

# Random mating in the brooding coral *Acropora palifera*

David J. Ayre<sup>1,\*</sup>, Karen Miller<sup>1,2</sup>

<sup>1</sup>Institute for Conservation Biology, School of Biological Sciences, University of Wollongong, Wollongong, New South Wales 2522, Australia

<sup>2</sup>Marine Research Laboratory, Tasmanian Aquaculture and Fisheries Institute, University of Tasmania, Private Bag 49, Hobart, Tasmania 7001, Australia

**ABSTRACT:** For marine invertebrates such as corals, restricted dispersal of sperm and/or larvae have been invoked to explain large heterozygote deficits and population subdivision apparent in many genetic surveys. Equally though, for the many corals and other invertebrates that are hermaphroditic, inbreeding through self-fertilisation may also account for heterozygote deficits. Flexibility of mating systems to allow at least some level of self-fertilisation may be favoured by selection, as this would facilitate the founding of new populations by low numbers or densities of colonists. While tests for self-compatibility are relatively easy for broadcast-spawning corals, experimentally determining the level of selfing in corals that have internal fertilisation is near impossible; ironically, it is these brooding species that are considered good colonists and hence the most likely to display a tolerance for self-fertilisation. Here we used allozyme data to provide the first rigorous estimate of outcrossing rates in a brooding coral *Acropora palifera*, and compare these values with indirect estimates of mating system based on adult genotype frequencies. We found that within each of 2 sites (150 and 300 m<sup>2</sup>) at Wistari Reef on the southern Great Barrier Reef, estimated outcrossing rates were not significantly less than rates expected from random mating ( $t = 0.96 \pm 0.07$  and  $t = 0.92 \pm 0.09$ ). Levels of biparental inbreeding (0.02 and 0.15) and correlated paternity estimates (0.14 and 0.39) were intermediate to low, implying that broods typically had multiple male parents. The adult populations at both sites showed evidence of greater levels of heterozygote deficits than could be explained based on levels of outcrossing estimated from the genotypes of broods, implying that either outcrossing rates vary over time or that population genetic structure is strongly influenced by other factors such as restricted larval dispersal.

**KEY WORDS:** Gamete dispersal · Population structure · Allozymes · Internal fertilisation · Inbreeding · Outcrossing

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## INTRODUCTION

It is increasingly evident that for many marine invertebrates such as brooding scleractinian corals, a capacity for rapid settlement of larvae, together with extended competency periods, results in a bimodal pattern of larval dispersal (Jackson & Coates 1986, Grosberg 1987, Richmond 1987, Raimondi & Keough 1990, Ayre & Hughes 2000, Krug 2001, Miller & Mundy 2003). However, while theory predicts that genetically different kinds of larvae should be optimal for localised colonisation of the parental habitat versus long-

distance dispersal to new or unpredictable habitats (Williams 1975, Shields 1982, Knowlton & Jackson 1993), little is known about the genotypic composition of coral broods.

For tropical corals, tactics such as asexual reproduction and inbreeding (including self-fertilisation for hermaphroditic species) that favour preservation of the parental genotype may be favoured for localised recruitment, while outcrossing with increased genotypic novelty may be favoured for long distance dispersal or settlement within a spatially or temporally heterogeneous environment. Therefore, if the geno-

types of brooded coral larvae could be matched to the bimodality of dispersal distances then broods might typically reflect a mixed mating strategy with outcrossed larvae being the more widely dispersed. It is of course unlikely that within a brood dispersal distance will be determined by genotype. Moreover, simplistic predictions of links between dispersal distances and modes of reproduction are confounded by the fact that tropical coral reefs are typically both physically and biologically diverse and unstable (Connell et al. 1997), and that the success of brooding corals as colonists of isolated reefs (Veron 1992, Harriott 1992, Harriott et al. 1995, Ayre & Hughes 2004) requires that successful colonizing genotypes are both well adapted to their new habitat and able to establish a self-sustaining population from one or a few initial colonists. We argue that the optimal life-history for brooding corals is likely to be a mixed mating strategy involving at least some selfing or biparental inbreeding, as is the case for many plants. Such flexibility may favour outcrossed sexual reproduction when both outcross and self-sperm are available (Willson & Burley 1983), but may allow for greater inbreeding or asexual reproduction at low adult densities.

