Contributed Paper

Protection of Genetic Diversity and Maintenance of Connectivity among Reef Corals within Marine Protected Areas

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Abstract: *High-latitude coral reefs (HLRs) are potentially vulnerable marine ecosystems facing well-documented threats to tropical reefs and exposure to suboptimal temperatures and insolation. In addition, because of their geographic isolation, HLRs may have poor or erratic larval connections to tropical reefs and a reduced genetic diversity and capacity to respond to environmental change. On Australia's east coast, a system of marine protected areas (MPAs) has been established with the aim of conserving HLRs in part by providing sources of colonizing larvae. To examine the effectiveness of existing MPAs as networks for dispersal, we compared genetic diversity within and among the HLRs in MPAs and between these HLRs and tropical reefs on the southern Great Barrier Reef (GBR). The 2 coral species best represented on Australian HLRs (the brooding* Pocillopora damicornis *and the broadcast-spawning* Goniastrea australensis*) exhibited sharply contrasting patterns of diversity and connectedness. For* P. damicornis*, the 8-locus genetic and genotypic diversity declined dramatically with increasing latitude (*N_a *= 3.6–1.2,* H_e *= 0.3–0.03,* N_g:N *= 0.87–0.06), although population structure was consistent with recruitment derived largely from sexual reproduction (*G_o:G_e *= 1.28–0.55). Genetic differentiation was high among the HLRs (*F_{ST} *[SD] = 0.32 [0.08],* $p < 0.05$*) and between the GBR and the HLRs (*$F_{ST} = 0.24$ *[0.06],* $p < 0.05$*), which indicates these temperate populations are effectively closed. In contrast for* G. australensis*, 9-locus genetic diversity was more consistent across reefs (*N_a *= 4.2–3.9,* H_e *= 0.3–0.26,* N_g:N *= 1–0.61), and there was no differentiation among regions (*F_{ST} *= 0.00 [0.004],* $p > 0.05$*), which implies the HLRs and the southern GBR are strongly interconnected. Our results demonstrate that although the current MPAs appear to capture most of the genetic diversity present within the HLR systems for these 2 species, their sharply contrasting patterns of connectivity indicate some taxa, such as* P. damicornis*, will be more vulnerable than others, and this disparity will provide challenges for future management.*

Keywords: gene flow, *Pocillopora damicornis*, *Goniastrea australensis*, larval dispersal, range limits, MPA networks

Protección de la Diversidad Genética y Mantenimiento de la Conectividad entre Arrecifes de Coral en Áreas Marinas Protegidas

Resumen: *Los arrecifes de coral de latitudes alta (ACLA) son ecosistemas marinos potencialmente vulnerables que enfrentan amenazas bien documentadas y exposición a temperaturas subóptimas e insolación. Adicionalmente, debido a su aislamiento geográfico, los ACLA pueden tener conexiones larvarias pobres o erráticas con arrecifes tropicales y una diversidad genética y capacidad para responder a cambios ambientales reducidas. En la costa oriental de Australia se ha establecido un sistema de áreas marinas protegidas (AMP) con la finalidad de conservar ACLA, en parte mediante el aprovisionamiento de fuentes de larvas colonizadoras. Para examinar la efectividad de las AMP existentes como redes para dispersión, comparamos la diversidad genética dentro y entre los ACLA en áreas marinas protegidas y entre esos ACLA y arrecifes tropicales en el sur de la Gran Barrera Arrecifal (GBA). Las 2 especies de coral mejor representadas en*

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*los ACLA australianos ((*Pocillopora damicornis *y* Goniastrea australensis*) exhibieron patrones de diversidad y conectividad muy contrastantes. En* P. damicornis *la diversidad genética y genotípica en 8 locus declinó dramáticamente con el incremento de la latitud (*N_a *= 3.6–1.2,* H_e *= 0.3–0.03,* N_g:N *= 0.87–0.06) aunque la estructura de la población fue consistente con el reclutamiento derivado principalmente de la reproducción sexual (*G_o:G_e*=1.28–0.55). La diferenciación genética fue alta entre los ACLA (*F_{ST} *[SD] = 0.32 [0.08],* $p <$ *0.05) y entre la GBA y los ACLA (*F_{ST} *= 0.24 [0.06],* $p <$ *0.05), lo cual indica que estas poblaciones templadas están cerradas efectivamente. En contraste para* G. australensis*, la diversidad genética fue más consistente en los arrecifes (*N_a *= 4.2–3.9,* H_e *= 0.3–0.26,* N_g:N *= 1–0.61), y no hubo diferenciación entre regiones (*F_{ST} *= 0.00 [0.004],* $p >$ *0.05), lo cual implica que los ACLA y el sur de la GBA están estrechamente interconectados. Nuestros resultados demuestran que aunque parece que las AMP actuales capturan la mayor parte de la diversidad genética de estas 2 especies en los sistemas de ACLA, sus patrones de conectividad tan contrastantes indican que algunos taxa, como* P. damicornis*, serán más vulnerables que otros, y esta disparidad determinará retos para el manejo futuro.*

