in a broadcast-spawning (Acropora tenuis) and a brooding (Seriatopora hystrix) coral at isolated reef systems off northwest Australia. Congruent with expectations based on life histories, levels of genetic subdivision among populations were markedly higher in the brooder than in the broadcast spawner. Additionally, significant subdivision for both species between systems (>100 km), and between (>10 km) or within reefs (<10 km) within systems, indicated that many reefs or reef patches are demographically independent. There was also a clear distinction in the scale of genetic structure between the different systems; at the more geographically complex of the systems, a much finer scale structure was detected in both species. This suggested that the hydrodynamics associated with these complex reefs restrict distances regularly traveled by larvae. The primary implication is that short-term recovery of these coral communities after severe disturbance requires the input of larvae from viable communities kilometers to a few tens of kilometers away. Therefore, to be self-sustaining, we suggest that coral reef protected areas need to be large enough to encompass these routine dispersal distances. Further, to facilitate recovery from severe disturbances, protected areas need to be replicated over these spatial scales. However, specific designs also need to account for size, complexity, and isolation of reefs, which will either restrict or enhance dispersal within this range.

Key words: Acropora tenuis; disturbance; gene flow; genetic connectivity; marine protected areas; marine reserves; microsatellites; recruitment; reef-building coral; Rowley Shoals, northwest Australia; Scott Reef, northwest Australia; Seriatopora hystrix.

Introduction

Coral reefs around the world are threatened by an increasing variety, number, and severity of disturbances (Hughes et al. 2003). Marine reserve networks have been advocated as a powerful tool for managing resilience of coral reefs to these disturbances (Bellwood et al. 2004) and conserving threatened marine systems in general (Lubchenco et al. 2003), but effective design of reserve networks must incorporate a spatially explicit understanding of larval dispersal (Palumbi 2003). Direction, distance, and frequency of dispersal will influence the size and spacing of reserves, because protected areas need to be large enough to be self-sustaining, and close enough not only to promote persistence of protected communities through dispersal among them, but also to supplement recruitment to communities outside reserves (Sale et al. 2005). Further, scales of larval dispersal need to be considered in relation to scales of disturbance. For example, a community that does not receive a regular and large supply of recruits from outside the range of a severe disturbance will recover slowly, and may undergo a dramatic transition in the stable state of dominant taxa if the disturbance occurs frequently. Recent progress has been made in understanding the different spatial and temporal scales of disturbances that affect coral reef communities (Nystrom et al. 2000), from the local patchy impacts of intense storms, to chronic regional effects of overfishing, to the global and long-term impacts of raised seawater temperatures, but our current understanding of scales of dispersal of coral larvae is inadequate (van Oppen and Gates 2006).

An important factor influencing the dispersal of marine organisms is their reproductive mode, which affects the time larvae spend in the water column.
Across a range of taxa, larval duration is positively correlated with their dispersal distance (Bohonak 1999, Shanks et al. 2003). For example, populations of scleractinian corals that release brooded larvae that are competent to settle immediately are generally more genetically subdivided than species that spawn their gametes externally and whose larvae develop within the plankton (e.g., Ayre and Hughes 2000, Nishikawa et al. 2003, Whitaker 2004, 2006). However, recent evidence indicates that even in marine species with larvae having the potential to spend weeks or months in the plankton, dispersal may not be as far as initially thought, and retention to natal reefs or reef patches may be common (reviewed by Levin 2006). Recent studies of broadcast-spawning corals support this changing paradigm, indicating that dispersal between regions or reefs is often limited (Hellberg 1996, Ayre and Hughes 2000, Hughes et al. 2001, Nishikawa et al. 2003, Ayre and Hughes 2004, Whitaker 2004, Baums et al. 2005).

Although a general correlation exists between distances moved by larvae and reproductive mode in marine species, dispersal is also influenced by the interaction of other physical and/or biological factors (Swearer et al. 2002). Specifically, local variation in hydrogeographic features arising from the interaction between reefs, land masses, and water currents can either promote or restrict dispersal, and accounts for some of the variation in patterns of larval dispersal observed over different spatial and temporal scales (Largier 2003). For example, gene flow between islands in an intertidal snail, Austrococclia constricta, is not continuous over local scales (<2 km), despite a high degree of connectedness among populations over larger scales (~50 km) (Johnson and Black 2006). Thus, oceanographic conditions associated with complex island systems may promote the retention of planktonic larvae and enhance local isolation of some populations. Similarly, prevailing currents influence the degree of retention of larvae of Thalassoma bifasciatum (bluehead wrasse) to natal island reefs in the Caribbean; larvae that recruit to leeward areas are produced locally, while most recruits to windward areas come from more distant sources (Swearer et al. 1999). In scleractinian corals, the interactive effects of variation in oceanographic conditions and biological fluctuations in reproductive output and recruitment can also influence dispersal patterns, as evidenced in a study on two sympatric species of Montastraea with the same reproductive mode but strikingly different patterns of genetic subdivision (Severance and Karl 2006). Additionally, favorable oceanographic conditions and high reproductive output in the coral Seriatopora hystrix apparently facilitate occasional dispersal of brooded larvae over relatively large distances (>10 km), despite most larvae recruiting to their natal site (<100 m) (Underwood et al. 2007).

