



Genetic diversity and differentiation among high-latitude broadcast-spawning coral populations disjunct from the core range

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ABSTRACT: Little is known regarding the maintenance of range-edge populations in the absence of gene flow from core populations. In this study, we used 7 microsatellite markers to investigate genetic diversity and differentiation of the broadcast-spawning coral species *Acropora solitaryensis* among range-edge populations that are disjunct from the core range, and cautiously infer what this means in terms of connectivity. *Acropora solitaryensis* in sub-tropical eastern Australia is effectively isolated from conspecifics thousands of kilometers away and cannot rely on immigration from core populations for population maintenance. The range-edge region in this study consists of nearshore (Solitary Island) and offshore (Lord Howe Island) populations separated by >630 km. Despite the presence of null alleles, genetic diversity was within the range of that observed in other *Acropora* species. Nearshore and offshore populations were found to be genetically differentiated, with some indication of a small number of long-distant migrants in both directions. From both a demographic and a genetic perspective, this result may be important for the long-term persistence of *A. solitaryensis* at this range edge.

KEY WORDS: *Acropora solitaryensis* · Range edge · Long-distance dispersal · Genetic maintenance · Disjunct distribution

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INTRODUCTION

Range-edge populations are hypothesized to be more vulnerable to extirpation compared with larger core populations. The underlying factors for this increased risk can be grouped into 2 broad categories: (1) demographic instability arising from marginal habitats, small populations, and random stochastic events (e.g. Hardie & Hutchings 2010); and (2) genetic erosion (e.g. high inbreeding, low genetic diversity) that can contribute to lower fitness (Sexton et al. 2011 and references therein). Nevertheless, many ecologically and demographically marginal, genetically unique range-edge populations have survived over extended time scales (e.g. Budd & Pandolfi 2010).

While many studies describe demographic and genetic relationships between range-edge and core populations (reviewed by Hardie & Hutchings 2010), few studies have examined the mechanisms underlying maintenance of genetic diversity and population persistence at range edges, especially in the absence of immigration from a core range (reviewed in Eckert et al. 2008). Genetic as well as demographic factors must be taken into account when considering long-term persistence of range-edge populations disjunct from the core. At the scale of individual populations, several hypotheses have been proposed for long-term persistence at range boundaries. For example, genetic isolation in a substantially different (often marginal) habitat compared with the core range may preserve mutations and local adaptations that favor

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population persistence at that site (Kawecki 2008). Introgressive hybridization can also increase a species' genetic diversity, and is generally more common at species boundaries where species abundances tend to be lower compared with core populations (Thompson et al. 2010, Budd & Pandolfi 2010). Finally, gene flow between genetically differentiated populations within a range edge can provide substantial genetic benefits, such as decreasing the effects of inbreeding and improving fitness (e.g. Sexton et al. 2011).

Extended metapopulations of reef corals may be maintained by gene flow among large numbers of interconnected reefs (e.g. Great Barrier Reef; Ayre & Hughes 2000) or along 'stepping stone' populations (e.g. southeast African coast; Ridgway et al. 2008). For non-continuous reef areas (e.g. across a continental shelf), rare long-distance migration events may be significant in maintaining a metapopulation over evolutionary time scales (e.g. Underwood et al. 2009, Nakajima et al. 2012). Surrounding populations can be vital for recolonization after a localized extirpation in one population due to a stochastic event. Thus, dispersal between populations that are disjunct from the core range is likely to have positive demographic as well as genetic consequences.

This study provides population genetic data on subtropical populations of the broadcast-spawning coral *Acropora solitaryensis* (Acroporidae; Veron & Wallace 1984). This species is one of the most ecologically important and numerically dominant coral species on subtropical Eastern Australian reefs and coral communities (Harriott et al. 1999). *Acropora solitaryensis* occurs at high-latitude Eastern Australian locations, is extremely rare on the Great Barrier Reef (GBR), but is common in the Coral Triangle, Japan, and in Western Australia (Wallace 1999). Hence, *A. solitaryensis* populations in subtropical Eastern Australia are both range edge and effectively isolated from conspecific core populations in the Coral Triangle, as the GBR is an improbable source and the next nearest populations are 1000s of kilometres distant.