Palabras Clave: dispersión de larvas, flujo génico, límites de rango de distribución, *Goniastrea australensis*, *Pocillopora damicornis*, redes de AMP

Introduction

Marine ecosystems worldwide are facing increasing threats from a plethora of sources, including habitat degradation, climate change, and pollution. To counter these threats, a global initiative is underway that aims to generate a comprehensive, adequate, and representative network of marine protected areas (MPAs) (Kelleher et al. 1995), and Australia has responded by creating a national representative system of MPAs (NRSMPA). Nevertheless, both in Australia and elsewhere, little has been done to assess the value of these initiatives (Pomeroy et al. 2005). Inherent in the development of MPAs is the assumption that protected areas will act as sources of recruits and that there will be sufficient dispersal among MPAs to maintain connectivity (Palumbi 2003; Shanks et al. 2003). In some marine systems, including tropical reefs, high levels of connectivity among populations separated by hundreds of kilometers have been demonstrated (e.g., Benzie 1994; Doherty et al. 1995; Shulman & Bermingham 1995; Ayre & Hughes 2000). Nevertheless, there is a lack of empirical data underpinning connectivity within and among MPAs worldwide (Botsford et al. 2001; Palumbi 2003), and this problem is especially acute for the high-latitude coral reef (HLR) systems on Australia's eastern coast. In contrast to tropical reefs, the conservation status of HLRs has received little attention, although they may be more susceptible to environmental change. In addition to the threats facing tropical reefs (e.g., Hughes et al. 2003), HLRs typically have suboptimal temperatures and insolation for coral growth, are isolated from centers of coral diversity, and are at the margins of species ranges.

The HLRs of southeastern Australia are diverse communities that support a mix of tropical and temperate species and contain several tropical corals representing key habitat-forming species (Harriott et al. 1994, 1995). The conservation value of these reefs has been recognized (Harriott et al. 1999), and almost all significant east coast coral populations are now represented in no-take MPAs. The HLRs form 2 geographic groupings: (1) the mainland chain of fringing reefs from Morton Bay in the north to Port Stephens in the south and (2) the oceanic group that includes Elizabeth and Middleton Reefs and Lord Howe Island (LHI) (Fig. 1). There is evidence of limited connections between the Great Barrier Reef (GBR) and LHI (Ayre & Hughes 2004); however, the origin and maintenance of corals on this and other HLRs remains uncertain because is it unclear what proportion of recruitment is from local stocks (self-seeding) and whether larvae travel directly from the GBR to offshore islands (path A) or along the mainland chain and then move offshore with the East Australian Current (EAC) (path B) (Fig. 1b). Larval connections along either path are difficult to predict for at least 3 reasons. Corals display enormous variation in early life history (Harrison & Wallace 1990), which affects dispersal potential (Ayre & Hughes 2000). Dispersal may decrease with distance from the GBR associated with declining strength of the EAC (Fig. 1b); but equally, dispersal may increase with decreasing temperature and associated delays in larval development times (O'Connor et al. 2007; but see Kelly & Eernisse 2007). Alternatively, some reefs may be ephemeral "sinks" maintained by long-distance colonists.

Because the tropical corals of Australia's southeastern HLRs occur toward the edge of their range, the strength of dispersal from the north will influence their genetic composition and likely resilience with consequences for the effectiveness of the MPAs. We predict that the genetic diversity of HLR coral populations will be low as a result of drift and founder events if they have small effective population sizes (N_e) and receive few migrants (Wright 1969; Frankham et al. 2002). Several lines of evidence suggest that dispersal from the GBR to the HLRs is either limited or episodic but that the nature of larval connections and recruitment processes may vary among locations. For example in the Solitary Islands, recruitment rates are very