Given the number of physical and biological factors contributing to the variability in the dispersal of larvae, significant advances in our understanding of their relative influence is required before patterns of dispersal can be incorporated in the design of marine reserve networks in a local context. Studies need to consider variation of dispersal not only in reproductive modes, but also in hydrogeographical features associated with the size, complexity, and isolation of reefs and reef systems. However, there are considerable practical challenges to measuring larval movements directly, and the indirect methods of inferring dispersal such as oceanographical, microchemical, and genetic analysis also have important limitations. Genetic methods have many conceptual and practical advantages and are commonly utilized, but careful application and interpretation of genetic data is crucial (Hellberg et al. 2002). In essence, genetic divergence of populations arises through isolation, and the degree of genetic differentiation provides insights into the degree of connectedness among those populations. If significant differentiation is detected in neutral genetic markers that are not affected by selection, then limitations to gene flow and restrictions to dispersal can be inferred. Importantly, however, the high rates of gene flow and potential for occasional long-distance dispersal in marine species can undermine the accuracy of estimating these parameters (Waples 1998). To obtain robust estimates of larval dispersal from genetic data, sources of error need to be reduced relative to the genetic signal. This requires detailed and geographically explicit sampling designs (Hellberg et al. 2002, Palumbi 2003), together with sensitive markers that utilize individual genotypes as the units of analysis (Hellberg 2007).

Inferences of dispersal from genetic data must also be interpreted over appropriate temporal scales (Mora and Sale 2002). For example, the anomalous long-distance migrant will be important for processes operating over evolutionary time, such as maintenance of genetic diversity, novel species invasions, or limitation of genetic differentiation and speciation, but will have little effect on community dynamics over ecological time. In contrast, rates of recovery of communities following major disturbances will be primarily influenced by the distances over which the majority of larvae disperse regularly. Given the rapid declines in health of coral reefs worldwide, managers are particularly interested in determining dispersal distances that are relevant to the short-term persistence of the reef-building coral communities that form the three-dimensional foundation of these diverse ecosystems.

In this study, we utilized high-resolution genetic markers to infer the dispersal patterns of reef-building corals with different reproductive modes, at reef systems with different hydrogeographical characteristics, relative to spatial scales and time frames that are applicable to the management of coral reefs. Our focus was to elucidate the distances over which viable coral communities can facilitate the short-term recovery of communities severely affected by disturbances. By short-term recovery, we mean a return to similar predisturbance diversity and cover within one to two decades. To this end, DNA microsatellite markers were used to quantify...
the genetic structure of the brooding hard coral *Seriatopora hystrix* and the broadcast-spawning hard coral *Acropora tenuis* within and among a set of discontinuous reef systems off northwest Australia that differ in size, complexity, and isolation. The unique geographic isolation of these reefs created the opportunity for a clear and measurable genetic signal of differentiation between and even within systems, allowing us to estimate from the genetic data the distances over which the vast majority of larvae routinely recruit, and therefore, the spatial scales of demographic independence among communities.

**Methods**

*Study site and genetic sampling*

In total, 576 colonies of the broadcast-spawning coral *Acropora tenuis* were collected from the Rowley Shoals and Scott Reef systems, and 476 colonies of the brooding coral *Seriatopora hystrix* were collected from the Rowley Shoals, Scott Reef, and Browse Island systems. (Although Browse Island is composed of only one reef, we refer to it as a system due to its isolation from other reefs.) These offshore coral systems are separated from each other and nearby reefs by hundreds of kilometers of open water (Fig. 1). Replicate sites were sampled at most reefs within each system, and samples were collected from the reef slope at the Scott Reef system in January 2004, Rowley Shoals in April 2005, and Browse Island in September 2006. The data for *S. hystrix* include the 287 individuals genotyped from Scott Reef in Underwood et al. (2007).