This species has been observed to broadcast spawn gametes at both the Solitary Islands and Lord Howe Island (Wilson & Harrison 2003, Harrison 2008). However, the large geographic distances between subtropical Eastern Australian nearshore coral communities and offshore reefs (>630 km) likely limit dispersal between these locations. The observation that 2 species of brooding reef coral among subtropical Eastern Australian locations showed limited gene flow supports this hypothesis (Miller & Ayre 2008,

Noreen et al. 2009). A large proportion of subtropical-dwelling corals are tropical species surviving at or near their range limit, and environmental stress is known to negatively affect coral reproduction as well as survival (Harrison 2011). However, 2 characteristics of *Acropora solitaryensis* may result in higher dispersal compared with brooding coral species in this region: (1) broadcast-spawning species generally have larger distances over which routine dispersal occurs compared with brooding corals (e.g. Ayre & Hughes 2000, Underwood et al. 2009), and (2) in contrast to many tropical species, *A. solitaryensis*'s reproduction appears to be adapted to the cooler subtropical water temperatures (Nozawa & Harrison 2007).

Using a population genetics approach, we examined (1) the genetic diversity of range-edge *Acropora solitaryensis* populations that are geographically isolated from conspecifics in the core range, and (2) the genetic differentiation between nearshore (Solitary Islands) and offshore (Lord Howe Island) range-edge locations. Our results are discussed in light of possible mechanisms underlying demographic and genetic maintenance of these *A. solitaryensis* populations and their overall persistence in this region.

MATERIALS AND METHODS

The 2 main locations sampled in this study were the nearshore Solitary Islands (29.9 to 30.2° S, 153.4° E) and offshore Lord Howe Island (31.5° S, 159.1° E; Fig. 1). Middleton (29.3° S, 159.1° E) and Elizabeth Reefs (29.6° S, 159.1° E) were surveyed in 2007 to conduct sampling for this study, but no *Acropora solitaryensis* colonies were observed. Samples from the northern limit of the southeastern Australian range (Flinders Reef; 27.0° S, 153.4° E) were also collected, but there were too few individuals for robust genetic analyses ($n = 8$). At Lord Howe Island, where species identification is more uncertain, larger voucher specimens were taken for subsequent verification of species identity, and C. C. Wallace was consulted *in situ* during the latter of 2 sample collections. The identity of the sampled corals was confirmed using the Australian Institute of Marine Science *Scleractinia of Eastern Australia Monograph Series* reference collection at the Museum of Tropical Queensland. Only confirmed *A. solitaryensis* samples were included in the study, which resulted in low sample sizes at Lord Howe Island. Pooling of sites occurred if they were adjacent (<2 km distant), in similar habitat, located on the same side of the island (east or