Surveys of the genetic composition of populations of both broadcast spawning and brooding corals on the Great Barrier Reef (GBR) imply that populations are typically maintained by localised dispersal of larvae and/or gametes. Indeed, populations of many coral species are highly genetically subdivided and show massive heterozygous deficits that may be explained through inbreeding and self-fertilisation (Knowlton & Jackson 1993, Ayre & Dufty 1994, Ayre & Hughes 2000, Ayre & Miller 2004). Like many brooding invertebrates, brooding scleractinian corals are hermaphroditic and thus may have the ability to self-fertilise (Knowlton & Jackson 1993). However, for most broadcast spawning coral species, mating trials have shown that self-fertilisation is rare (Miller & Babcock 1997, Willis et al. 1997). By inference, inbreeding in brooding species would also seem likely to reflect the effects of limited dispersal of sperm and larvae (Black et al. 1991, Oliver & Babcock 1992, Miller & Mundy 2003) rather than self-fertilisation. Alternatively, asexual production of brooded larvae may be relatively common. While the sexual production of brooded larvae has been confirmed genetically for only 3 coral species (Ayre & Resing 1986, Hellberg & Taylor 2002), another 3 species have been shown to generate their broods asexually (Stoddart 1983, Ayre & Resing 1986, Ayre & Miller 2004).

The extent of outcrossing, biparental inbreeding and self-fertilization in brooding reef corals that use sexual reproduction to generate their broods is

unknown because valid genetic comparisons of adults and their broods have been restricted to 1 colony of *Seriatopora hystrix* and 11 isoporan colonies from a number of local populations (Ayre & Resing 1986). These isoporans may have belonged to either or both of the cryptic species pair *Acropora palifera* and *A. cuneata* (Ayre et al. 1991). The small number of broods examined, the absence of reliable single species estimates of the genotypes of surrounding conspecifics, and the pooling of data from multiple populations invalidate Carlon's (1999) estimate of low levels of outcrossing ( $t = 0.246$ ) in *A. palifera* using Ayre & Resing's (1986) published data. Estimates of allele frequencies of adults within the pool of potential male parents are essential to such studies of mating systems, as outcrossing rates are estimated by comparing genotype frequencies within progeny arrays with those expected given the maternal genotype and a random sampling of available sperm (Ritland 2002). Brazeau et al. (1997) also claimed to demonstrate moderate levels of self-fertilization in the Caribbean brooders *Favia fragum* and *Porites asteroides*; however, their study was based on genetic comparisons of adults and their broods using a dominant DNA marker (RAPDs) with no objective means of predicting the genotypes expected under different mating systems, and again with no estimates of allele frequencies in the surrounding set of potential male parents.

*Acropora palifera* is one of the most obvious targets for investigation of mating systems in brooding corals. It is one of the most abundant brooders on the GBR (Kojis 1986) and allozyme studies have revealed large and consistent heterozygous deficits within local populations spread along the length of the GBR ( $F_{IS} = 0.12$ , Benzie et al. 1995;  $F_{IS} = 0.22 \pm 0.05$ , Ayre & Hughes 2000), which could be explained by substantial levels of self-fertilization and/or biparental inbreeding. *Acropora palifera* is hermaphroditic (Kojis 1986) and has been a successful colonist of isolated island and reef systems (Harriott 1992, Veron 1992). Moreover, *A. palifera* has unusually large and conspicuous larvae (~2 mm and pink-tipped) that have almost invariably settled within 5 m on experimental release (Best & Resing 1987).

Here we used allozyme electrophoresis to determine the multi-locus genotypes of *Acropora palifera* adults and sets of brooded larvae from 2 sites on Wistari Reef on the southern GBR. We then used these data to make direct and indirect estimates of outcrossing rates and correlated outcrossed paternity (numbers of male parents contributing to broods), to establish if self-fertilisation or bi-parental inbreeding might explain the observed population genetic structure in this brooding coral.