At each site (except the two at Browse Island), the exact locations of the sampled colonies relative to a 300-m transect were recorded, along with the GPS coordi-
Genotyping

Genomic DNA was extracted with DNase kit for animal tissue (Qiagen, Valencia, California, USA) or by a standard salting-out protocol (see Appendix B). Details of genotyping procedure of eight microsatellite loci from Seriatopora hystrix are described in Underwood et al. (2006), and further modified in Underwood et al. (2007). (Microsatellites are tandemly repeated nucleotide sequences that vary in number of repeats among individuals at a particular locus.) Data for Acropora tenuis were collected for seven microsatellite loci developed from a genomic DNA library from Acropora millepora (van Oppen et al. 2007). Five of these loci were optimized for A. millepora and described by van Oppen et al. (2007), and two loci were optimized specifically for A. tenuis. Two multiplex polymerase chain reactions (PCRs) were performed per individual using fluorescently labelled primers. (Details of multiplex PCR, loci characteristics, and GenBank accession numbers are given in Appendix C.) PCR products from both species were analyzed on a MegaBACE 1000 capillary sequencer (GE Healthcare, Chalfont St. Giles, UK), and the resulting electropherograms were scored using the program MegaBACE Genetic Profiler v2.2 (Sponaugle et al. 2002). 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 size of PCR product in base pairs. A genotyping error rate was estimated per reaction according to Bonin et al. (2004) as the ratio between the observed number of allelic differences and the total number of allelic comparisons across all loci when 24 genotypes from each species were repeated. S. hystrix had a very low error rate of 0.21%, while A. tenuis had a higher error rate of 2.68%. These error rates are unlikely to significantly bias our results because they are appropriate to the precision of analyses performed for each species: population structure and individual assignment analyses for S. hystrix, and population structure analyses only for A. tenuis (Bonin et al. 2004).

Allelic frequencies, allelic patterns, and expected heterozygosities under Hardy-Weinberg equilibrium, and the number of private alleles were calculated in GenAIEx v6 (Peakall and Smouse 2006) (see Appendix A). Tests for Hardy-Weinberg and linkage disequilibrium were conducted using FSTAT v2.9.3 (Goudet 1995), and significance levels were 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 sites and over all sites using the inbreeding coefficient $F_{IS}$. Of the 273 tests for linkage disequilibrium between pairs of loci at each site for A. tenuis, two were significant after Bonferroni correction. Of the 308 linkage disequilibrium tests that were performed for S. hystrix, one was significant after Bonferroni correction, indicating that loci vary independently in these populations. However, populations of both species were characterized by significant departures from Hardy-Weinberg equilibrium. Significant heterozygote deficits were detected in at least one locus at all sites for both species, except one S. hystrix site at Browse Island (Br2). Further, when data from all loci were combined, the two sites at Browse Island were the only sites that were in Hardy-Weinberg equilibrium. Lastly, there were only two loci for S. hystrix and one locus for A. tenuis, respectively, that did not exhibit significant heterozygote deficits in at least one site. Therefore, congruent with the majority of studies on corals (Ayre and Hughes 2000, Gilmour 2002, Mackenzie et al. 2004, Whitaker 2004, Nishikawa and Sakai 2005) and many other marine invertebrates (Tracey et al. 1975, Johnson and Black 1982, 1984, Andrade and Solferini 2007), heterozygote deficits are common features of these populations. Consequently, while we cannot rule out the presence of some null alleles, we attribute these deficits to biological factors associated with spatial and/or temporal admixture and nonrandom mating within sites. At least for S. hystrix, this conclusion is strongly supported by the detection of significant spatial structure of scales of tens of meters detected by Underwood et al. (2007). Further, significant differentiation among size classes (as measured by longest linear dimension) of A. tenuis was detected at some sites (data not shown), suggesting that Wahlund effects due to sampling a range of genetically distinct cohorts are probably a major cause of the observed heterozygote deficits for A. tenuis (e.g., Johnson and Black 1984). However, because we could not quantitatively assess whether all the heterozygote deficits were caused by biological factors, we also checked the data with the program MICRO-CHECKER (van Oosterhout et al. 2004). This program cannot distinguish whether heterozygote deficits are caused by null alleles or lack of panmixia unless an independent estimate of the inbreeding coefficient is available (van Oosterhout et al. 2006). As expected, possible null alleles were identified at all loci in disequilibrium. The AMOVA analysis was performed with the data adjusted for null alleles and importantly, results were congruent with the unadjusted data set (see Results).
Statistical analysis

A hierarchical Analysis of Molecular Variance (AMOVA) (Excoffier et al. 1992) was used to assess the amount of genetic variation that was geographically structured with respect to different alleles ($F_{ST}$). While it is recommended that microsatellite studies also estimate population structure with respect to the sum of squared size differences of the alleles, assuming a stepwise model of mutation ($R_{ST}$) (Balloux and Lugon-Moulin 2002), we do not present the results of this analysis, which were marginally higher, because general patterns were equivalent with the $F_{ST}$ estimates. Further, the effect of migration is likely to be strong relative to mutation in species with planktonic larvae that have a high dispersal potential (see Balloux and Lugon-Moulin 2002). Analysis was performed with GenAIEx v6 (Peakall and Smouse 2006) in two stages. First, the proportion of variation was calculated among sites within reefs ($F_{SR}$) and among reefs within each system ($F_{RT}(A)$) relative to the variation within each system. Second, the proportion of variation was calculated among systems ($F_{RT}(B)$), and among all sites ($F_{ST}$) relative to the total variance. Tests for statistical significance for all estimates were based on 1000 random permutations.