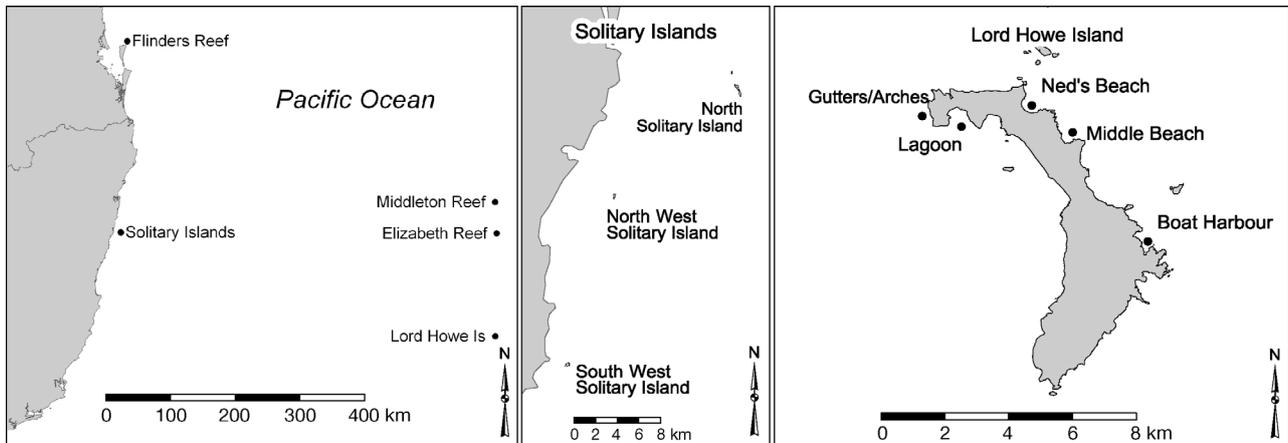


Fig. 1. *Acropora solitaryensis*. Sampling locations: Lord Howe Island and North, North West, and South West Solitary Islands. Sample sites at Lord Howe Island are indicated by black circles. Flinders Reef, Middleton Reef, and Elizabeth Reef were also visited for this study, but inadequate sample sizes were found at these locations

west), and not significantly genetically differentiated (based on F_{ST} values calculated in FSTAT v. 2.9.3; Goudet 1995, 2002; data not shown). This resulted in pooling 2 pairs of sites: Gutters/Arches $n = 13$ and Lagoon $n = 7$; and Ned's Beach $n = 9$ and Middle Beach $n = 6$.

Branches of *Acropora solitaryensis* with a base ca. 5 cm in width were collected using SCUBA and fixed in 95% ethanol. DNA was extracted following a standard Proteinase K and isopropanol-precipitation extraction (Wilson et al. 2002). Eight *Acropora* microsatellite loci (Baums et al. 2005, van Oppen et al. 2007) were amplified using fluorescently labeled primers in 2 multiplex PCRs (Table A1 in Appendix 1). Samples were genotyped with an internal size standard (ET 400-R) on a MegaBACE 1000 capillary and scored using a MegaBACE Genetic Profiler v. 1.2.

Data analysis

GIMLET v. 1.3.3 (Valière 2002) was used to assess the ratio of clones (N_g) to unique genotypes sampled (N) per population. If P_{random} was $p \leq 0.01$ for identical genotypes, all but one sample in the putative clone sets was removed prior to analyses. Tests for linkage disequilibrium (LD) and Hardy-Weinberg equilibrium (HWE) were conducted in the web-based package GenePop v. 4.0 (Raymond & Rousset 1995). Locus Amil2_018 was removed due to significant ($p < 0.0001$) LD with Amil2_010. As significant deviations from HWE were detected, Microchecker v. 2.2.3 (van Oosterhout et al. 2004) was used to test for the presence of null alleles, and significant null alleles were detected in many populations and loci (Table A1 in

Appendix 1). STRUCTURE v. 2.2 (Pritchard et al. 2000), a model-based clustering method, was used to visually represent a range of numbers of genetic clusters (K). Burn-in was 100 000 with 1 000 000 iterations for $K = 1$ to $K = 10$ replicated 5 times per K , and the most likely value of K was determined following Evanno et al. (2005) (Fig. A1 in Appendix 1). GeneClass v. 2.0 (Piry et al. 2004) was used to detect first-generation immigrants under the following conditions: likelihood ratio $L_{\text{home}}/L_{\text{max}}$ with 10 000 simulated individuals following the algorithm of Paetkau et al. (2004). This generated a probability of each individual being a putative migrant. Individuals with a p -value for being a migrant of ≤ 0.0001 were removed from the original populations, and tested against the sampled populations. Genetix v. 4.05.2 (Belkhir et al. 1996–2004) was used to construct an individual-based principal coordinates analysis (PCA). Two Solitary Island outliers were removed from the data set to facilitate visual interpretation of the PCA.