## MATERIALS AND METHODS

**Collection of colonies and brooded larvae.** In mid-January 2003, we collected *Acropora palifera* from 2 sites on the shallow back reef slope of Wistari Reef (23° 28' S, 151° 52' E) in the Capricorn Bunker Group of the GBR for larval collection and genotyping. These sites (1 and 2) were separated by about 200 m, spanned 4 to 8 m depth at low tide, and were approximately 150 and 300 m<sup>2</sup> in area, respectively. Within each site, we collected 2 cm branch tips from all adult *A. palifera* colonies (n = 40 at both sites) to allow determination of allozyme genotypes. We also did preliminary inspections of colonies to determine if brooded juveniles were visible on the cut surface of the branch. We subsequently collected 9 and 11 brooding colonies from Sites 1 and 2, respectively. Colonies we collected were expected to have a high probability of being *A. palifera*, but were also likely to include at least some morphologically similar *A. cuneata* (Ayre et al. 1991). However, we had first carried out surveys of colonies in adjacent shallow water reef crest sites (expected to be dominated by *A. cuneata*) and detected no brooding colonies, suggesting that only *A. palifera* was brooding at that time.

We collected planulae from 14 of the 20 brooding adults (6 and 8 for Sites 1 and 2, respectively) by placing them in individual aquaria within a flow-through sea water system for up to 3 d. Larvae were obtained either by pipetting them from the bottom of each aquarium or removing them from plankton mesh larval collectors placed at the aquarium outlets (e.g. Ayre & Miller 2004).

**Electrophoretic determination of genotypes.** We determined genotypes for adult tissue and whole planulae using allozyme electrophoresis. Following the methods of Ayre & Hughes (2000) for all adults and planulae we scored 3 loci: glucosephosphate isomerase (*Gpi* E.C. 5.3.1.9), malate dehydrogenase (*Mdh*<sup>1&2</sup> EC 1.1.1.37); for adults we also stained for 6 phosphogluconic acid dehydrogenase (*6pgd* EC 1.1.1.44) and leucyl tyrosine pepti-

dase (*Ltp* EC = 3.4.11) and used this information to confirm our experimental colonies were *Acropora palifera* rather than the morphologically similar *A. cuneata* (Ayre et al. 1991). Alleles at each locus were labelled according to their mobility relative to that of the most common allele.

**Analyses.** We used Ritland's (1990) multilocus mating system program (MLTR) to calculate allele frequencies and fixation indexes within the adult populations (incorporating the genotypes of all parents plus the neighbouring adults at each site), and to estimate single- and multi-locus outcrossing rates (*t*) and outcrossed correlated paternity (*r<sub>p</sub>*) for each of the broods. Standard errors for outcrossing rates and correlated paternity were estimated by bootstrapping using 1000 permutations. For all analyses we used only adults and larvae for which we had complete 3-loci genotypes.

## RESULTS

### Adult population structure and allele frequencies

Our samples of *Acropora palifera* adults displayed similar allele frequencies and hence similar levels of allelic diversity at both sites, with 2 common and 1 rare allele present at each locus (Table 1). On average we detected deficits of heterozygotes at each site, although for Site 1 the average inbreeding coefficient across all loci ( $f = 0.15 \pm 0.11$ ) was not significantly different to 0 (the expectation for Hardy-Weinberg equilibria). At Site 2, significant departures from Hardy-Weinberg equilibrium were detected ( $f = 0.29 \pm 0.06$ ,  $p < 0.01$ ) (Table 2).

