The Role of Hybridization in the Evolution of Reef Corals

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Abstract

The importance of hybridization in the evolution of plant species is widely accepted, but its contributions to animal species evolution remain less recognized. Here we review evidence that hybridization has contributed to the evolution of reef corals, a group underpinning the coral reef ecosystem. Increasingly threatened by human and climate-related impacts, there is need to understand the evolutionary processes that have given rise to their diversity and contribute to their resilience. Reticulate evolutionary pathways among the ecologically prominent, mass-spawning genus *Acropora* suggest that hybridization, although rare on ecological timescales, has been instrumental in their diversification on evolutionary timescales. Evidence that coral hybrids colonize marginal habitats distinct from those of parental species' and that hybridization may be more frequent at peripheral boundaries of species' ranges supports a role for hybridization in range expansion and adaptation to changing environments. We conclude that outcomes of hybridization are significant for the future resilience of reef corals and warrant inclusion in conservation strategies.

INTRODUCTION

Hybridization has long been considered a major creative force in the evolution of plant species (e.g., Anderson 1949, Anderson & Stebbins 1954, Grant 1981, Stebbins 1959), but traditionally, its role in the evolution of animal species has been thought to be inconsequential, or at most, significant only in terms of reinforcing barriers to interspecific fertilization (Dobzhansky 1937, Mayr 1963). However, as predicted in a comparatively recent review of animal hybridization (Dowling & Secor 1997), evidence is mounting that hybridization is more common among animal species than previously thought and occurs in the majority of phyla in both terrestrial and marine habitats (reviewed in Arnold 1997, Gardner 1997, Mallet 2005). Phylogenetic hotspots, where (as in British vascular plants) approximately 25% of animal species hybridize, include British duck and game bird species, and American warblers and butterflies, but overall, 6–12% of bird, butterfly, and mammal species hybridize naturally (Mallet 2005). There are comparatively few studies of hybridization in modular, sessile marine animals (Gardner 1997), whose modes of speciation are more likely to resemble those of plants given similarities in their life histories. For example, both have sessile modular adults, frequent hermaphroditism, absence of mating behavior, broadcast spawning of gametes, passive dispersal of juveniles, and extensive asexual reproduction. Further studies of animals with plant-like life histories will enhance current understanding of the evolutionary significance of hybridization in animals.

On tropical coral reefs, the simultaneous mass spawning of many species of stony corals (Harrison et al. 1984) represents a unique breeding strategy among animals and suggests that hybridization might have played a role in the evolution of this functionally important group, the cornerstone of the coral reef ecosystem. In the past two decades, an upsurge of studies on the reproduction of scleractinian corals has shown that synchronized spawning among more than two species (i.e., mass spawning sensu Willis et al. 1985) occurs in the majority of reef regions (e.g., Baird et al. 2002, Carroll et al. 2006, de Graaf et al. 1999, Gittings et al. 1992, Guest et al. 2002, Hayashibara et al. 1993, Simpson 1991). In highly synchronized events, up to 35 species in sympatry may spawn within two hours of each other (e.g., mass spawning of corals on Australia's Great Barrier Reef (GBR); Babcock et al. 1986, Willis et al. 1985). In combination, the apparent absence of temporal barriers to interspecific breeding provided by mass spawning events, the co-occurrence of large numbers of coral species on reefs where currents mix positively buoyant gametes in a thin layer at the sea surface, and the reliance of the mate recognition system on interactions among gametes for assortative fertilization (Palumbi 1994) provide outstanding opportunities for hybridization. Concurrence in the timing of spawning among many coral species and the global nature of the mass-spawning phenomenon suggest that the Scleractinia provide a novel system for gaining insights into the role that hybridization has played in the evolution of animal species.

Understanding the evolutionary processes that have shaped modern reef corals and given rise to their diversity has become urgent as the number and intensity of threats to the biodiversity and resilience of coral reef ecosystems escalate against a backdrop of global climate change (e.g., Harvell et al. 2002, Hoegh-Guldberg 1999, Hughes

et al. 2003). Estimates that recent declines in coral cover and colony numbers have been greater than 97% for two of the three Atlantic species of the once-common coral genus *Acropora* and predictions that the downward trajectory may continue (*Acropora* Biological Review Team 2005) have led to their listing as threatened and endangered wildlife under the U.S. Endangered Species Act (ESA). However, evidence that the third coral, *Acropora prolifera*, is a hybrid and thus fails to meet the ESA definition of a species disqualifies it from consideration for protection under the act. If appropriate management strategies are to be developed for the Scleractinia, greater understanding of the evolutionary processes giving rise to their biodiversity is needed, particularly in relation to the role that hybridization has played in adaptive radiation and evolution within the group. The recent publication of a body of reproductive, morphological, ecological, and molecular data for mass-spawning corals in both the Indo-Pacific and Caribbean (see references in sections below) provides new perspectives on coral evolution and has prompted the present review of the evolutionary importance of hybridization within the Scleractinia.

HYBRIDIZATION AS AN EVOLUTIONARY PROCESS

Introgressive hybridization, here defined as the exchange of genes between genetically differentiated species, may have a variety of contrasting outcomes. Extensive and prolonged episodes of introgressive hybridization may lead to the merging of species and ultimately to the extinction of pure parental species along with their morphological, behavioral and/or ecological distinctions. This process of genetic mixing may provide increased genetic diversity, new traits, and heterosis for the emerging species, but may carry the cost of a net loss of species diversity. Regardless of contrasting perspectives on the fate of species following merging and homogenization of gene pools (i.e., the loss of current species versus the emergence of new ones), the comparative speed with which new traits and species can arise suggests that, in some cases, there may be positive selective pressure for hybridization and introgressive events [e.g., among diversifying species of sunflowers (Ungerer et al. 1998) and cyprinid fish (Rosenfield & Kodric-Brown 2003)].

Hybridization may also give rise to new species that are reproductively isolated from parental species through either polyploid speciation or recombinational speciation, both processes representing mechanisms for the rapid evolution of genetic novelty without the loss of parental species. Polyploid speciation involves the production of allopolyploids, which by definition contain three or more sets of chromosomes from two different species and thus achieve immediate reproductive isolation from parental species. Allopolyploid species are common in plants (Grant 1981, Ramsey & Schemske 1998, Soltis & Soltis 1999) and account for 2–4% of angiosperm species and 7% of fern species (Otto & Whitton 2000). In studies so far, animal allopolyploids are much rarer and are predominantly parthenogenic rather than sexually reproducing (Bullini 1994, Dowling & Secor 1997, Otto & Whitton 2000, White 1978). However, because uniparental species may contribute sexual propagules capable of introgressing with other species (e.g., diploid, hemiclonal species in the hybridogenetic fish

Poeciliopsis; Mateos & Vrijenhoek 2002) and may have greater distributional ranges than their bisexual ancestors (e.g., *Bacillus* stick insects, Bullini 1994), lack of sexual viability is not grounds for dismissing the evolutionary potential of asexual hybrid lineages.