RESULTS

A relatively high frequency of null alleles was observed for most loci studied (Table A1 in Appendix 1), which can skew HWE (and hence the inbreeding coefficient F_{IS}) (e.g. Chakraborty et al. 1992) and therefore affect data interpretation. Hence, these 2 genetic indices were not assessed here. Despite the presence of null alleles at most loci, moderate genetic diversity was detected at both locations (allelic richness $R = 4.02$ – 4.99 , expected heterozygosity $H_e = 0.548$ – 0.696) and this was not significantly different

between locations for either parameter (t -tests, $p = 0.25$ and 0.68 , respectively). Low levels of clonality were recorded among samples from the Solitary Islands, but no clonality was observed at Lord Howe Island, where all samples were sexually produced (Table 1).

The most likely value of K in STRUCTURE was 3, with 2 admixed genetic clusters dominant at the Solitary Islands, and another genetic cluster dominant at Lord Howe Island (Fig. 2). A small proportion of individuals at both the Solitary Islands and Lord Howe Island were admixed and showed assignment to the non-local genetic cluster (Fig. 2). The PCA also showed 2 distinct yet overlapping groups (Fig. 3), further supporting genetic differentiation between nearshore and offshore locations overlaid by a low level of gene flow.

Seven putative migrants ($p \leq 0.0001$) were identified in GeneClass: one sampled at Lord Howe Island, and 6 sampled at the Solitary Islands (Table 2). The single migrant identified at Lord Howe Island had moderate re-assignment probabilities to each of the 3 Solitary Islands (0.23–0.64). Four of the Solitary

Islands' putative migrants, all sampled at North West Solitary Island, could be assigned to one or 2 sites at Lord Howe Island at a low to moderate probability (0.16–0.36). The low relative bias of null alleles in assignment testing compared with other analyses (such as F_{ST} ; Carlsson 2008) provide confidence in these results despite the technical issues (i.e. null alleles). In addition, while the low sample sizes and the potential for unsampled Solitary Island or Lord Howe Island populations increase uncertainty in assignment, there are few other locations harbouring substantial *Acropora solitariaensis* populations in this region (e.g. Byron Bay; also see 'Discussion' regarding Middleton and Elizabeth Reefs) and this species is extremely rare to absent on the GBR.

DISCUSSION

The results of this study show that *Acropora solitariaensis* populations at Lord Howe Islands and the Solitary Islands are genetically differentiated, with the possibility of rare long-distance migration between these locations. These occasional dispersal events may play an important role in the persistence of these range-edge populations by maintaining genetic diversity as well as providing a mechanism for recolonization at an extirpated (or novel) site.

Genetic diversity

Low levels of clonality were recorded in populations at the nearshore Solitary Islands but the populations at

Table 1. *Acropora solitariaensis*. Sample size (N), mean observed (H_o) and expected (H_e) heterozygosity, the ratio of unique genotypes to sample size (N_g/N), number of private alleles, and mean allelic richness (R). LHI: Lord Howe Island

	N	H_o	H_e	N_g/N	Private alleles	R
North Solitary Island	45	0.396	0.569	0.93	4	4.12
North West Solitary Island	55	0.348	0.551	0.93	2	4.23
South West Solitary Island	27	0.388	0.548	0.93	–	4.02
LHI Gutters/Arches–Lagoon	20	0.567	0.667	1.0	6	4.21
LHI Ned's–Middle Beach	15	0.454	0.696	1.0	3	4.99
LHI Boat Harbour	11	0.566	0.695	1.0	1	4.15