Table 1. *Acropora palifera*. Allele frequencies at 3 variable loci for adults collected from 2 sites on the southern Great Barrier Reef: a, b and c represent alleles labelled in order of decreasing electrophoretic mobility

	n	<i>Mdh</i> <sup>1</sup>			<i>Mdh</i> <sup>2</sup>			<i>Gpi</i>		
		a	b	c	a	b	c	a	b	c
Site 1	37	0.39	0.58	0.03	0.03	0.62	0.35	0.01	0.72	0.27
Site 2	37	0.36	0.57	0.07	0.17	0.55	0.28	0.04	0.65	0.31

Table 2. *Acropora palifera*. Mating system parameters ( $\pm$  SE) estimated from progeny arrays at each of 2 sites on Wistari Reef. Genotypes were determined for each of 3 variable allozyme loci.  $t_m$  = multi-locus outcrossing rate,  $t_s$  = mean single-locus outcrossing rate,  $r_p$  = correlated outcrossed paternity,  $f$  = fixation index based on adult genotypes frequencies

Location	Broods genotyped	Mean brood size	Adults genotyped	$t_m$	$t_s$	$t_m - t_s$	$r_p$	$f$
Site 1	6	10.8 $\pm$ 1.9	37	0.96 $\pm$ 0.07	0.94 $\pm$ 0.11	0.02 $\pm$ 0.09	0.14 $\pm$ 0.14	0.15 $\pm$ 0.11
Site 2	8	8 $\pm$ 0.8	37	0.92 $\pm$ 0.09	0.77 $\pm$ 0.12	0.15 $\pm$ 0.08	0.39 $\pm$ 0.33	0.29 $\pm$ 0.06

### Direct estimates of outcrossing and correlated paternity

Our comparisons of adults and their brooded juveniles revealed high levels of outcrossing at both sites, although we detected no alleles among larval genotypes that were not present in the neighbouring adult populations (Table 2). Estimates of  $t$  based on the mean of the 3 loci ( $t_s = 0.94 \pm 0.11$  and  $0.77 \pm 0.12$  at Sites 1 and 2, respectively) were high to moderate and our multi-locus estimates of  $t$  ( $t_m = 0.96 \pm 0.07$  and  $0.92 \pm 0.09$  at Sites 1 and 2, respectively) were not significantly different to 1 (the expectation for random mating;  $p > 0.05$ ).

Where inbreeding is evident in a population, the difference between the multi-locus and single-locus estimates of outcrossing ( $t_m - t_s$ ) can be used to characterise the level of biparental inbreeding (mating between close relatives) as opposed to selfing. For each of our sites biparental inbreeding was low ( $t_m - t_s = 0.02 \pm 0.09$  and  $0.15 \pm 0.08$  at Sites 1 and 2, respectively).

### DISCUSSION

Our electrophoretic comparisons of adult *Acropora palifera* and their brooded planulae revealed that broods within each of 2 sites at Wistari Reef were generated almost exclusively by outcrossing. Moreover, at Site 1, most larvae appeared likely to have had different sires and the inbreeding coefficient that we estimated for the adult population was not significantly greater than 0 (the expectation for random mating). These results (particularly those from Site 1) conflict with our expectation that limited sperm dispersal (Levitan & Petersen 1995), limited dispersal of larvae (Best & Resing 1987) and self-compatibility (Knowlton & Jackson 1993) would together lead to a high level of self-fertilization and biparental inbreeding in a brooding coral. Indeed, our data show that selfing and/or biparental inbreeding were relatively rare within both sites, and in both cases outcrossing rates were not significantly different to expectations for random mating. These results support and extend Ayre & Resing's (1986) observation of the outcrossed generation of isoporan broods, and contrast with Carlon's (1999) estimate of only 26% outcrossing in this species (though see earlier comments on the validity of this estimate). Interestingly, the average level of heterozygous deficiency that we detected at Wistari Reef ( $f = 0.22$ ) exactly matched the average value reported by Ayre & Hughes (2000) for sites on other parts of the GBR.

The 'snap shot' of the realised mating system (Richardson et al. 2000) provided by our data imply that, as

for broadcast spawning corals, self-fertilisation in the brooder *Acropora palifera* was unlikely to explain the heterozygote deficits in this and previous genetic studies of this species (Benzie et al. 1995, Ayre & Hughes 2000). Additionally, the low levels of biparental inbreeding would not appear to account for heterozygote deficits in adult populations. If we assume that the mating system was at equilibrium, the levels of outcrossing that we inferred for Sites 1 and 2 ( $t_m = 0.96$  and  $0.92$ , respectively) would be expected to equate to inbreeding coefficients of  $f_e = 0.02$  and  $0.04$  (using the relationship  $f_e = (1 - t)(1 + t)^{-1}$ , Hedrick 1985). This is considerably less than the values of  $f$  that we calculated for adults within these sites ( $f = 0.15$  and  $0.29$ , Table 2).