In addition to the standard AMOVA analyses, to validate the results, we conducted two other analyses of subdivision based on transformed data. First, to check for the possible influence of null alleles, we conducted an AMOVA with allele frequencies adjusted for null alleles with MICRO-CHECKER (van Oosterhout et al. 2004), according to the Brookfield 1 equation. Second, to check whether differences in within-population diversity between species were influencing estimates of $F_{ST}$, we calculated a standardized measure of $F_{ST}$ according to the method of Meirmans (2006). Because genetic differentiation is dependent upon number of migrants per generation, which in turn is a product of population size and migration rate, it is possible that large differences in population sizes of these two species may have influenced these results. Although quantification of population sizes is practically impossible in this system, observations in the field suggested that the densities and distributions of populations of the two species were similar, indicating that large differences in population sizes were not driving these patterns of genetic structure. In addition, the standardization method of Meirmans (2006) should also account for differences in effective population sizes.

To quantify further the relationships among sites, the genotype likelihood ratio distance, $D_{LR}$ (Paetkau et al. 1995), was calculated for pairs of sites for both species with the online calculator Doh (Brzustowski 2002). This measure of genetic distance is the mean genotype log-likelihood ratio across individuals from the two populations, and performed particularly well for measuring fine-scale population structure in an empirical study (Paetkau et al. 1997). To illustrate these genetic relationships among sites, we used a multidimensional approach; a Principal Coordinates Analysis (PCA) graph was constructed from the $D_{LR}$ genetic distance matrix in GenAIEx v6.

To focus on the ecologically important effects of dispersal by determining the fine-scale geographic structuring of genetic variation, we employed a spatial autocorrelation analysis in addition to the AMOVA and the genetic distance analysis. This method was also performed in GenAIEx v6. Unlike $F$ statistics and genetic distance measures that are based on summary statistics of gene frequency from predefined populations, spatial autocorrelation utilizes the spatial position and genetic identity of each individual as data. This method provides a direct measure of genetic structure that is sensitive to recent dispersal processes, does not require the assumption of equilibrium, and is particularly useful for the exploration of fine-scale population structure (Clark and Richardson 2002, Double et al. 2005, Epperson 2005). A pairwise genetic distance matrix from all loci for samples collected from the Rowley Shoals and Scott Reef systems was calculated along with a linear pairwise geographic distance matrix from the $x$ and $y$ coordinates of the location of each colony. From these matrices, an autocorrelation coefficient ($r$) was generated for all pairs of individuals whose geographic separation fell within a specified distance class. The autocorrelation coefficient provides a measure of genetic similarity, and when it is plotted over a range of distance classes as a “correlogram,” the relative balance between the homogenizing effects of gene flow (yielding positive $r$ values) can be assessed relative to the random influence of genetic drift (yielding $r$ values of zero). When gene flow is restricted and local loci are utilized, the autocorrelation coefficient will be positive at short distance classes, and will subsequently decline through zero and become negative at larger distance classes (Sokal and Wartenberg 1983, Epperson and Li 1996, Smouse and Peakall 1999, Peakall et al. 2003, Double et al. 2005). Therefore, the distance where $r$ first crosses the $x$ intercept provides an estimate of the extent of the positive genetic structure, revealing the distance where the random effects of genetic drift, not gene flow, are the primary determinants of genetic composition. Additionally, the point where $r$ begins to decline after an initial plateau indicates the extent of the genetic neighborhood where the larval pool is no longer completely mixed and gene flow first becomes limited. To test for statistical significance of $r$ at each distance class, a 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. Although GenAIEx provides an alternative and less conservative test for significance via a permutational method (Double et al. 2005), no differences in these two tests were detected, so we present only the bootstrapped confidence intervals.

The high levels of subdivision among populations of *S. hystrix* meant that there was enough information in the data to assign individuals to their population of
Table 1. Hierarchical Analysis of Molecular Variance (AMOVA) calculated with respect to different alleles (FST) from Acropora tenuis and Seriatopora hystrix corals sampled at Scott Reef, Rowley Shoals, and Browse Island, northwest Australia.