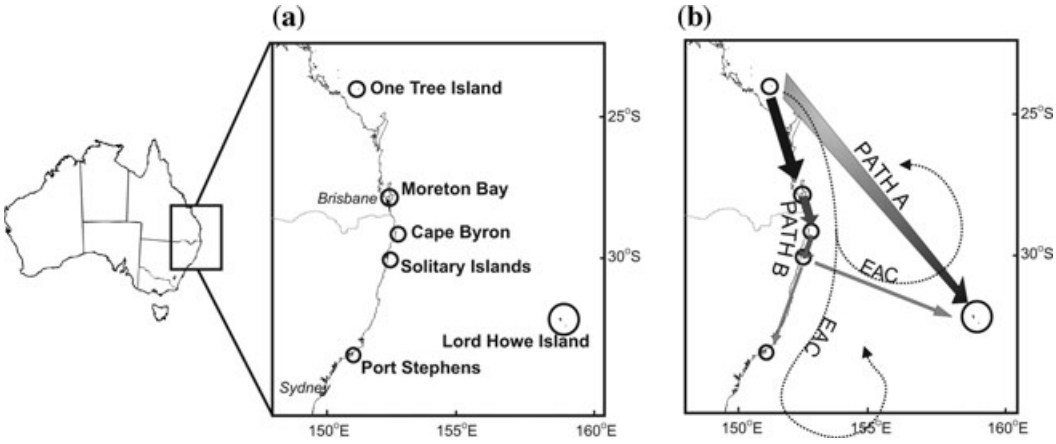

Figure 1. (a) Approximate location of the 6 marine protected areas (MPAs) on the east coast of Australia sampled in this study and (b) hypothesized larval dispersal pathways (path A direct from the southern Great Barrier Reef [One Tree Island] to Lord Howe Island and path B along the chain of coastal reefs with the southward flow of the East Australia Current [EAC], but with decreasing magnitude as the current weakens from north to south).

low (e.g., 6.7 cf. 44–242 larvae/pair of settlement plates on the southern GBR [Harriott & Banks 1995; Hughes et al. 1999], although recruitment rates at LHI (48.5 larvae/pair of plates) are close to the lower end of the range reported on the southern GBR (Harriott 1992). Genetic data show that LHI is effectively isolated from the GBR and genetically depauperate (Ayre & Hughes 2004; Miller & Ayre 2004). Nevertheless, no genetic data exist for the other HLRs and nothing is known either about the links between the GBR and coastal HLRs or among the HLRs.

To determine the nature of connections among HLRs and the GBR, we compared the genetic composition of populations of 2 species with strikingly different early life histories: the brooding and potentially clonal *Pocillopora damicornis* (Ayre & Miller 2004) and the broadcast-spawning *Goniastrea australensis* (Wilson & Harrison 1998). These species are numerically dominant on HLRs and are important habitat-forming species. Specifically, we tested for evidence of reduced genetic diversity with increasing latitude and inferred the likely effectiveness of existing MPAs as sources of larvae or networks of interconnected populations.

Methods

Study Species, Study Sites, and Sample Collections

P. damicornis is a fast-growing bushy coral and is a characteristic early-successional species. Colonies are hermaphroditic and are thought to broadcast spawn gametes, although the only recorded reproductive output in this species on the east coast of Australia are brooded larvae generated through asexual reproduction (Ayre & Miller 2004). Brooded larvae can settle upon release, although results of laboratory studies suggest they can remain planktonic and competent to settle for up to 100 days (Richmond 1987). Genetic studies of *P. damicornis* from the east coast of Australia show localized recruitment of asexual larvae is limited and that populations are maintained largely through sexual reproduction (Benzie et al. 1995; Ayre & Miller 2004; Miller & Ayre 2004; Sherman et al. 2006), although clonal populations may exist in some locations (Miller & Ayre 2004; Sherman et al. 2006).

G. australensis has a massive or hemispherical growth form and is a slow-growing, late-successional species. It reproduces through the broadcast-spawning of gametes and has external fertilization. Larvae of congeneric species with similar reproduction are competent to settle from 2 to 4 days after spawning (Babcock & Heyward 1986; Miller & Mundy 2003), and larvae remain competent to settle for up to 56 days in laboratory trials (Wilson & Harrison 1998). Asexual reproduction through fission or fragmentation is rare in massive species (although see Foster et al. 2007; Miller & Ayre 2008).

We collected tissue samples of both species from sites within MPAs from 4 regions along the east coast of mainland Australia: the GBR Marine Park (4 sites on One Tree Reef), Moreton Bay Marine Park (1 site each at Flat Rock, Shag Rock, Amity Point, and Peel Island), Cape Byron Marine Park (1 site at Julian Rocks), and the Solitary Islands Marine Park (1 site each at Split, South-West, and South Solitary Islands). We also sampled *P. damicornis* from the Port Stephens-Great Lakes Marine Park (1 site each at Cabbage Tree Island and Fingal Island), which is the southern-most extent of this species on mainland Australia, and the LHI Marine Park (7 sites), an isolated HLR over 600 km offshore and representing the southern limit of reef-building corals on the east coast of Australia (Fig. 1). All these MPAs are multiple use, but our sites were within the highest protection zone of each park

(generally no-take areas), with the exception of Moreton Bay, where all sites were in conservation zones that are closed only to trawling.

We collected small (approximately 2 × 2 cm) tissue samples from up to 60 colonies of each species at each site (see Supporting Information), sampling only from corals that were independent (hence, unlikely to be the product of fission or fragmentation) and within as small an area as possible at each site (typically 100 m^2). In Cape Byron Marine Park, we collected samples from only 16 *P. damicornis* colonies because it was less abundant there than at other locations. Samples were frozen in liquid nitrogen and stored at −70 °C prior to analysis.