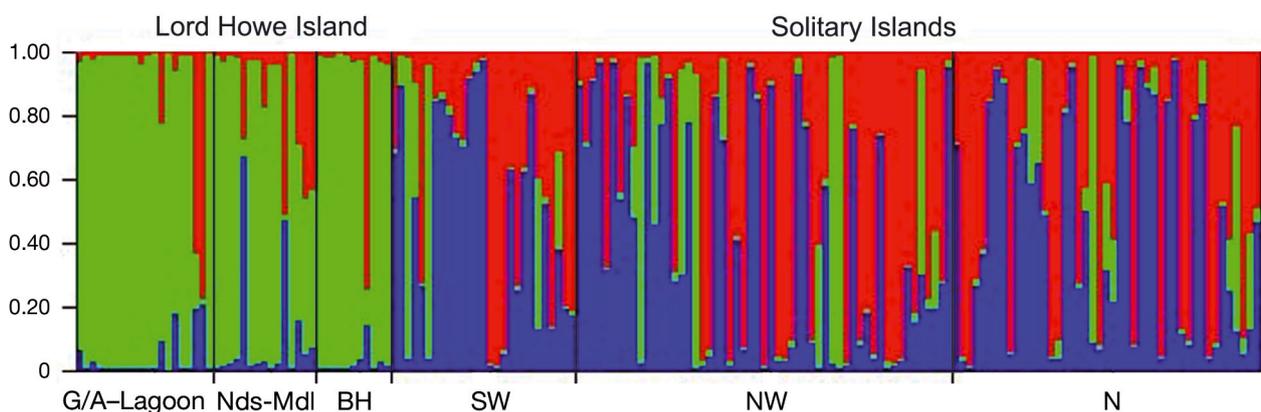


Fig. 2. *Acropora solitariaensis*. STRUCTURE bar plot for *A. solitariaensis* ($K = 3$). Each vertical line represents the assignment probability of a single individual to genetic cluster(s) without reference to where that individual was sampled

Table 2. *Acropora solitaryensis*. Assignment of putative migrants. Site at which the individual was sampled (Site sampled), the p-value for being a migrant (p migrant), the putative origin site(s), and the assignment probability for each site. LHI: Lord Howe Island; SOL: Solitary Island

Site sampled	p migrant	Putative origin	Assignment p
LHI Boat	0.0001	SOL SW	0.23
Harbour		SOL NW	0.34
		SOL N	0.62
		None	<0.01
SOL SW	<0.0001	None	<0.01
SOL NW	<0.0001	LHI Ned's–Middle Beach	0.16
SOL NW	<0.0001	LHI Ned's–Middle Beach	0.13
		LHI Boat Harbour	0.20
		LHI Ned's–Middle Beach	0.35
SOL NW	<0.0001	LHI Boat Harbour	0.36
		LHI Boat Harbour	0.21

Lord Howe Island were completely sexual (Table 1). In contrast, the congener *Acropora valida* is highly clonal at Lord Howe Island (Ayre & Hughes 2004). Fragmentation is a likely cause for clonality in *Acropora solitaryensis*, as it has a broadcast-spawning reproductive mode and does not develop asexually produced larvae (Harrison 2008, 2011). Despite the null alleles detected for most loci and populations, which cause an underestimation of genetic diversity, expected heterozygosity was moderately high ($H_e > 0.50$) at both the Solitary Islands and Lord Howe Island. The H_e and R detected in this study were within the range of values for *Acropora* species on the GBR and elsewhere (Underwood 2009, van Oppen et al. 2011, Richards & van Oppen 2012). In addition, a similar high-latitude study in Japan on *Acropora* sp. 1 also found that for 2 subtropical loca-

tions at the same latitude and separated by ~1500 km of open ocean, genetic diversity was not substantially depressed for either population (Nakajima et al. 2012).

Genetic differentiation and gene flow

Two previous studies showed significant genetic differentiation of *Acropora* populations separated by extensive areas of open ocean and interpreted 'rare' (northwest Australia; Underwood 2009) or 'infrequent' (Japan; Nakajima et al. 2012) dispersal.

In our study, the PCA (Fig. 3) as well as the STRUCTURE results (Fig. 2) support a similar conclusion: *A. solitaryensis* populations at the Solitary Islands and Lord Howe Island are genetically distinct, but with evidence of low levels of gene flow and admixture among them (Fig. 2, Table 2).