<table>
<thead>
<tr>
<th>Allele</th>
<th>Scott</th>
<th>Rowley</th>
<th>All</th>
<th>Scott</th>
<th>Rowley</th>
<th>Browse</th>
<th>All (excluding Browse)</th>
</tr>
</thead>
<tbody>
<tr>
<td>FST: within reefs</td>
<td>0.010***</td>
<td>0.003</td>
<td></td>
<td>0.107***</td>
<td>0.001</td>
<td>0.018*</td>
<td></td>
</tr>
<tr>
<td>FST(A): among reefs</td>
<td>0.010***</td>
<td>0.027***</td>
<td></td>
<td>0.000</td>
<td>0.085***</td>
<td>NA</td>
<td></td>
</tr>
<tr>
<td>FST(B): among systems</td>
<td>0.012***</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FST: among all sites</td>
<td>0.034***</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Notes: Analyses estimated the proportion of variance among sites within reefs [FST(R)] and among reefs within each system [FST(A)] relative to the variation within each system, and the proportion of variance among systems [FST(B)] and among all sites [FST] relative to the total variance. Tests for statistical significance were based on 1000 random permutations. NA means not applicable. Levels of statistical significance for the F values are indicated by asterisks.

* P < 0.05; ** P < 0.01.

Origin using the assignment/exclusion method computed in GENECLASS 2 (Piry et al. 2004). The likelihood that an individual belongs to a particular population was computed with a partially Bayesian criterion of Rannala and Mountain (1997). Then, to identify a statistical threshold beyond which individuals are excluded from a given reference population, this likelihood was compared to a distribution of likelihoods of 10^6 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 >95% (P ≤ 0.05). Individuals excluded from their sampling site were assigned to another site when the likelihood that they originated from that site was >10% (P ≥ 0.1). These individuals were classified as putative long-distance migrants, while individuals that were excluded from all sites remained "unassigned." A more detailed discussion of this analysis is given in Underwood et al. (2007). Due to the lower level of genetic subdivision among A. tenuis populations (FST < 0.1), this analysis could not be performed with any degree of confidence for this species (Berry et al. 2004).

RESULTS

The genetic structure of Seriatopora hystrix and Acropora tenuis indicated a clear lack of panmixis across the scale of the study, with significant subdivision detected between systems, between reefs, and even within some reefs (Table 1). However, major differences in levels of subdivision were detected between the two species. FST values were far higher for the brooding coral (FST(excluding Browse) = 0.191) compared with the broadcast spawner (FST = 0.034). This pattern remained when FST estimates were adjusted for null alleles (S. hystrix FST (excluding Browse) = 0.198; A. tenuis FST = 0.059), and when FST estimates were standardized for differences in within-population diversity between the two species (S. hystrix FST (excluding Browse) = 0.312; A. tenuis FST = 0.080). Further, genetic distances between pairs of populations were also much larger for S. hystrix (D_{LR} ranged from 0.58 to 10.93, average D_{LR} = 6.34) than for A. tenuis (D_{LR} ranged from 0.02 to 0.12, average D_{LR} = 0.06) (for pairwise genetic distance matrices; see Appendix D). The PCA plots illustrate these genetic relationships among sites (Fig. 2). For S. hystrix, each of the three systems formed a distinct cluster, with large genetic distances between the Scott

![Plot Fig. 2.](https://example.com/plot2.png)

FIG. 2. Plots of Principal Coordinate Analysis (PCA) calculated with GenAIEx v6 (Peakall and Smouse 2006), illustrating the genetic relationships among sites from Scott Reef, Rowley Shoals, and Browse Island for Seriatopora hystrix and Acropora tenuis. Each plot illustrates the major axes of variation in two dimensions (Coordinates 1 and 2) located within a multidimensional matrix of standardized genetic distances that was derived from pairwise D_{LR} estimates between sites calculated with the online calculator Doh (Brzustowski 2002). The first two axes explain 86% of the variation for S. hystrix, and 82% of variation for A. tenuis.
Reef system, Rowley Shoals, and Browse Island. For *A. tenuis*, there was less separation of clusters of sites among the Rowley Shoals and Scott Reef systems, but sites from the two systems did not overlap.

At a more local scale, the spatial autocorrelation analysis emphasized further the differences in genetic subdivision between the two species (Fig. 3). At Scott Reef and the Rowley Shoals, the positive values of the genetic autocorrelation coefficients \(r\) were much larger for *S. hystrix*, and declined and first crossed the x-axis, at smaller distance classes than for *A. tenuis*. For example, \(r\) values began to decline over distances >100 m for *S. hystrix*, and had an x intercept of at most 20 km. In contrast, \(r\) values were relatively constant over the length of the transects (300 m) for *A. tenuis*, then declined to cross the x-axis within 60 km. These results show that the genetic neighborhood, and the extent of positive genetic structure, is considerably smaller in *S. hystrix*. Thus, larvae are routinely recruiting over much smaller distances in the broader corals compared with the broadcast spawner.