Allozyme Electrophoresis

We genotyped colonies with allozyme electrophoresis. Tissue was ground in an extractant solution (10 g sucrose, 0.1 g bromophenol blue, 0.1 mL β-mercaptoethanol to 100 mL Tris HCl) prior to loading on 11% weight/volume starch gels. For *P. damicornis*, we stained for 6 enzymes and scored 8 loci: glucosephosphate isomerase (*Gpi* E.C. 5.3.1.9); malate dehydrogenase ($Mdh^{1\&2}$ EC 1.1.1.37); mannose phosphate isomerase (*Mpi* E.C. 5.3.1.8); phosphoglucomutase (Pgm^2 E.C. 2.7.5.1; assayed with TC8 buffer no. 5 of Selander et al., 1971); hexokinase ($Hk^{1\&2}$ E.C. 2.7.1.1); and leucyl tyrosine peptidase (Ltp^2 E.C. 3.4.11) (assayed with TEB buffer no. 6 of Selander et al., 1971). For *G. australensis*, we stained for 8 enzymes and scored 9 loci: glucosephosphate isomerase (*Gpi* E.C. 5.3.1.9); malate dehydrogenase ($Mdh^{1\&2}$ EC 1.1.1.37); phosphoglucomutase (*Pgm* E.C. 2.7.5.1; assayed with TC8 buffer no. 5 of Selander et al., 1971); mannose phosphate isomerase (*Mpi* E.C. 5.3.1.8); hexokinase (*Hk* E.C. 2.7.1.1); 3 peptidases with the substrates leucyl-tyrosine, leucyl-glycylglycine; and leucyl-proline (Lt^2 Lgg^1 and Lp^2 E.C. 3.4.11; assayed with TEB buffer no. 6 of Selander et al. 1971). Alleles at each locus were numbered by decreasing mobility. We found no linkage among any loci in either species (tested with Genepop, version 3.4; Raymond & Rousset 1995).

Data Analyses

To investigate the contributions of sexual and asexual reproduction, we used chi-square tests to determine whether the number of observed and expected heterozygotes were significantly different from the predictions of Hardy–Weinberg equilibria, with exact p values estimated by the Markov chain method in the software Genepop (version 3.4; Raymond & Rousset 1995). We then used Wright's (1965) fixation index (f) to determine the nature of departures from random mating; positive values represent heterozygote deficits and negative values represent excesses. Deficits are expected from inbreeding or self-fertilization, whereas asexual reproduction should produce both heterozygous excesses and deficits (Willis & Ayre 1985). Where possible, we compared the observed and expected genotypic diversity (G_O:G_E) (Stoddart & Taylor 1988) at each site. Values of G_O:G_E <1 should reflect the combined effects of departures from single-locus Hardy–Weinberg equilibria and multilocus linkage disequilibria, which are a predictable consequence of asexual reproduction. Departures of G_O:G_E from unity were assessed with t tests (Stoddart & Taylor 1988).

For regions with ≥3 sampled sites we used analysis of variance (ANOVA) to test for heterogeneity of genetic diversity on the basis of allelic diversity (N_a—the number of alleles per locus) and expected heterozygosity (H_e). Connectivity among sites and regions was estimated with hierarchical F_{ST}, calculated as Weir and Cockerhams' θ with TFPGA (Miller 1997). Mean θ (SE) was calculated by jackknifing over loci. Departures from panmixis were tested with the 95% CI of θ, calculated by bootstrapping over loci. Pairwise F_{ST} values were used to calculate N_em under an island model ($N_em = (1/F_{ST} - 1)/4$; Wright 1969) to estimate the magnitude of gene flow among MPAs (data pooled across sites).

Because F_{ST} varied across loci, we tested for evidence of selection at each locus with the F_{ST} outlier approach of Beaumont and Nichols (1996) implemented with the selection–detection workbench LOSITAN (http://popgen.eu/soft/lositan). We based predictions on 10,000 simulations, and tests for neutrality were determined on the basis of 95% CIs.

Results

Population Structure

For *P. damicornis* patterns of single-locus heterozygosity was largely consistent with each population being derived from sexual reproduction with some inbreeding. Mean values of f were large, and multilocus H_o was $<H_e$ in 19 of 20 populations sampled (Supporting Information). Indeed, 85 of 160 possible tests across 8 loci and 20 sites revealed heterozygote excesses in only 21 cases *cf.* 63 heterozygous deficits. Of these, only 2 excesses and 15 deficits were significant after sequential Bonferroni corrections (Hochberg 1988) (data not shown). Levels of multilocus genotypic diversity were also consistent with sexual recruitment with G_o:G_e typically >0.55 within all sites for which we could perform valid tests (see Supporting Information).

For *G. australensis* mean f values were also large, and multi-locus H_o was $<H_e$ in all 10 populations (see Supporting Information). In 73 tests across 9 loci and 10 sites, we detected 10 heterozygous excesses and 63 deficits of which 27 remained significant after Bonferroni correction (data not shown).