Clearly, factors other than self-fertilisation and biparental inbreeding must have contributed to the observed heterozygote deficits in the adult populations. Possible explanations for this discrepancy might include restricted dispersal of larvae, post-settlement processes that select against heterozygous individuals, or Wahlund effects (resulting from variation in allele frequencies among demes or over time) (Ayre & Dufty 1994, Ayre & Hughes 2000). Realistically, since mating systems within unstable habitats such as a coral reefs (Connell et al. 1997) are unlikely to be at equilibrium, it may be safer to acknowledge that there is no clear match between mating system and fine-scale population structure. Indeed, this mismatch is also apparent for the asexual brooding coral *Pocillopora damicornis* (Ayre & Miller 2004, Miller & Ayre 2004a) as well as for the broadcast-spawners *Goniastrea favulus* and *Platygyra daedalea* (Miller & Ayre 2004b).

Our results also have interesting implications for the understanding of sperm dispersal in corals. For broadcast spawning scleractinian corals, limited dispersal of sperm and subsequent fertilisation among close neighbours (Oliver & Babcock 1992) is considered to account for at least some degree of non-random mating (e.g. Miller & Benzie 1997). For marine invertebrates in general, successful sperm dispersal is typically thought to occur only over distances of up to a few metres (Levitan & Petersen 1995). However, where sperm density is maximised through high fecundity or synchronous spawning, fertilisation can be achieved hundreds of metres from a spawning source; e.g. Babcock et al. (1994) and Yund (2000) have argued that sperm limitation in natural populations may be relatively rare. Here we found multiple paternity within our broods indicating that *Acropora palifera* sperm were dispersed successfully over at least tens of metres, since we found only ~40 colonies in the 150 m<sup>2</sup> area at Site 1 and a similar number in 300 m<sup>2</sup> at Site 2, and at both sites it was rare to find more than 2 or 3 colonies in close proximity. However, we detected no unique alleles in any of

the broods, suggesting that even for those broods that had multiple sires, all sires could well have come from within our relatively small sites. More precise estimates of sperm dispersal must await detailed paternity analyses, but this pattern is similar to that reported by Lasker & Gutierrez-Rodriguez (2002) for an externally brooding gorgonian.

While our data show that *Acropora palifera* was highly outcrossed at 2 sites in 2003, it is important to emphasize that our data did not demonstrate self-incompatibility. We still predict that even on the GBR the mating system of *A. palifera* may be flexible with levels of outcrossing dependent upon the effective local density and diversity of conspecifics. Self-fertilisation rates and levels of biparental inbreeding may well be higher in sites or situations such as the initial colonisation of isolated sites or high flow regimes, where outcrossed sperm is less readily available or limiting. In the present study we chose back reef sites on Wistari Reef with moderate densities of colonies that were large enough to be prolific brooders, within an area that supported a diverse array of species and clearly had not experienced any recent major disturbance. These sites might be expected to be among the more highly outcrossed. Within the better studied broadcast spawning Acroporiids, selfing is reduced or delayed—but not prevented—by a system of gametic incompatibility that breaks down a few hours after spawning (Willis et al. 1997); however, for broadcast spawning Faviids self-incompatibility mechanisms persist for an extended period (Miller & Babcock 1997). Moreover, in brooding invertebrates such as the ascidian *Botryllus schlosseri*, realized mating systems have been shown to be dependent on the diversity and density of surrounding colonies (Grosberg 1987, 1991, Yund & McCartney 1994). Further studies are required to investigate temporal and spatial variation in the level of outcrossing, and will further our understanding of mating systems and the factors that ultimately influence the genetic structure of coral populations.

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