Recombinational species (Grant 1981), also called homoploid hybrid species, are hybrid species that have the same number of chromosomes as their parent species but are reproductively isolated from them and are true breeding (Grant 1981, Rieseberg 1997). The number of clear-cut cases of recombinational speciation identified suggests that it may be rare in both plants and animals (Coyne & Orr 2004, Rieseberg 1997). For example, Rieseberg (1997) identified only eight well-documented cases of recombinational speciation in plants, three of which are *Helianthus* sunflower species. However, by its very nature, recombinational speciation, which requires that fit, interfertile recombinant hybrid genotypes be produced that are reproductively isolated from their sympatric parent species, is difficult to identify (Rieseberg 1997, Coyne & Orr 2004). The discovery of increasing numbers of diploid hybrid species with the advent of improved molecular techniques suggests that the real number of cases may be much higher than generally thought (Seehausen 2004). Seehausen argues that hybridization is particularly significant where ecological conditions favor adaptive radiations, such as where there are underutilized niches following disturbance or at the ecological or geographical peripheries of species ranges, and based on the prevalence of hybridization in studies of more recent adaptive radiations [e.g., Darwin's finches (Freeland & Boag 1999), African cichlids (Salzburger et al. 2002), Hawaiian crickets (Shaw 2002)], its contributions to past species diversifications have been underestimated. Evidence of transgressive segregation, in which phenotypic variation in hybrid populations is greater than the combined variation of parent populations (e.g., enhanced salt tolerance of hybrid *Helianthus* sunflowers through acquisition of different parental loci with additive effects; Lexer et al. 2003), provides a mechanism by which recombinational species can have greater fitness than parental species. When recombinational speciation does occur, empirical and theoretical evidence suggests that it does so rapidly and is often accompanied by ecological divergence that promotes reproductive isolation (Buerkle et al. 2000, McCarthy et al. 1995, Rieseberg et al. 2003). This further impedes the detection of past hybridization events in the origin and transfer of novel adaptations. Although hybrid zones provide valuable microcosms in which current, ongoing evolutionary processes can be studied (Hewitt 2001), the lack of a similar window on past hybridization events makes more distant contributions of hybridization events difficult to detect.

There is wide acceptance among botanists that the transfer of genes between taxa through introgressive hybridization potentially provides more raw material for evolution than can be produced directly by mutation (Anderson 1949, Anderson & Stebbins 1954, Arnold 1997), and hybridization is estimated to have produced a significant fraction (~11%) of flowering plant lineages (Rieseberg 1997). Even though cases of hybridization in animals continue to be described, the prevalent view is that hybridization has not played a major creative role in the evolution of animal species. This may be partly due to difficulties in identifying the products of hybrid speciation in past events. Even in contemporary studies, hybrid taxa or lineages may

be difficult to detect because they may be much closer genetically or morphologically to one parental species than the other (Jiggins & Mallet 2000, Naisbit et al. 2003). Moreover, establishing that hybrid lineages constitute distinct evolutionary entities that are reproductively isolated from parent species requires multiple lines of evidence including morphological, reproductive, molecular, and chromosomal karyotype data. Without such evidence of effective reproductive isolation, hybrid lineages are hybrids and not hybrid species. In summary, the variety of ways in which hybridization may contribute to the evolution of lineages attests to its scope as an evolutionary process, but evidence of its past contributions may be elusive.

MATING SYSTEMS OF MASS-SPAWNING CORALS

The mating systems of corals are based on either broadcast spawning of gametes for external fertilization or internal fertilization followed by larval brooding, with approximately two thirds of species (n = 227) utilizing the former, external mode of development (Harrison & Wallace 1990). The breeding periods of broadcast-spawning corals may be temporally isolated on scales that range from hours (Fukami et al. 2003, Knowlton et al. 1997, Levitan et al. 2004, van Oppen et al. 2002) to weeks or months (Wolstenholme 2004; B.L. Willis, unpublished data), but most corals spawn in tightly synchronized breeding events that overlap with those of a number of species, most commonly congeners (Harrison & Wallace 1990, Richmond & Hunter 1990). Opportunities for interspecific breeding in the mating systems of corals thus vary in response to breeding times that range from complete temporal isolation to complete overlap, with the dominant breeding strategy of synchronized mass spawning providing unparalleled potential for hybridization. Interpreting this potential for hybridization, however, requires knowledge of both prezygotic (including fine-scale temporal barriers and gamete incompatibility) and postzygotic isolating barriers.

Next we review isolating barriers for the dominant reef-building genera in two of the major ocean basins: the *Acropora* in the Indo-Pacific and the *Montastraea* in the Western Atlantic. The Indo-Pacific *Acropora* constitute a highly diverse group of more than 100 species, up to 76 of which can occur in sympatry (Wallace 1999; **Figure 1a**) and at least 35 of which are known to participate in synchronized mass-spawning events (Babcock et al. 1986, Willis et al. 1985). This genus has undergone the greatest adaptive radiation of any scleractinian genus in the Indo-Pacific, where it commonly dominates coral communities. In contrast, there are only 3 extant species of *Acropora* in the Western Atlantic (**Figure 1b**), indicating that different processes have shaped the evolution of this genus in these two biogeographic regions.

Prezygotic Isolating Barriers: Mating Precedence in Sperm Choice Experiments

Tests of gamete compatibility in laboratory crosses between mass-spawning species have had variable outcomes. Although the data are as yet fragmentary, there are some basic differences in interspecific gamete compatibility between those Indo-Pacific and Caribbean corals for which data are available. Among species of *Acropora*

Figure 1

Comparison of *Acropora* (Order: Scleractinia) assemblages on (*a*) Indo-Pacific reefs, where the genus attains the greatest diversity (more than 100 species) of all extant corals and typically dominates coral communities (almost all corals in the assemblage pictured are species of *Acropora*); and (*b*) Caribbean reefs, where there are only 3 extant species: *A. cervicornis* (*top right*); *A. palmata* (*bottom right*); and the hybrid *A. prolifera* (*bottom left*).

from the central GBR, outcomes of colony crosses between 38 pairs of species have spanned the complete spectrum of fertilization success from high (50–100%) between 8 pairs, through moderate (10–50%) between 7 pairs, to low (3–10%) between a further 3 pairs of species (van Oppen et al. 2002, Willis et al. 1997). Overall, one third of species pairs of Indo-Pacific *Acropora* crossed experimentally (n = 73 species combinations) have resulted in greater than 10% fertilization in some colony pairings, based on studies combined from the central GBR (van Oppen et al. 2002, Willis et al. 1997), northern GBR (Wolstenholme 2004), and Japan (Fukami et al. 2003, Hatta et al. 1999). The fraction rises to more than 45% if species pairs with low gamete compatibility (3–10% interspecific fertilization success) in at least some colony crosses are included. Thus the capacity to hybridize appears to be a common feature of mating systems in the Indo-Pacific *Acropora*, and this feature is consistent over large geographic areas. Similarly, breeding trials between seven morphospecies in the Indo-Pacific genus *Platygyra* have shown high levels of interspecific fertilization on the GBR (Miller & Babcock 1997, Willis et al. 1997). The lack of genetic distinctiveness among morphospecies of *Platygyra* in allozyme studies (Miller & Benzie 1997) suggests that hybridization may be more common in this genus than in the Indo-Pacific *Acropora*.