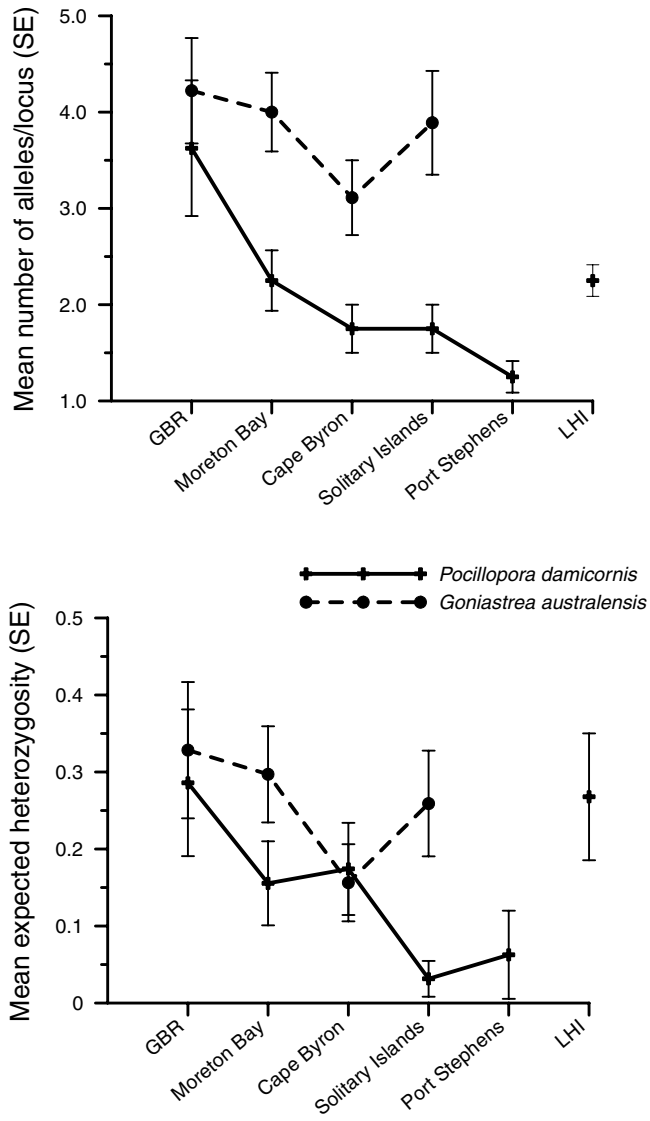

Figure 2. Trends in genetic diversity with increasing latitude in Pocillopora damicornis *and* Goniastrea australensis *from the east coast of Australia. Lord Howe Island is an offshore, oceanic reef and is plotted independent of the chain of near-shore reefs.*

Genetic Diversity and Latitude

Allelic diversity and expected heterozygosity declined with increasing latitude in both species (Fig. 2). Nevertheless, the variation among regions with ≥ 3 sampled sites was only significant for *P. damicornis* (ANOVA df = 3, $p < 0.0006$), where the mean (SE) N_a ranged from 3.6 (0.7) to 1.3 (0.2) and the mean H_e from 0.28 (0.1) to 0.03 (0.02) from the GBR to the Solitary Islands, respectively (Fig. 2). For *P. damicornis*, the lowest values of N_a and H_e were within the southern-most Port Stephens Marine Park, but these were not included in the ANOVA because only 2 sites were sampled in this region. Values of N_a and H_e in *P. damicornis* populations on the offshore LHI were greater than on the coastal HLRs (Fig. 2).

Connectivity within and among MPAs

HIERARCHICAL *F* STATISTICS

For *P. damicornis*, we detected great and significant genetic subdivision within MPAs (mean [SD] $F_{SM} = 0.34$ [0.06], $p < 0.05$) and among all MPAs ($F_{MT} = 0.28$ [0.05], $p < 0.05$) (Table 1). This reflects, in part, subdivision between our tropical and temperate sites. Nevertheless, separate analysis for just the temperate populations revealed even greater variation within ($F_{SM} = 0.46$ [0.09]) and among ($F_{MT} = 0.39$ [0.08]) the 5 high-latitude MPAs (Table 1). Tests for selection indicated 7 of 8 loci were acting as neutral markers, but that *Mpi* was likely to be under positive selection ($p < 0.05$). Nevertheless, because mean *F* statistics were calculated as weighted averages, our results were unaffected by the omission of the outlier locus (Table 1).

In contrast, *G. australensis* displayed only low levels of genetic subdivision within and among MPAs. We detected small but statistically significant differentiation within MPAs (mean [SD] $F_{SM} = 0.09$ [0.03], $p < 0.05$), but no significant differentiation among MPAs ($F_{MT} = 0.03$ [0.03]). Nevertheless, even these small levels of subdivision were arguably inflated by one outlier locus *Mpi*, which displayed an order of magnitude more variation than all other loci, and simulations suggested it is under positive selection ($p < 0.05$). Removal of *Mpi* reduced estimates to $F_{SM} = 0.06$ (0.02) and $F_{MT} = 0.00$ (0.004) (Table 2), but did not change the significance of the results. Tests for selection also indicated *Hk* was likely to be under balancing selection ($p < 0.05$).