The local dispersal of *S. hystrix* was further supported by the Bayesian analysis; 94% of the 468 *S. hystrix* colonies were assigned to the site from which they were sampled. Of the remaining 30 colonies that were excluded from their sampled site, four were assigned to another site within the same reef (three at Rowley Shoals and one at Browse Island), six were assigned to sites from other reefs within the same system, and 20 could not be assigned to a sampled site (Table 2). No colonies were assigned to sites from different systems.

In addition to these differences between species, differences in spatial scale of genetic subdivision were detected between the two major systems investigated. For both species, subdivision was significant among sites located on the same reef (\(F_{SR}\)) at the Scott Reef System, but not at the Rowley Shoals (Table 1). Differences in spatial scale of genetic structure between the two major systems are also illustrated by the spatial autocorrela-
Table 2. Numbers of individual colonies of *Seriatopora hystrix* excluded (immigrants) from their sampling sites and their most likely population of origin (assigned population), calculated with GENECLASS 2.

<table>
<thead>
<tr>
<th>Sampling locality</th>
<th>Number excluded</th>
<th>Assigned population</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>SL1 SL2 SL4 SL5 SS1 SS3 RS1-L RS2-2 RS2-S Br1 Br2</td>
<td>Not assigned</td>
</tr>
<tr>
<td>SL1</td>
<td>3 0 0 0 0 0 0 0 0 3</td>
<td></td>
</tr>
<tr>
<td>SL2</td>
<td>4 0 1 0 0 0 0 0 0 3</td>
<td></td>
</tr>
<tr>
<td>SL4</td>
<td>4 0 0 0 0 0 0 0 0 4</td>
<td></td>
</tr>
<tr>
<td>SL5</td>
<td>5 0 2 1 0 0 1 0 0 1</td>
<td></td>
</tr>
<tr>
<td>SS1</td>
<td>1 0 0 1 0 0 0 0 0 0</td>
<td></td>
</tr>
<tr>
<td>SS3</td>
<td>1 0 0 0 0 0 0 0 0 0</td>
<td></td>
</tr>
<tr>
<td>RS1-L</td>
<td>4 0 0 0 0 0 0 0 0 4</td>
<td></td>
</tr>
<tr>
<td>RS2-2</td>
<td>3 0 0 0 0 0 0 0 2 2</td>
<td></td>
</tr>
<tr>
<td>RS2-S</td>
<td>4 0 0 0 0 0 0 0 2 0</td>
<td></td>
</tr>
<tr>
<td>Br1</td>
<td>1 0 0 0 0 0 0 0 0 1</td>
<td></td>
</tr>
<tr>
<td>Br2</td>
<td>0 0 0 0 0 0 0 0 0 0</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>30 2 3 0 1 0 2 1 0 20</td>
<td></td>
</tr>
</tbody>
</table>

Notes: Individual colonies were excluded from their sampling site if the likelihood of their genotype occurring in that site was <0.05 when compared to a distribution of 10^6 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 probability was below 0.10, then the individual was assumed to have originated from a population that was not sampled (unassigned). Numbers in boldface type indicate immigrants assigned to another site on the same reef.

Discussion

This study used microsatellite data to measure the genetic structure and infer the spatial scales of routine dispersal in two species of reef-building coral with contrasting reproductive modes at isolated offshore systems of northwest Australia. The results support three primary broad conclusions from previous genetic research on corals. First, differences in the reproductive mode of coral species influence levels of genetic subdivision (Hollenberg 1996, Ayre and Hughes 2000, Nishikawa et al. 2003, Whitaker 2004, 2006). Second, many coral reefs are genetically differentiated (Gilmour 2002, Ayre and Hughes 2004, Whitaker 2004, 2006). Third, panmixia is only generally observed over scales of tens of kilometers or less (reviewed by van Oppen and Gates 2006). Moreover, we extend this earlier work by using an analysis of fine-scale genetic structure to provide quantitative estimates of the distances over which the vast majority of larvae disperse regularly in reef systems with unique hydrogeographical characteristics. These estimates have direct applications to the design of marine reserves in the region, and also make an important contribution to a fundamental understanding of dispersal that is essential for the effective management of coral systems worldwide.