Migration from Lord Howe Island to the Solitary Islands and vice versa is consistent with potential larval dispersal pathways. For example, fish larvae can disperse from nearshore sites to Lord Howe Island (e.g. Patterson & Swearer 2008); and a satellite-tracked drifter released during a coral spawning event at the Solitary Islands arrived at Lord Howe Island 25 d later (Wilson & Harrison 1998), well within the extended competency period of *Acropora solitaryensis* (65 to 72 d; Nozawa & Harrison 2002). In addition, the formation of large gyres south of 32° S

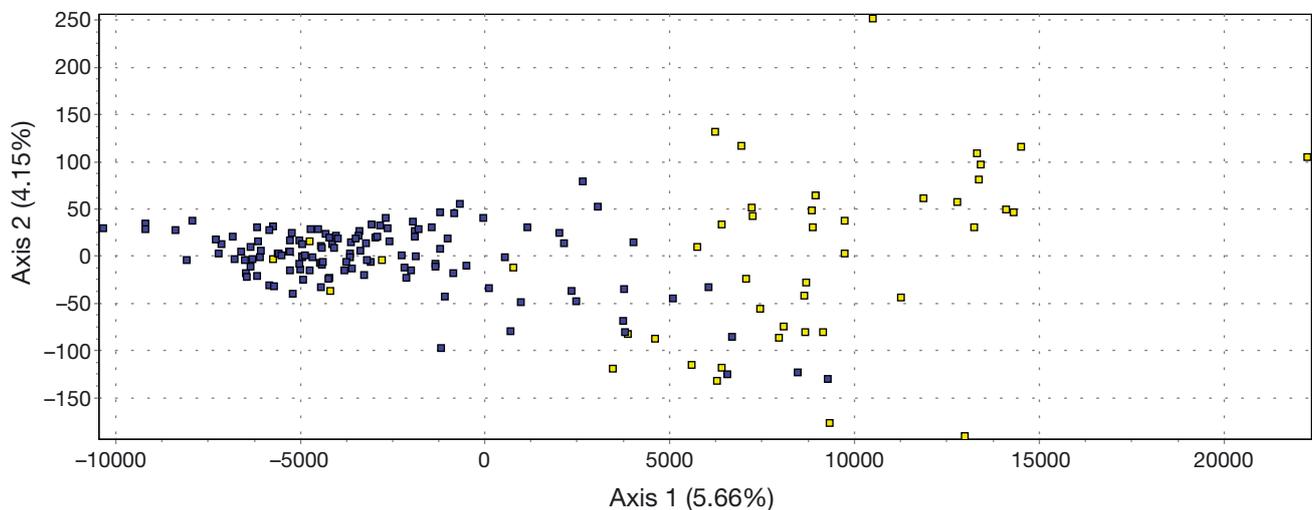


Fig. 3. *Acropora solitaryensis*. Principal coordinates analysis of Solitary Island (blue squares) and Lord Howe Island (yellow squares) samples

could also provide transport for propagules in the opposite direction, from offshore to nearshore locations.

The STRUCTURE analysis indicated 3 as the most likely number of genetic clusters (Fig. A1 in Appendix 1) instead of 2, and appears to result from 2 admixed clusters present in the Solitary Islands (Fig. 2). The relatively tight group formed by the Solitary Islands in the PCA and the nearly equal re-assignment given to each of the 3 Solitary Island sites in GeneClass indicate genetic similarity among sites. Supporting this interpretation, the broadcast-spawning coral *Goniastrea australensis* showed low differentiation along several hundred kilometers of the subtropical Eastern Australian coastline (including the Solitary Islands) (Miller & Ayre 2008). In addition, low population differentiation of broadcast-spawning *Acropora* species among a series of islands (over much larger spatial scales) has been detected at their northern range limit in Japan (Nishikawa et al. 2003, Nakajima et al. 2010). Many coral populations located along strong directional flows, such as the Kuroshio Current, the Agulhas Current (southeastern Africa), or the Eastern Australian Current have adequate dispersal and gene flow to prevent significant genetic differentiation over extended distances (100s of kilometres) (e.g. Ayre & Hughes 2000, Ridgway et al. 2008, Nakajima et al. 2010). In contrast, significant population differentiation between sites at Lord Howe Island has previously been detected in 3 brooding and one broadcast-spawning reef coral species (Ayre & Hughes 2004, Miller & Ayre 2004, 2008, Noreen et al. 2009). In this study, the STRUCTURE results show that most Lord Howe Island samples belong to the same genetic cluster (Fig. 2), although the low sample size at Lord Howe Island prevents definitive interpretations on the population structure of *A. solitaryensis* among sites.