Although laboratory crosses in which eggs are provided only with the opportunity to mate with heterospecific sperm demonstrate that gametes are compatible, significant variation in the relative frequency of inter- and intraspecific fertilization success and dramatic variation among individual pairs of colonies (from 0% to 100% in some species crosses; Fukami et al. 2003, van Oppen et al. 2002, Willis et al. 1997) imply that prezygotic isolating barriers may exist among the *Acropora*. In order to test for evidence of premating isolation under conditions that more closely resemble in situ mass-spawning events, we carried out a series of sperm-choice breeding trials. We incubated eggs with both conspecific and heterospecific sperm in lab crosses, where sperm came from parents (*Acropora millepora* and *A. pulchra*) that were alternately homozygous for allozyme genotypes. Some 14 different sperm-choice crosses were performed, involving 3 cases in which *A. millepora* was the mother and 11 cases in which *A. pulchra* was the mother. Electrophoretic analyses of individual larval offspring demonstrated that, in the 11 trials in which *A. pulchra* was the mother, all offspring (n = 475 larvae) tested were the result of intraspecific fertilizations. Similarly, in 2 of 3 sperm-choice trials involving *A. millepora* as the mother, all offspring (n = 117 larvae) tested were purebreds. However, in one trial where *A. millepora* was the mother, all offspring (n = 120) tested were *A. millepora* × *A.pulchra* hybrids. It is conceivable that the colony used as the source of intraspecific sperm in this latter trial (which resulted in hybrid offspring) had been misidentified and was actually *A. spathulata*, a cryptic species that has recently been separated from *A. millepora* (Wallace 1999) on the basis of incompatibility in breeding trials (Willis et al. 1997). However, either hybridization was favored over conspecific fertilization (assuming that the fathers were correctly identified as *A. millepora* and *A. pulchra*) or, given a choice between sperm from two different species (*A. spathulata* and *A. pulchra*), *A. millepora* eggs were fertilized by the species with the more compatible sperm. These results suggest that, although eggs of many Indo-Pacific species of *Acropora* are compatible with heterospecific sperm in no-choice lab crosses, prezygotic isolating mechanisms exist that favor

conspecific mating in these species at least most of the time. Species specificity in gamete recognition and binding proteins has been found in other marine invertebrates, for example, in abalone (Vacquier et al. 1990) and sea urchins (Metz & Palumbi 1996) and would be a fruitful area of research to further understand the mating systems of mass-spawning corals.

Because many species of *Acropora* are able to hybridize in no-choice experimental crosses, the lack of hybrid offspring produced in the presence of conspecific sperm in the few sperm-choice trials so far performed suggests that prezygotic isolating barriers are semipermeable based on a hierarchy in gamete compatibility. Decreasing gamete compatibility, in rank order from intraspecific to closely related interspecific, and lastly to more distantly related interspecific matings, offers an alternative avenue for reproductive success if mates are scarce, such as in marginal or disturbed environments. At the same time, precedence of conspecific mating limits gene flow between species, thus maintaining species boundaries and morphologically recognizable species. Regardless of whether the capacity for hybridization under these circumstances is an artifact of their mating systems or a selected feature, the net result is a form of bet-hedging. Although interspecific pairings can lead to gamete wastage, there is ample evidence that they may also result in offspring that, if not sexually viable, are nevertheless able to found clonal lineages that may be ecologically successful (Bullini 1994, Kearney 2005, Spolsky et al. 1992).

In the Caribbean, there are no published studies of interspecific gamete compatibility for the genus *Acropora*, but studies of the *Montastraea* species complex have found generally low interspecific gamete compatibility between species that have overlapping spawning times. In Panama, evidence of gamete incompatibility in laboratory crosses provides corroborative evidence that *M. faveolata*, previously thought to be a morphological variant of *M. annularis*, is a cryptic species (Knowlton et al. 1997, Levitan et al. 2004). A second cryptic species (*M. franksi*) had moderate (~40–60%) gamete compatibility with *M. annularis*, but gametes age rapidly so that fine-scale (two hours) temporal isolation in spawning times provides a reasonably effective reproductive barrier. Significantly, the two species that have the more compatible gametes and are most closely related genetically (i.e., *M. franksi* and *M. annularis*) show strong temporal isolation, whereas the two species that spawn together (*M. annularis* and *M. faveolata*) have incompatible gametes and are genetically most different (Fukami et al. 2004, Levitan et al. 2004). Thus a suite of isolating barriers maintains species boundaries in this group in Panama.

Contrasting patterns of gamete compatibility were found at a site near the northern geographical periphery of the ranges of these western Atlantic species. In the Florida Keys, *M. faveolata* hybridized well with both *M. franksi* and *M. annularis* (Szmant et al. 1997). Genetic differences among these three taxa were also weaker in the Bahamas than in Panama (Fukami et al. 2004), potentially reflecting the occasional moderate to high numbers of viable larvae found in some experimental crosses, particularly with aged eggs, between pairs of these three species (Fukami et al. 2004). Similarly, consistent differences in patterns of corallite morphology were detected among these three species across their distributional ranges. Distinct corallite morphologies among all three species in Panama, in contrast to overlapping corallite

morphologies in the Bahamas, led Fukami et al. (2004) to speculate that a gradient in hybridization exists; the strongest introgression occurred at northern sites. Differences in gamete compatibility and morphologies among the same species at different geographic locations provide support for Veron's (1995) suggestion that species may interact differently through hybridization across their ranges. Morphological analyses of fossil specimens from Panama and the Bahamas suggest that present patterns of greatest introgressive hybridization and least morphological differentiation among *Montastraea* species in the Bahamas have persisted throughout the geological history of this species complex (Budd & Pandolfi 2004). Such persistent differences in the extent of interspecific breeding over broad geographic ranges throughout evolutionary histories are consistent with the notion that semipermeable barriers at the extremities of species' ranges afford increased opportunities for mating.