PAIRWISE ESTIMATION OF GENE FLOW

Pairwise estimates of F_{ST} revealed little or no gene flow between most MPAs for *P. damicornis*. The lowest level of differentiation, and hence highest level of inferred gene flow, was between GBR and LHI, ($N_em = 7.8$ genetically effective migrants/generation) and Moreton Bay/Cape Byron ($N_em = 4.9$) (Fig. 3). All other pairs of MPAs were highly differentiated, exchanging <3 migrants/generation. Nevertheless, the inferred connections between some MPAs should be treated with caution because we were only able to collect 16 specimens from Cape Byron and the Solitary Island and Port Stephens MPAs each displayed little allelic variation (Fig. 1; Appendix S1).

For *G. australensis*, pairwise estimates of F_{ST} revealed minimal genetic differentiation among the 4 MPAs, with estimates of gene flow ranging from moderate to high ($N_em = 4.2$–18.9 migrants/generation; Fig. 3).

Table 1. The F_{ST} values for *Pocillopora damicornis* calculated as Weir and Cockerham's Θ among sites within each marine protected area (MPA) (F_{SM}) and among MPAs (F_{MT}) along the east coast of Australia.*

	F_{SM}		F_{MT}	
Locus	*all regions*	*temperate regions*	*all regions*	*temperate regions*
Gpi	0.35	0.47	0.32	0.44
Hk[1]	0.24	0.35	0.17	0.26
Hk[2]	0.05	0.06	0.02	0.02
Ltt[2]	0.24	0.36	0.20	0.29
Mdh[1]	0.01	0.01	0	0
Mdh[2]	0.20	0.21	0.15	0.15
Mpi	0.47	0.63	0.38	0.54
Pgm[2]	0.06	0.05	0	0
Over all loci	0.33	0.44	0.27	0.37
Mean (SD)	0.34 (0.06)	0.46 (0.86)	0.28 (0.05)	0.39 (0.08)
95% CI	0.19–0.41	0.26–0.54	0.14–0.33	0.19–0.47
After removal of *Mpi*				
mean (SD)	0.28 (0.05)	0.37 (0.07)	0.24 (0.06)	0.32 (0.08)
95% CI	0.16–0.32	0.22–0.43	0.11–0.29	0.16–0.39

**The 95% CI represents the 95% confidence interval around the mean* F_{ST}.

Discussion

As predicted the marginal HLR populations of both the bushy and asexually viviparous *P. damicornis* and the massive *G. australensis* displayed less genetic diversity than tropical populations closer to their range centers. Nevertheless, despite their similar ranges, the 2 species displayed contrasting population structures and patterns of connectedness. Overall our data imply that the HLR populations of *P. damicornis* are largely isolated and are the genetically deficient products of rare colonization events. Even within the mainland chain of HLRs, populations of *P. damicornis* were highly genetically differentiated but lacked within-population allelic variation, which suggests that existing marine parks do not provide a network of larval connections for this species. In contrast, HLR populations of *G. australensis* retained relatively high levels of genetic diversity, and all appeared moderately to highly interconnected by gene flow.

Table 2. The F_{ST} values for *Goniastrea australensis* calculated as Weir and Cockerham's Θ among sites within each marine protected area (MPA) (F_{SM}) and among MPAs (F_{MT}) along the east coast of Australia.*

Locus	F_{SM}	F_{MT}
Gpi	0.07	0
Hk	0.02	−0.01
Lgg[1]	0.14	−0.01
Lp[2]	0.03	0.01
Ltp[2]	0.03	−0.02
Mdh[1]	0.05	0.02
Mdh[2]	0.03	0.01
Mpi	0.19	0.15
Pgm	0.05	−0.01
Over all loci	0.09	0.03
mean (SD)	0.09 (0.03)	0.03 (0.03)
95% CI	0.04–0.14	−0.01–0.09
After removal of *Mpi*		
mean (SD)	0.06 (0.02)	0 (0.004)
95% CI	0.03–0.10	−0.01–0.01

**The 95% CI represents the 95% confidence interval around the mean* F_{ST}.

Connectivity among Existing MPAs

The life history of the asexually viviparous *P. damicornis* has been the subject of more intense scrutiny than any other coral. This reflects both its complex and variable life history (see Ayre & Miller 2004; Miller & Ayre 2004) and its abundance on many of the world's shallow tropical and temperate reefs. Results of earlier studies show that on the GBR, this species has the least large-scale (1200 km) genetic differentiation of 5 brooding and 4 broadcast-spawning species (Ayre & Hughes 2000). Moreover, almost all sites were highly genotypically diverse (Benzie et al. 1995; Ayre et al. 1997; Ayre & Miller 2004; Sherman et al. 2006), which implies that the GBR populations are well connected by sexually produced larvae. In contrast, our data, together with the results of Ayre and Hughes (2004), demonstrate dramatically greater differentiation between tropical and temperate reefs and among temperate reefs, which implies much less gene flow than for the GBR. Indeed, levels of genetic differentiation for the HLRs are so great that, with the exception of LHI, we conclude they are effectively self-seeding. Similar conclusions have been drawn from the nature of larval recruitment to these reefs (e.g., Harriott 1992).