Reproductive mode and routine dispersal

Levels of subdivision were markedly higher in the brooding coral *Seriatopora hystrix* (FST excluding Browse = 0.191) than in the broadcast-spawning coral *Acropora tenuis* (FST = 0.034). These results are similar to genetic data from the Great Barrier Reef (Ayre and Hughes 2000) and the Red Sea (Maier et al. 2005) for *S. hystrix*, and for *A. tenuis* in Japan (Nishikawa et al. 2003), and reflect expectations based on the life histories of these corals. Laboratory experiments indicate that, if a suitable substrate is present, *S. hystrix* larvae are competent to settle within six hours of release (Isomura and Nishihira 2001), whereas *A. tenuis* are competent after 3–4 days (Nishikawa et al. 2003). Our data suggest that most *S. hystrix* larvae settle within 100 m of their parent colony, while most *A. tenuis* larvae are dispersed within reefs over distances of kilometers to a few tens of kilometers (Fig. 3). Thus, the precompetency periods of larvae seem to be a primary determinant of the distances of routine dispersal on a generation-by-generation basis in these two species.

Reproductive mode and rare dispersal

Although precompetency periods are a primary determinant of the distances moved by the majority of
larvae, the upper competency periods also influence patterns of connectivity, but over larger spatial and temporal scales. In laboratory experiments, both brooded and broadcast-spawned larvae are capable of settling after many weeks (reviewed by Harrison and Wallace 1990), but survival decreases rapidly the longer larvae spend in the water column (e.g., Nishikawa et al. 2003). Further, reduced larval concentrations due to predation and diffusion are likely to be much higher in the open ocean compared with the closed laboratory environment. For example, Cowen et al. (2000) estimated that concentrations of coral fish larvae were diluted by six orders of magnitude within 30 days as a result of diffusion alone, and these rates increased when mortality was included in the model. Therefore, long-distance migrants are unlikely to contribute significantly to recruitment over ecological time scales.

In addition to the effects of routine dispersal on genetic structure observed here, we also detected a genetic signature of rare longer-distance dispersal in both species, although the scales differed between the brooder (tens of kilometers) and spawner (hundreds of kilometers). For S. hystrix, little differentiation between some sites (e.g., RS2-2 and RS2-S; see Appendix D) separated by tens of kilometers was evident, and the assignment tests identified a few recent migrants that dispersed over these distances both within and between reefs at each system. Further, in contrast to subdivision of S. hystrix within reefs ($F_{SR}$), subdivision between reefs ($F_{RT}$) was not significant at Scott Reef (Table 1). This result demonstrates that processes influencing localized recruitment primarily operate within reefs in this species, and further suggests that once outside these local influences, larvae occasionally disperse between reefs. However, the prodigious differentiation between the Scott Reef, Rowley Shoals, and Browse Island systems suggests that dispersal of S. hystrix larvae over hundreds of kilometers is very rare, even over evolutionary time. In contrast, there was less differentiation between Scott Reef and Rowley Shoals for A. tenuis, indicating that there is sufficient dispersal to limit major genetic divergence between systems. It is important to note that the small degree of differentiation between some sites from the Scott Reef and Rowley Shoals systems, relative to the differentiation observed within the systems for A. tenuis (Fig. 2), is not a result of more gene flow between than within systems, but rather illustrates the homogenizing influence of rare long-distance migration over multiple generations on genetic structure when considering large spatial scales and population sizes (see Ayre and Hughes 2004, Johnson and Black 2006).

**Hydrogeographic complexity and dispersal**

Comparisons between the genetic structures of the two major systems studied show that factors other than larval duration also affect dispersal of these brooded and spawned larvae, and in similar ways. For both species, we detected limitations to gene flow at the reef scale at Rowley Shoals, but within reefs at the Scott Reef system. We hypothesize that differences in the hydrogeographical characteristics of the two systems are driving these results. In particular, the large size and semicircular structure of the southern Scott reef is likely to modify water circulation patterns by increasing friction and therefore reducing circulation on the northern side of the reef and creating recirculating flows and eddies. This is likely to favor the retention of larvae to their natal reef patch at some sites, and accounts for the large (Appendix D) and significant (Table 1) genetic differences between sites located on the same reef relative to within-reef comparisons between sites at the Rowley Shoals. This pattern was consistent for all such comparisons (four within-reef comparisons at Scott Reef vs. three at the Rowley Shoals for A. tenuis, and three at Scott Reef vs. one at Rowley Shoals for S. hystrix), but differentiation between SL1 and SS1 (see Fig. 1) provides the most striking comparison; the genetic distance between these two sites separated by a few kilometers was 10 times greater for S. hystrix, and nearly two times greater for A. tenuis, than the genetic distances between sites on the same reef separated by more than 10 kilometers at Rowley Shoals (Appendix D). However, oceanographic data on local circulation patterns within these two systems, combined with temporal genetic data, are required to provide a rigorous test of this hypothesis.