Patterns of temporal barriers to interbreeding in relation to species relatedness within the Caribbean *Montastraea* are the inverse of those within the Indo-Pacific *Acropora*; temporal isolating barriers are strongest between the most closely related species of Caribbean *Montastraea* (i.e., *M. franksi* and *M. annularis*; Levitan et al. 2004) but weakest between closely related species of Indo-Pacific *Acropora*, where temporal barriers reflect the greatest genetic divergence among species (Fukami et al. 2003; van Oppen et al. 2001, 2002; Wolstenholme 2004). Similarly, patterns of synchronous spawning with gamete compatibility differ between the two reef regions; synchronous spawning in Panama occurs between *Montastraea* species with the least compatible gametes (Levitan et al. 2004), whereas many Indo-Pacific *Acropora* and *Platygyra* species that spawn synchronously have compatible gametes (Miller & Babcock 1997, Fukami et al. 2003, Willis et al. 1997). Gametes of at least some Indo-Pacific species of *Platygyra* and *Acropora* remain competent for a significantly longer period of time (6–8 hours post spawning; Miller & Babcock 1997, Willis et al. 1997) than do those of their Caribbean counterparts (1–2 hours, Levitan et al. 2004), contributing to differences between the two regions in the degree of temporal isolation among species that spawn on the same night.
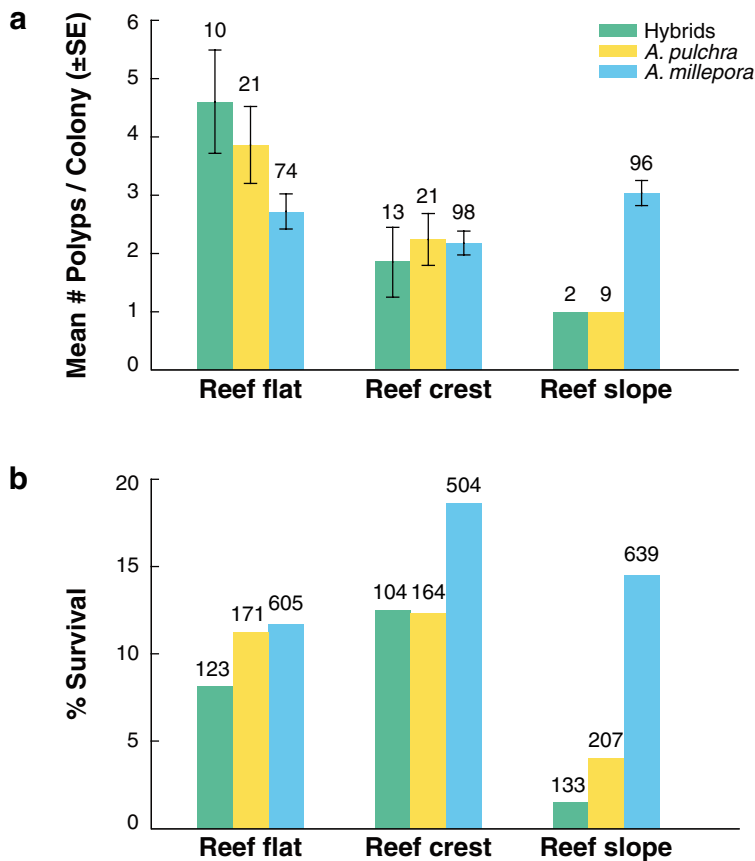
Postzygotic Isolating Barriers: Developmental Competence of Coral Hybrids

Studies of postzygotic isolating barriers among coral species are scarce, largely because of their long pre-reproductive periods (Harrison & Wallace 1990). In the Indo-Pacific, hybrid offspring from two different species crosses (*Acropora millepora* × *A. pulchra* and *A. hyacinthus* × *A. cytherea*) are developmentally competent and have been successfully reared for three years (**Figure 2**). Moreover, in a large-scale grow-out program on Orpheus Island reefs in the central GBR, patterns in the survival and growth of three-month-old hybrids of *A. millepora* × *A. pulchra* in three habitats (i.e., the intertidal, inner reef-flat habitat of *A. pulchra*, the reef-slope habitat of *A. millepora*, and an intermediate reef-crest habitat) indicate that, at this early life history stage, their fitness does not differ from that of purebred offspring reared in the reef-flat and reef-crest habitats (**Figure 3**). Generally, purebred offspring survived best in the habitat where the corresponding parental species was most abundant. Thus offspring
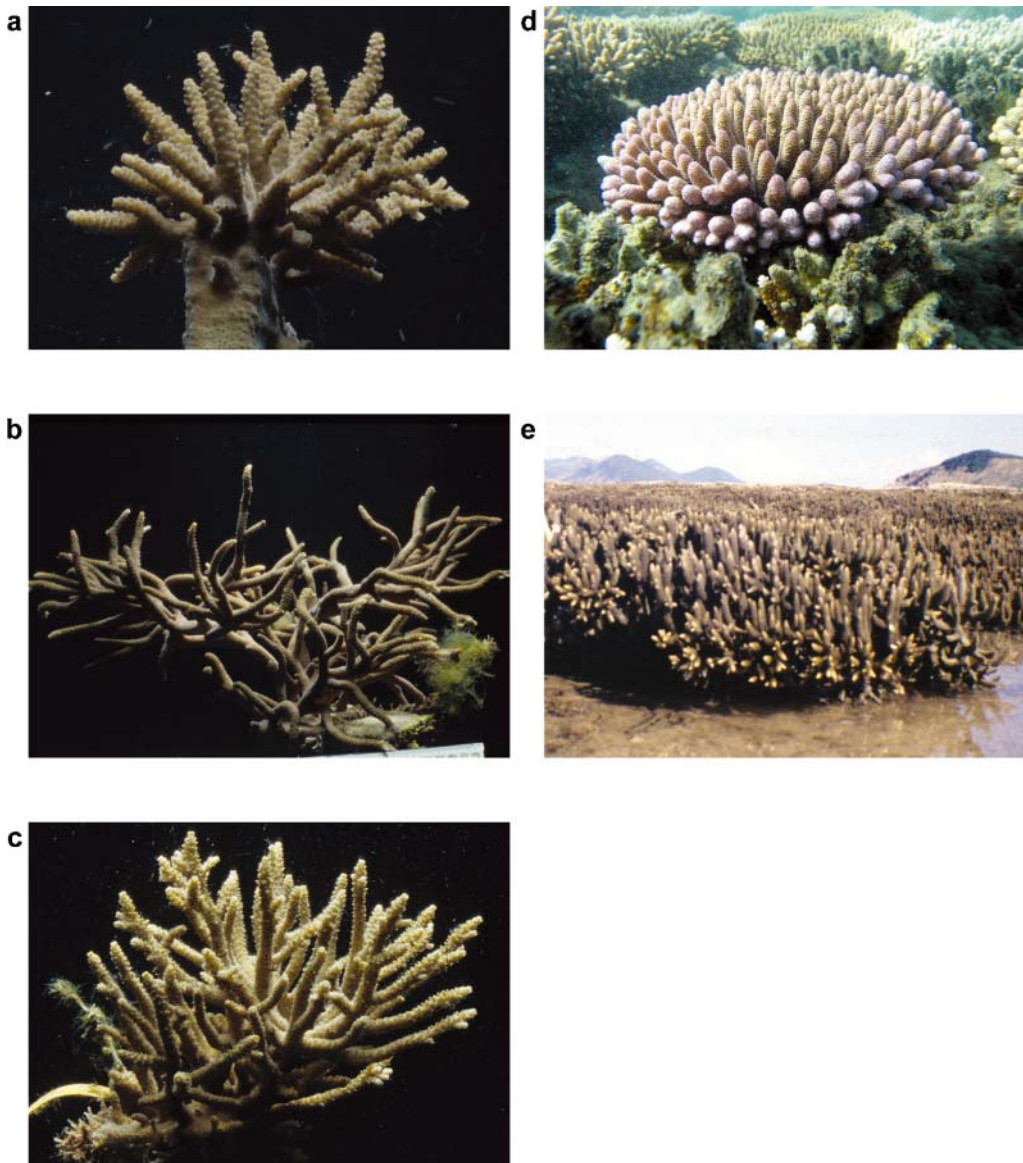
Figure 2