From a conservation perspective, perhaps the second-most striking feature of the high-latitude populations of *P. damicornis* is their lack of genetic and genotypic diversity. This is a predictable consequence of their extreme geographic and genetic isolation and implies extreme vulnerability to environmental change (Frankham et al.

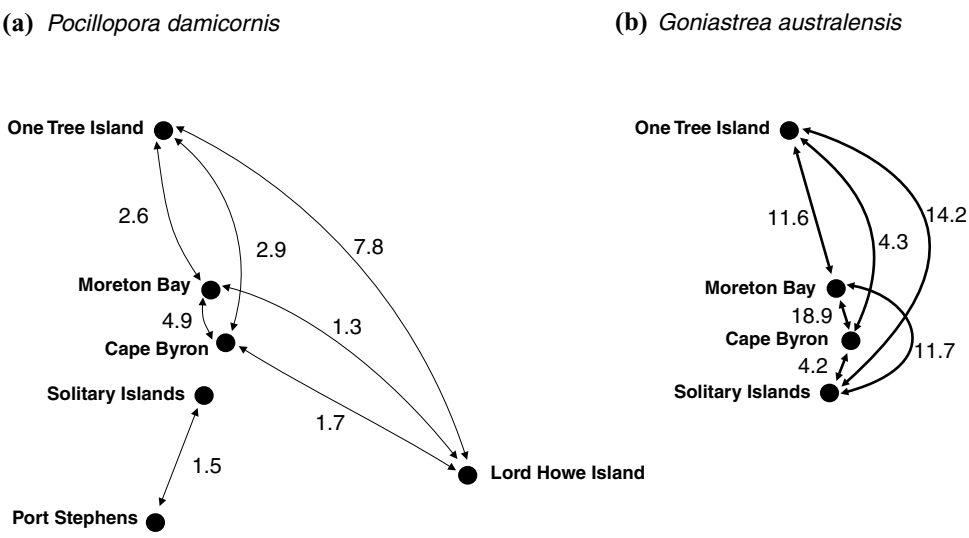

Figure 3. Estimates of gene flow (calculated as N_em*) between marine protected areas (MPAs) on the basis of sites pooled within MPAs for (a)* Pocillopora damicornis *and (b)* Goniastrea australensis*. Where there is no connecting line between MPAs,* $N_em \leq 1$*. Calculations for* G. australensis *exclude the outlier locus* Mpi.

2002). Given its life history, a lack of genetic variation could also be expected from localized proliferation of clones as reported for temperate reefs of Western Australia (Stoddart 1984) and Hawaii (Stoddart 1986). Nevertheless, our analyses imply that asexual reproduction makes little contribution to recruitment at any of our sites. Although low sample sizes or lack of genetic variation within the Cape Byron, Solitary Islands, and Port Stephens Marine Parks prevented valid testing of the importance of clonality, it seems unlikely that populations from these 3 MPAs should be more reliant on asexual reproduction that the other high-latitude and tropical populations surveyed.

Because our results for *P. damicornis* are clearly not driven by recruitment of asexually generated brooded larvae, the observed population differentiation must reflect the limited dispersal of broadcast-spawned, sexually produced larvae (Ward 1992; Tanner 1996). It is surprising then that our results for *G. australensis* contrast so starkly with those obtained for *P. damicornis*. Our data suggest considerable gene flow among HLRs and between the GBR and HLRs for *G. australensis*, although we did find small but significant subdivision among sites within MPAs, which most likely reflects some level of isolation at local scales (i.e., hundreds of meters to <10 km). Indeed, this pattern (whereby genetic subdivision is apparent at small scales, but not at larger scales) is seen often in marine invertebrates, including corals (e.g., Hellberg 1995; Ayre & Hughes 2000), and may reflect spatial and temporal variation in recruitment resulting in apparently chaotic genetic patchiness (Johnson & Black 1982), stabilizing selection, or ongoing gene flow across evolutionary timescales to maintain effective panmixia (Hughes et al. 1992). Nevertheless, the role of long-lived massive corals such as *G. australiensis* as "ecosystem engineers" (Cameron & Endean 1985; Foster et al. 2007) may confound estimation of gene flow because even if dispersal occurs only rarely over large geographic scales, the persistence of individual genotypes for hundreds of years in a population will skew genetic estimates of connectivity.