**Implications for managing resilience of coral communities**

The applicability of our results for inferring dispersal in other species of corals and other reef systems remains to be determined, particularly given the importance of variation in hydrogeographical conditions and larval duration. Species of spawning corals can have different competency periods (Baird 2004), which may be an important reason why genetic structure of spawners varies among species and regions (Márquez et al. 2002, Ayre and Hughes 2004). Further, although the tendency for many spawning corals to produce larvae at similar times following mass spawning means that the physical conditions to which they are exposed within a given reef system may be similar, stochastic variation in larval production and settlement success may contribute to substantial variation in dispersal of these species (Severance and Karl 2006). For brooding corals, larvae are often released over several months, so different oceanographic conditions (i.e., wind speeds, tidal amplitudes, and strengths of prevailing currents) during the time of larval release are likely to enhance the dispersal variance among species and regions. Additionally, brooders are often characterized by a diverse range of reproductive strategies, such as asexual production of larvae and self-fertilization, which complicates both realized and inferred patterns of larval dispersal (e.g., Sherman et al. 2006). It is also important to note that the isolated reef systems in this study do not provide the opportunity for stepping-stone recolonization events,
which may be more important to the short-term recovery of coral communities in continuous reef systems.

Regardless of the extent to which our results apply precisely to other corals and reefs, the patterns of connectivity described here add to a growing body of evidence from a wide range of oceanographic (e.g., Wolanski and Hammer 1988, Black et al. 1991, Largier 2003), ecological (e.g., Hughes et al. 2000, Grantham et al. 2003), biochemical (e.g., Swearngin et al. 1999, Jones et al. 2005), theoretical modelling (e.g., Hastings and Botsford 2006), and genetic (e.g., Ayre and Hughes 2000, Taylor and Helberg 2003, Baums et al. 2005) studies suggesting that dispersal among marine populations is often localized. These studies also highlight that generalizations of dispersal patterns based on simple life history traits such as pelagic larval duration may be misleading (see also Leis 2002, Bay et al. 2006, Ramon et al. 2008). More specifically, our estimates of routine distances of dispersal of *A. tenuis* and *S. hystrix* larvae fall within the lower range of the 10–100 km predicted by the latest biophysical models for fish species (Cowen et al. 2006), and a reanalysis of several genetic studies on marine species that specifically accounted for geographic distance (Palumbi 2003). These estimates are also concordant with recent work on coral reef fish, which suggest that a high proportion of larvae self-recruit to a small reef area (less than a square kilometer), even in species with planktotrophic larvae and varied pelagic larval durations (Almany et al. 2007, Gerlach et al. 2007). In the context of coral reef resilience, the implication is that recovery of many coral reef communities from disturbances whose impacts are localized or patchy (e.g., cyclones) should be rapid, provided unaffected communities are protected from chronic stressors (e.g., decreased water quality, overfishing) that affect growth and reproductive output. However, when an entire reef or reef system is severely affected by a disturbance such as widespread thermal-induced bleaching, recovery will be compromised.

Our results have important ramifications for the effective design of coral reef reserves. We demonstrated significant restrictions to gene flow among *A. tenuis* populations over distances of 20 km at Rowley Shoals, and <10 km at Scott Reef. Therefore, short-term recovery of these broadcast-spawning communities after severe disturbances may be facilitated largely by the recruitment of larvae produced by viable communities separated by these distances. For the broader, interpretation of the genetic structure for management applications is not so straightforward. Fine-scale genetic structure was detected at much smaller distances for *S. hystrix*, but the prolific reproductive output and highly philopatric dispersal of this species means that local and rapid recovery may be largely facilitated by a few survivors or the occasional long-distance migrant produced a few tens of kilometers away. Thus, to be self-sustaining, we suggest that coral reef protected areas need to be large enough to encompass routine dispersal distances of coral larvae of kilometers to a few tens of kilometers. Additionally, to facilitate recovery from severe disturbances that affect an entire protected area, replicate protected areas are needed over these spatial scales. However, specific designs need to account for size, complexity, and isolation of reefs that will either restrict or enhance dispersal within this range.

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**Literature Cited**


**APPENDIX A**

Details of the eight *Seriatopora hystrix* and seven *A. tenuis* microsatellite markers from offshore reefs in northwest Australia (*Ecological Archives* A019-002-A1).

**APPENDIX B**

Protocol for DNA extraction from coral fragments (*Ecological Archives* A019-002-A2).

**APPENDIX C**

Characteristics of microsatellite loci for *Acropora tenuis* (*Ecological Archives* A019-002-A3).

**APPENDIX D**

Genetic distances of $D_{R}$ calculated with the online calculator Doh, and geographic distance between pairs of sites for *S. hystrix* and *A. tenuis* in northwest Australia (*Ecological Archives* A019-002-A4).