Three-year-old coral offspring produced from experimental crosses demonstrate that coral
hybrids are developmentally competent. (*a*) *Acropora millepora* purebred juvenile; (*b*) *A. pulchra*
purebred juvenile; (*c*) *A. pulchra* (mother) × *A. millepora* (father) hybrid juvenile; (*d*) adult *A.
millepora* showing typical corymbose (pillow) morphology and subtidal, reef-slope habitat; and
(*e*) adult *A. pulchra* showing typical arborescent (branching) morphology and intertidal,
reef-flat habitat. Offspring were reared in flow-through tanks at Orpheus Island Research
Station, Central Great Barrier Reef, but died in a bleaching event before reproductive
competency could be assessed.

a

b

of *A. pulchra* survived best on the inner reef flat and reef crest, which are the habitats to which it is largely restricted as an adult. Moreover, *A. pulchra* offspring grew fastest on the inner reef flat (**Figure 3**), where the species is most abundant and typically forms monospecific stands. There was a trend toward poorest survival of *A. millepora* offspring in the intertidal reef-flat habitat, where adults are typically not found, although their growth in the first three months was not markedly different among the three habitats. Interestingly, patterns of hybrid offspring survival and growth were most similar to those of *A. pulchra*. Hybrids grew faster than *A. millepora* on the inner reef flat (**Figure 3a**) and also survived better there and on the reef crest than on the reef slope. Although results for F_2-generation hybrids are unknown, results for F_1 hybrids are consistent with a review of hybrid fitness by Arnold & Hodges (1995), who found that existing evidence does not support a general pattern of reduced hybrid fitness and concluded that the role of hybridization in the process of evolutionary diversification has been underestimated. The greater growth and survival of hybrids in the more environmentally variable reef-flat and reef-crest habitats suggest a potential role for hybrids in providing a source of variation for adaptation to new or extreme environments.

In summary, there are few apparent pre- or postzygotic isolating mechanisms that would preclude hybridization from contributing to the evolutionary diversification of at least some of the Indo-Pacific mass-spawning *Acropora*, particularly when mating opportunities with conspecifics are scarce. However, parallel studies suggest that hybridization has played a different role in the evolution of the dominant Caribbean coral genera. Within the Caribbean *Acropora*, it has been suggested that postzygotic selection against hybrid genotypes (reviewed below) may be acting as a strong filter against genetic mixing and hence the potential for further evolutionary diversification among the three Caribbean species (Vollmer & Palumbi 2002). Similarly, a variety of mechanisms acting in concert are thought to render hybridization among the three species in the *Montastraea* complex unlikely in Panama (Levitan et al. 2004), although it appears to have played a greater role in the Bahamas (Fukami et al. 2004). Studies of the fitness of hybrid offspring would shed further light on the nature of postzygotic isolating mechanisms within these two Caribbean species complexes.

MOLECULAR EVIDENCE OF HYBRIDIZATION IN CORALS

Hybrid Origin of Coral Species in the Caribbean *Acropora*: *A. prolifera* Case Study

The only scleractinian coral known to be of hybrid origin, so far, is the Caribbean species *Acropora prolifera*. Three species of *Acropora* are known from the Caribbean, all of which are endemic: *A. cervicornis*, *A. palmata* and *A. prolifera* [collectively referred to as the *A. cervicornis* group (Wallace 1999)]. *A. cervicornis* and *A. palmata* are sister species with good fossil records, the earliest fossils being approximately 6.6 (Budd & Johnson 1999) and 3.6–2.6 (McNeill et al. 1997) Myr old respectively. In contrast, *A. prolifera* is of recent (Holocene) origin and has no fossil record (Budd et al. 1994). The three species are differentiated by colony growth form (**Figure 1b**) and habitat preference (Cairns 1982, Rützler & Macintyre 1982). *Acropora cervicornis* has an arborescent, staghorn morphology and occurs in comparatively sheltered fore- and back-reef habitats. *Acropora palmata* has a robust, elkhorn morphology and occurs primarily in more exposed, reef-crest habitats. The third described species, *Acropora prolifera*, has a fused-branched morphology that is intermediate between the two species, and has been further differentiated into co-occurring palmate and bushy morphs at one location (in Puerto Rico, Vollmer & Palumbi 2002). It is rarer than the other two Caribbean *Acropora* species and tends to occur in marginal, shallow-water, back-reef and reef-crest habitats that the other species do not occupy. All three species are sympatric throughout the Caribbean (Adey et al. 1977, Budd et al. 1994, Goreau 1959, Rützler & Macintyre 1982, Wallace 1999) and, although they generally occupy different reef zones, their depth distributions may overlap (Adey et al. 1977, Goreau 1959). Despite their distinct morphologies and ecological niches, the taxonomic status of these three species has been debated for over a century (Cairns 1982, Gregory 1895, Vaughan 1901, Wells 1973). The intermediate morphology of *A. prolifera* and the restriction of its distribution to reefs on which both *A. palmata* and *A. cervicornis* co-occur suggest that it may be a hybrid of the other two species.