Surprisingly, we found no evidence of stepping-stone connections along the coast for either coral species, as might be expected on the basis of our knowledge of the direction and speed of the prevailing current (Ridgeway & Dunn 2003) and the settlement competency periods of coral larvae. For *P. damicornis*, recruitment to LHI appears more likely to occur directly from the GBR (path A, Fig. 1b), rather than along coastal reefs via the EAC (path B, Fig. 1b), although even direct dispersal will be infrequent. Certainly the limited data available suggest that the overall pattern of isolation we found for *P. damicornis* may be more typical of HLR populations than the apparent panmixis displayed by *G. australensis*. Ayre and Hughes (2004) reported that LHI populations of 4 additional coral species (3 brooders and 1 broadcast spawner) are significantly less genetically diverse than on the GBR, and their high levels of genetic subdivision imply that for each species, LHI received <1 colonist/generation from the GBR. Similarly, Benzie and Stoddart (1992) report that LHI populations of the crown of thorns starfish (*Acanthaster planci*) are also highly differentiated from populations on the GBR. Although Booth et al. (2007) report strong links between the EAC and dispersal of fish larvae from the tropics to southern New South Wales, recruitment appears to be linked to local features, such as eddies, and larval behavior and is not directly predictable from the EAC.

Conservation of Genetic Diversity within the Current System of MPAs

Our data raise several key questions about the effectiveness of the current MPA network along the east coast of Australia and the most appropriate strategies for future conservation and management of HLR corals.

From a theoretical perspective, the contrasting population structures exhibited by our target species pose radically different challenges for conservation. For the largely self-seeding *P. damicornis*, conservation efforts need to focus on protecting existing adults to ensure an adequate supply of recruits for local population maintenance. For the more widely dispersed *G. australensis*, the emphasis must be on protecting source populations and ensuring larval recruitment. These 2 strategies seem at odds; however, the comprehensive nature of the existing MPAs (which at least partially protect corals within most of the known HLRs and include multiple reefs within each MPA) means that the conservation of both species may hinge simply on ensuring that the existing MPAs continue to favor the growth and settlement of coral. Because few other notable coral populations exist outside existing MPAs, any protection beyond the current system of MPAs would seem unnecessary.

Because genetic diversity is a strong predictor of capacity to adapt to environmental change (Frankham et al. 2002), we predict that the less genetically variable and isolated populations of *P. damicornis* will be more vulnerable than the genetically variable and interconnected populations of *G. australensis*. Arguably, however, the population structures displayed by both species may indicate that conservation should have a low priority in each case because for *P. damicornis*, the HLRs contain only a tiny proportion of the variation present on the GBR, whereas for G. *australensis*, the HLRs appear to be simply a smaller but representative sample of the larger population of the GBR.

We argue, however, that conservation may be more important and vulnerability more difficult to predict in the face of climate change and predicted variation in the EAC (Cai et al. 2005). Our data show that links between the GBR and HLRs are weak at best and so the likelihood that the GBR will act as a source of recruits to the HLRs following catastrophic events is negligible and only likely to occur over long timescales. In addition, it is likely that HLR populations support valuable locally adapted genotypes. Selection was evident at *Mpi* in both species, and the lack of gene flow among *P. damicornis* populations also increases the likelihood that local adaptation occurs (see Ayre [1985, 1995] for evidence of localized adaptation of clones despite infrequent recruitment). Locally adapted genotypes may be crucial to the persistence of HLR populations under current conditions and are likely to be important sources of genetic novelty in the future. Certainly, climate-change models predict water temperatures will rise, which may release previously unsuitable habitats for coral recruitment and growth. As we have demonstrated, the probable source of larvae is from nearby populations, so any range extension of these corals is likely to rely on recruits from existing HLRs.

Overall, the picture that emerges from our analysis of the population structure for 2 corals that are common and widespread on Australia's HLRs is that they must now and for a long time have been subject to sharply contrasting patterns of realized dispersal and that they consequently pose equally contrasting challenges for any MPA system. There is little evidence that the chain-like suite of MPAs along the east coast of Australia forms a network for dispersal of coral larvae, although the protection of part of almost all significant coral populations within MPAs may arguably be the best conservation measure currently available. The contrasting genetic patterns displayed by *P. damicornis* and *G. australensis* imply that comparable surveys are required for other coral species and their associated flora and fauna for more meaningful conservation strategies that are relevant at the community level. In addition, the role of offshore reefs such as Elisabeth and Middleton Reefs as stepping stones between the GBR and LHI remains an important gap in our knowledge of the nature of links among high-latitude MPAs.

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Supporting Information

Allele frequency data for *Pocillopora damicornis* (Appendix S1) and *Goniastrea australensis* (Appendix S2) are available as part of the on-line article. The authors are responsible for the content and functionality of these materials. Queries (other than the absence of material) should be directed to the corresponding author.

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