Implications for genetic maintenance

Our results are consistent with several possibilities regarding genetic maintenance of subtropical *Acropora solitaryensis* populations. The genetic diversity of *A. solitaryensis* in this region, measured with genetic markers that included null alleles, was generally on par with other *Acropora* species (e.g. Underwood 2009, van Oppen et al. 2011, Richards & van Oppen 2012). One or more of several explanations could account for this, of which the most probable may be long-distance dispersal and/or interspecific hybridization. For example, a single successfully

dispersed and ultimately reproductive migrant per generation can contribute substantially to genetic diversity in small populations (e.g. Mills & Allendorf 1996, see also Sexton et al. 2011). Alternatively, hybridization between some *Acropora* species occurs occasionally (e.g. Willis et al. 2006) and range-edge populations of many plant and coral species may display more introgressive hybridization compared with populations in the core range (Thompson et al. 2010, Budd & Pandolfi 2010). For example, at Lord Howe Island, likely *Pocillopora damicornis* × *Stylophora pistillata* hybrids were detected (Miller & Ayre 2004). The difficulty of identifying unambiguously *A. solitaryensis* at some high latitude locations (Wallace 1999, C. C. Wallace pers. comm.) may reflect inter-specific hybridization events.

Implications for demographic maintenance

Our data show consistent genetic distinctions, albeit with some apparent mixture, which indicate the demographic independence of geographically isolated subtropical *Acropora solitaryensis* populations. Previous studies of tropical coral species at Lord Howe Island predicted that coral populations would have 'extremely lengthy' replenishment time scales after extirpation (Ayre & Hughes 2004, Miller & Ayre 2008). Our results support this hypothesis, as do field observations: Middleton and Elizabeth Reefs, 180 and 235 km north of Lord Howe Island (respectively), harboured substantial populations of *A. solitaryensis* during the first detailed taxonomic study of these reefs in 1981 (Hutchings 1992, J. E. N. Veron pers. comm.). However, a severe crown-of-thorns starfish outbreak occurred at Middleton and Elizabeth Reefs in the mid-1980s (J. E. N. Veron pers. comm.), and no colonies of *A. solitaryensis* were observed at either location in 2007 during >11 h diving at 7 sites and in suitable habitats (A. Noreen pers. obs.). This indicates either that *A. solitaryensis* is restricted to habitats at Elizabeth and Middleton Reefs that were not surveyed in 2007, or that the time scale for recolonization is >20 yr. However, in the absence of complete simultaneous region-wide extinction, we hypothesize that replenishment will occur eventually (i.e. decades to centuries), as long as a source population within the region remains.