The putative parent species, *Acropora palmata* and *A. cervicornis*, spawn synchronously once or twice a year in August and/or September (de Graaf et al. 1999, Szmant 1986; S.V. Vollmer, personal observation) and have compatible gametes in experimental crosses (B.L. Willis, unpublished data); thus opportunities for interspecific hybridization exist. Genetic data confirm that *A. prolifera* has indeed had a hybrid origin (van Oppen et al. 2000, Vollmer & Palumbi 2002). Allele frequencies of a nuclear intron (*PaxC* 46/47 intron) were significantly different between sympatric colonies of the parental species; *A. cervicornis* carried two alleles that were not present in *A. palmata* at a frequency of 0.769 and 0.039, respectively, confirming that they are distinct species (van Oppen et al. 2000). All colonies of *A. prolifera* were heterozygous for this locus, the expected outcome if two species with very distinct allele complements and frequencies (i.e., *A. palmata* and *A. cervicornis*) hybridize. Ribosomal DNA ITS sequence types were shared among all three species, confirming that *A. prolifera* is a hybrid between the other two species that backcrosses at low frequency. At two additional nuclear loci, all *A. prolifera* were also heterozygous for both species' alleles, indicating that *A. prolifera* colonies are most likely first generation (F_1) hybrids (Vollmer & Palumbi 2002, 2004). Moreover, maternally inherited mitochondrial DNA demonstrated that hybridization occurs in both directions (Vollmer & Palumbi 2002). Three mtDNA haplotypes were observed (A, B, and C), with haplotypes A and C occurring only in *A. cervicornis* and *A. prolifera*, whereas haplotype B occurs in all three species. Using phylogenies and Bayesian coalescent models, Vollmer & Palumbi (2002) demonstrated that backcrossing occurs with only one of the parental species, *A. cervicornis*, thereby passing genes from *A. palmata* to *A. cervicornis*. Even limited unidirectional flow of genes may represent a significant mechanism for evolutionary change (Mallet 2005), thus by providing a conduit for gene flow; *A. prolifera* may provide a mechanism for the acquisition of novel genes for at least one (*A. cervicornis*) of the Caribbean *Acropora*.

Interestingly, *A. prolifera* lacks a fossil record (Budd et al. 1994) suggesting that either hybridization between *A. palmata* and *A. cervicornis* is a relatively recent phenomenon or that environmental conditions have only recently favored survival of the hybrid *A. prolifera*. The current Caribbean-wide distribution of *A. prolifera* (Veron 2000, Wallace 1999) suggests that whatever triggers hybridization between its parental species has operated over a large geographic scale.

A Polyploid or Recombinational Hybrid Species?

Karyotype data for corals are few (Heyward 1985, Kenyon 1997); however, there is evidence of polyploidy in multiple species groups of Pacific *Acropora* (Kenyon 1997). In several scleractinian genera (*Acropora*, *Fungia*, *Gonipora*, *Lobophyllia*, and *Montipora*), the diploid chromosomal number is 28 (Heyward 1985, Kenyon 1997). Of 22 *Acropora* species sampled, 3 apparent cases of polyploidy were identified—*A. elseyi*, *A. ocellata*, and *A. valida*. The last of these 3 species is a probable triploid, whereas the others are likely tetraploids (Kenyon 1997). Without additional molecular or morphological data, it is not clear if these 3 species are allopolyploid hybrid species or autopolyploids (i.e., polyploids produced by the same species). However,

the number of polyploid species found in the single study and aforementioned evidence for hybridization implies the existence of polyploid hybrids among Indo-Pacific *Acropora* species and suggests that this phenomenon may not be uncommon among corals.

Although no karyotype data are yet available for the three Caribbean *Acropora*, *A. prolifera* is unlikely to be polyploid because hybrids never had more than two alleles at single copy nuclear loci (S.V. Vollmer, unpublished data). Although known to be of hybrid origin, it is unclear whether *A. prolifera* is reproductively isolated from its parent species. In laboratory crosses, *A. prolifera* is both self-fertile and cross-fertile with *A. cervicornis* (backcrosses with *A. palmata* have not yet been completed; S.V. Vollmer, unpublished data). However, genetic evidence showing limited one-way gene flow from *A. palmata* to *A. cervicornis* implies that hybrids backcross with *A. cervicornis* at only low levels (Vollmer & Palumbi 2002). Both lines of evidence suggest that *A. prolifera* is not reproductively isolated from *A. cervicornis*. Moreover, the fact that all colonies of the hybrid *A. prolifera* so far tested appear to be F_1 hybrids (Vollmer & Palumbi 2002) suggests that hybrids are not interbreeding at high frequency. Thus, the available genetic and reproductive evidence suggest that *A. prolifera* is a hybrid and not a hybrid species.

Although *A. prolifera* may not strictly constitute a recombinational hybrid species, its ability to propagate clonally via asexual fragmentation allows these coral hybrids to persist locally, potentially over long periods of time (Vollmer & Palumbi 2002). The ability to persist through asexual propagation makes coral hybrids similar to clonal parthenogenic taxa (Miller & van Oppen 2003) that have been shown to be ecologically successful in a variety of animal groups (Bullini 1994, Vrijenhoek 1984). Indeed, *A. prolifera*, although generally rare, is most abundant in marginal and shallow water environments where neither of the parental species occurs (Cairns 1982; S.V. Vollmer, personal observation). Thus, these hybrids appear to be successful in an ecological niche that is distinct from that of the parent species. Similar habitat diversification is shown to be important in the evolution of plant hybrid species (Arnold 1997, Rieseberg et al. 2003). The recent detection of *A. prolifera*'s hybrid status raises the possibility that further molecular studies will reveal other coral morphospecies to be either hybrids or hybrid species that have diversified to occupy new habitats (Vollmer & Palumbi 2002). Recent evidence that the European temperate soft coral *Alcyonium hibernicum* harbors the ITS variants of two congeners, *A. coralloides* and *A.* sp. *M2*, and consequently is a hybrid of the two species (McFadden & Hutchinson 2004) supports this view. Despite its exclusively asexual mode of reproduction, *A. hibernicum* has a considerable distribution beyond the northern margins of the putative parent species' distributions, highlighting the potential role that hybrid lineages may have for range expansion beyond the limits of parental species' distributions. If climate change and other human-related pressures on Caribbean reefs continue at present levels or escalate, the survival of coral species may be increasingly dependent on their ability to colonize marginal habitats, highlighting the potentially increasing significance of hybrids and hybrid species.

Para- and Polyphyly in Molecular Phylogenies of Indo-Pacific Mass-Spawning Species of *Acropora*

In contrast to the low diversity of the Caribbean *Acropora*, there are more than 100 species of Indo-Pacific *Acropora* and up to 76 of these have been recorded from a single area (Wallace 1999). This complexity effectively precludes direct extrapolation of conclusions drawn on the basis of the much simpler, three-species Caribbean system to the Indo-Pacific *Acropora*. In particular, unlike the Caribbean fauna, there are no clear cases of species with morphologies intermediate between two putative parent species and, so far, molecular approaches have identified only two likely first- or early-generation hybrids (van Oppen et al. 2002, Wolstenholme 2004). The lack of obvious morphological hybrids may be partly explained by high levels of morphological variation within many coral species, which makes it difficult to locate species borders within morphological space, a prerequisite for distinguishing potential hybrids from intraspecific variation. Recently, however, morphs that have affinities to two species have been identified within the *A. humilis* group (Wolstenholme 2004, Wolstenholme et al. 2003). Evidence from molecular and reproductive studies suggests that species boundaries may be at various stages of formation among a group of five species and seven intermediate morphs and that some of this morphological variation may have arisen through hybridization (e.g., morphs intermediate between *A. digitifera* and *A. gemmifera;* Wolstenholme 2004). In contrast to the Caribbean, where opportunities for hybridization are limited to two species, in the Indo-Pacific, introgression between any pair of species can theoretically occur through backcrossing with a range of other species (and intermediate morphs). The high number of potentially interbreeding species, combined with intraspecific morphological variation, poses difficulties for unraveling molecular phylogenies within the Indo-Pacific *Acropora*.

Ribosomal DNA ITS phylogenies for Indo-Pacific *Acropora* spp. are consistent with interspecific hybridization and introgression in that they show sharing of highly divergent sequence types between a wide range of species (Marquez et al. 2003, Odorico & Miller 1997, van Oppen et al. 2002). A divergence of more than 20% has been observed between ITS1-5.8S-ITS2 sequences within species and even within individual corals, while at the same time some sequence variants show high similarity between species. In the *A. aspera* species group, one species, *A. aspera*, differs at least in some years in the timing of gamete release and harbors mainly a distinct and unique ITS type (van Oppen et al. 2002). The other four species that have been examined in this group spawn simultaneously every year and also share ITS types, supporting the view that synchronized spawning has led to hybridization and the sharing of ITS types. Furthermore, there is some evidence that some *A. pulchra* individuals may be recent generation hybrids (van Oppen et al. 2002). As ITS homogenization may proceed extremely slowly when divergent sequence types are combined in a single genome (Modrich & Lahue 1996), rDNA data cannot readily distinguish between ancient or recent hybridization events. Incomplete lineage sorting may further mimic hybridization signatures (Vollmer & Palumbi 2004). Nevertheless, phylogenies based on single-copy nuclear DNA (scnDNA) and mtDNA are broadly consistent with the rDNA analyses, also showing extended para- and polyphyly of a wide range of species

and resolving *A. aspera* from other members of the *A. aspera* species group (Hatta et al. 1999, van Oppen et al. 2001).

Within the *A. humilis* group, sequence data from the partial nuclear ribosomal large subunit DNA regions and the mitochondrial control region suggest that sequence types are shared between some species through occasional introgression without disrupting morphological boundaries (Wolstenholme 2004, Wolstenholme et al. 2003). Morphs intermediate between true species are possibly of hybrid origin based on fertilization tests, their morphological affinities, and their phylogenetic position in molecular phylogenies (Wolstenholme 2004, Wolstenholme et al. 2003). Paraphyly has also been observed for several other *Acropora* species at scnDNA and mtDNA markers (Hatta et al. 1999, Márquez et al. 2002b, van Oppen et al. 2001). In addition, some aspects of mtDNA and scnDNA phylogenies are inconsistent. Such patterns could be explained by interspecific hybridization and introgression, incomplete lineage sorting (i.e., shared ancestral polymorphism), or a combination of both. Two lines of evidence, however, lead us to believe that hybridization is at least partly responsible. First, as enumerated above, many mass-spawning species of Indo-Pacific *Acropora* are capable of successful cross-fertilization (Fukami et al. 2003, Hatta et al. 1999, van Oppen et al. 2002, Willis et al. 1997), and second, the genetic distinctiveness of a nominal species appears to be directly correlated with the extent of temporal or other reproductive barriers (Fukami et al. 2003, van Oppen et al. 2001, 2002, Wolstenholme 2004), with species having the most effective temporal isolating mechanisms containing distinct rDNA ITS1 variants, scnDNA alleles, and mtDNA haplotypes. For example, *A. donei* and *A. yongei* in Japan, which spawn 1–3 hours before other sympatric species, constitute a genetically distinct cluster based on *Mini-C* intron 2 sequences (Fukami et al. 2003, Hatta et al. 1999). *A. digitifera* on the GBR, which spawns three months after the main mass-spawning event, constitutes a separate clade from the other four species in the *A. humilis* group based on analyses of the mtDNA intergenic region (Wolstenholme 2004). Spawning of *A. yongei* in the central GBR was correctly inferred to coincide with that of *A. tenuis*, which similarly spawns 2–3 hours before congeners (Babcock et al. 1986) based on its phylogenetic position in the *PaxC* intron and control region trees (M.J.H. van Oppen, B.L. Willis, D.J. Miller, unpublished data). Moreover, ITS diversity correlates with the permeability of isolating mechanisms; ITS1 variability within and between most Indo-Pacific *Acropora* species is much higher than that observed among the three-species Caribbean *A. cervicornis* group. Thus, ITS1 p-distances range from 0% to ~13% in the *A. cervicornis* group, but are up to four times greater in the Indo-Pacific *A. aspera* group. *A. tenuis* has even lower ITS1 diversity (0–5.3%; M.J.H. van Oppen, unpublished data) and is genetically distinct based on scnDNA and mtDNA, which is consistent with its earlier spawning time and low interspecies fertilization success in vitro (Babcock et al. 1986, Willis et al. 1997). Similarly, *A. latistella* typically (but not always) spawns two weeks out of phase with most congeners (Babcock et al. 1986, Willis et al. 1985), and this species as well as *A. aspera* (which may spawn earlier than the mass spawning) both form distinct clusters in the molecular analyses. Thus transient reproductive barriers imposed by year-to-year variation in the lunar night of spawning may also contribute to the relative genetic distinction of *Acropora* species. In summary, a clear

pattern linking lack of temporal barriers to breeding with nonmonophyly in molecular phylogenies helps to build the case that hybridization has contributed to the evolution of the mass-spawning, Indo-Pacific *Acropora*.

Population Genetic Approaches Show that Some Nonmonophyletic Species are Genetically Distinct

Molecular phylogenies are extremely powerful tools for identifying likely cases of natural hybridization, but additional approaches are required to corroborate the occurrence and extent of introgressive hybridization. Although allele sharing in phylogenetic trees of the Indo-Pacific *Acropora* is strongly indicative of natural hybridization and introgression within the genus, such evidence alone cannot distinguish occasional hybridization between true species from the existence of a single, morphologically polymorphic species or from cases of incomplete lineage sorting. Because differences in allele frequencies occur more rapidly than mutational changes underlying phylogenetic analyses, population genetic approaches provide further insights into whether closely related cross-fertile species share the same gene pool or are connected through limited hybridization and introgression.