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Appendix 1

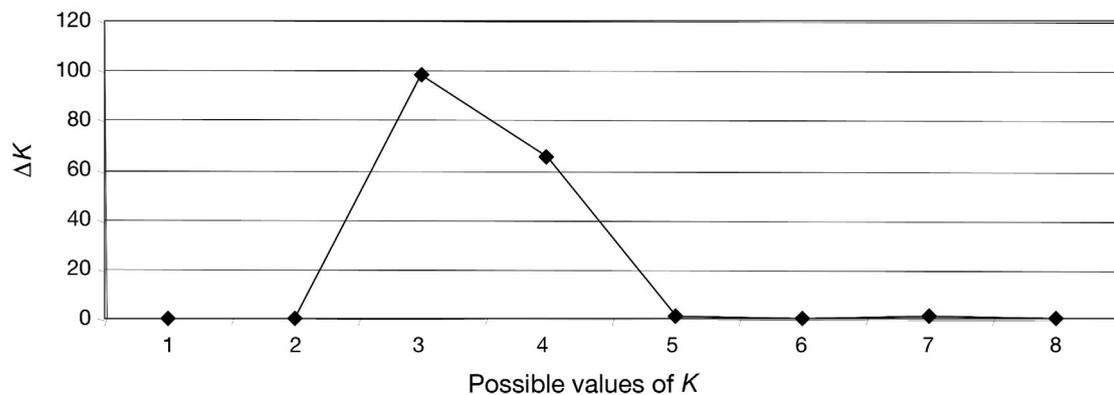


Fig. A1. ΔK values for STRUCTURE analysis

Table A1. Summary of *Acropora solitaryensis* data per population and locus. Number of alleles, observed heterozygosity (H_o), expected heterozygosity (H_e), inbreeding coefficients (F_{IS}), and loci with probable null alleles (Nulls)

	Locus	No. of alleles	H_o	H_e	F_{IS}	p	Nulls
Lord Howe Island							
Gutters/Arches–Lagoon	Amil2_002	7	0.350	0.781	0.569	0.000	Yes
	Amil2_010	7	0.550	0.689	0.225	0.002	Yes
	Amil2_006	5	0.300	0.466	0.378	0.005	Yes
	Amil2_023	2	0.250	0.219	-0.070	0.371	No
	Amil2_022	10	0.650	0.849	0.258	0.000	Yes
	Amil5_028	9	0.895	0.816	-0.118	0.755	No
Apam3_166	13	0.737	0.846	0.156	0.007	Yes	
Lord Howe Island							
Ned's Beach–Middle Beach	Amil2_002	6	0.667	0.796	0.195	0.124	No
	Amil2_010	6	0.467	0.644	0.307	0.073	Yes
	Amil2_006	3	0.267	0.604	0.582	0.002	Yes
	Amil2_023	3	0.133	0.127	-0.018	0.969	No
	Amil2_022	10	0.533	0.880	0.432	0.000	Yes
	Amil5_028	9	0.733	0.833	0.154	0.034	No
Apam3_166	11	0.500	0.885	0.465	0.000	Yes	
Lord Howe Island							
Boat Harbour	Amil2_002	7	0.455	0.744	0.420	0.048	Yes
	Amil2_010	6	0.545	0.657	0.216	0.070	No
	Amil2_006	3	0.182	0.483	0.652	0.007	Yes
	Amil2_023	2	0.364	0.397	0.096	0.101	No
	Amil2_022	8	0.889	0.815	-0.032	0.891	No
	Amil5_028	11	0.818	0.860	0.130	0.603	Yes
Apam3_166	9	0.636	0.831	0.278	0.044	No	
Solitary Island							
South West	Amil2_002	9	0.760	0.846	0.121	0.018	No
	Amil2_010	2	0.111	0.226	0.521	0.037	No
	Amil2_006	6	0.360	0.626	0.442	0.005	Yes
	Amil2_023	1	-	-	-	-	-
	Amil2_022	7	0.261	0.524	0.518	0.000	Yes
	Amil5_028	8	0.680	0.748	0.111	0.008	Yes
Apam3_166	9	0.263	0.852	0.704	0.000	Yes	
Solitary Island							
North West	Amil2_002	8	0.611	0.850	0.290	0.000	Yes
	Amil2_010	4	0.184	0.417	0.567	0.000	Yes
	Amil2_006	6	0.241	0.525	0.548	0.000	Yes
	Amil2_023	2	0.000	0.036	1.000	0.009	Yes
	Amil2_022	8	0.309	0.554	0.450	0.002	Yes
	Amil5_028	13	0.755	0.839	0.112	0.000	Yes
Apam3_166	12	0.278	0.894	0.697	0.000	Yes	
Solitary Island							
North	Amil2_002	11	0.705	0.850	0.182	0.004	Yes
	Amil2_010	5	0.190	0.357	0.476	0.000	Yes
	Amil2_006	5	0.227	0.500	0.553	0.000	Yes
	Amil2_023	1	-	-	-	-	-
	Amil2_022	9	0.378	0.568	0.344	0.000	Yes
	Amil5_028	11	0.750	0.802	0.076	0.031	Yes
Apam3_166	16	0.432	0.897	0.528	0.000	Yes	