Population genetic studies of two corals, *A. cytherea* and *A. hyacinthus*, which have highest interspecific fertility in experimental crosses (Willis et al. 1997) and share alleles extensively in phylogenetic analyses (Márquez et al. 2002b), demonstrate that these two taxa do not represent a single morphologically plastic species (Márquez et al. 2002a). Although very low, levels of genetic differentiation between these two species in sympatry were significant at eight polymorphic allozyme loci. Higher levels of gene flow between conspecific, widely allopatric (eastern versus western Australian) populations of these species in comparison to interspecific gene flow between them in sympatry support the conclusion that *A. cytherea* and *A. hyacinthus* constitute distinct entities (Márquez et al. 2002a). The question of whether incomplete lineage sorting is responsible for the small genetic divergences is more difficult to address. Based on the absence of a fossil record for either *A. cytherea* or *A. hyacinthus* prior to the Pleistocene (Wallace 1999), both species are assumed to be of relatively recent origin. The lack of fixed allelic differences and low allele frequency differences between these two species are both consistent with natural hybridization and introgression (i.e., interspecific gene flow following secondary contact) occurring infrequently, but could also be explained by them being incipient species with incomplete reproductive barriers and retention of ancestral polymorphisms (Márquez et al. 2002b).

Low, but distinct genetic differentiation in population genetic studies of the *A. nasuta* group (MacKenzie 2005) provides a second example of infrequent hybridization events potentially contributing to the evolution of species in the Indo-Pacific *Acropora*. Three species in this group, *A. nasuta*, *A. valida*, and *A. secale*, showed highly significant indices of pairwise genetic differentiation, both in sympatry and in allopatry (F_{st} values based on two nuclear introns and one microsatellite locus ranged from 0.08–0.09, 0.24–0.37, and 0.38–0.42 between *A. secale* and *A. valida*, *A. nasuta* and *A. valida*, and *A. nasuta* and *A. secale*, respectively) (MacKenzie 2005). Of the three species studied, two (*A. nasuta* and *A. valida*) were included in the *PaxC* intron phylogeny (van Oppen et al. 2001) and showed para- and polyphyly, respectively.

These examples illustrate that nominal *Acropora* species constitute genetically distinct entities, some of which are likely to exchange genes with congeneric species (as recognized within the current taxonomic framework; Wallace 1999) at low frequencies through introgressive hybridization. Thus, although no-choice cross-fertilization trials demonstrate mating compatibilities (Hatta et al. 1999, Miller & Babcock 1997, Szmant et al. 1997, van Oppen et al. 2002, Willis et al. 1997), sperm-choice trials are a much better predictor of the extent of hybridization occurring under natural conditions, where eggs are exposed to complex mixtures of con- and heterospecific sperm that compete to fertilize eggs. Nevertheless, even rare hybridization events on ecological timescales are likely to be significant on evolutionary timescales.

Hybridization in Other Mass-Spawning and Brooding Corals

There have been few genetic studies of mating systems in other mass-spawning coral genera on Indo-Pacific reefs, but the one study that has explored the potential for hybridization in a nonacroporid coral found evidence of extensive interspecific breeding. The genus *Platygyra* (Faviidae) on the GBR comprises seven recognized morphospecies, and estimates of pairwise genetic differences among species based on allozymes are low (Miller & Benzie 1997). Although corroborative evidence from additional molecular markers is required, low allozyme divergence (Nei's D range from 0.032 to 0.057) combined with the fact that the species show overlap in spawning times and are reproductively compatible in experimental breeding trials (Miller & Babcock 1997) suggest that introgressive hybridization has also played a role in the evolution of this genus. In contrast to the Indo-Pacific *Acropora*, however, natural hybridization may be operating to homogenize morphospecies within the *Platygyra*. Alternatively, recent speciation has occurred with or without ongoing hybridization (Miller & Benzie 1997).

Molecular studies of Caribbean species in the genus *Madracis* suggest that hybridization may also occur among brooding corals. Mixed paraphyly and site-specific polymorphisms, including additivity at nine sites, were interpreted as provisional evidence of hybridization among *M. decactis*, *M. pharensis*, and *M. formosa* (Diekmann et al. 2001). Interestingly, a recent allozyme study in the Indo-Pacific of two brooding scleractinian corals, *Pocillopora damicornis* and *Stylophora pistillata*, at the edge of their ranges on high latitude reefs of Lord Howe Island (beyond the southern extremity of the GBR), revealed a small proportion of apparently introgressed hybrids (Miller & Ayre 2004). Such hybridization among brooding coral species may yet prove to be as widespread as for mass-spawning species. Alternatively, such events may be more prevalent in areas such as Lord Howe Island, where conspecific sperm may occur at unusually low densities.

COMPARATIVE BIOGEOGRAPHIC PATTERNS AND THE GEOGRAPHIC SCALE OF HYBRIDIZATION

Molecular studies reviewed in the above sections demonstrate that hybridization events have occurred throughout the evolutionary history of corals on both Caribbean and Indo-Pacific reefs; however, the frequency and outcomes of hybridization appear

to vary between the two regions and between genera. In the Indo-Pacific *Acropora*, allele and haplotype sharing indicate that hybridization occurs between many pairs of species on evolutionary timescales, but these hybridization events appear to be rare on ecological timescales. Because a few hybrids can provide a means for transferring alleles between species, even rare events on ecological timescales may represent a significant mechanism for evolutionary change (Mallet 2005). Such events may have contributed significantly to adaptive radiation of the Indo-Pacific *Acropora*, particularly as they colonized new shallow-water habitats on continental shelves following frequent sea-level transgressions during the Pleistocene (Veron 1995). In contrast, hybridization between two of the three Caribbean *Acropora* species appears to be common, resulting in a hybrid that is recognized as the separate morphospecies, *A. prolifera*, although the outcome of hybridization appears to be limited to the production of F_1 hybrids. One factor that may contribute significantly to apparent differences in the frequency of hybridization is the comparative species richness of these two biogeographic regions. In the Caribbean, there are only three species within the genus *Acropora* and the coral fauna overall is quite small; around 30 scleractinian genera are present (Veron 2000), but each characteristically contains few species. This contrasts markedly with the Indo-Pacific fauna, where there are more than 100 species of *Acropora* and more than 80 genera overall (Veron 2000). When many congeneric species spawn simultaneously in sympatry, there may be stronger selection for efficient gamete recognition, whereas in locations where gametes of fewer species have an opportunity to interact, selection may be less stringent. However, as discussed above, even on Indo-Pacific reefs, isolating mechanisms are not absolute; many species of *Acropora* retain options for opportunistic interspecific mating.

Limited evidence suggests that there may also be variation in the frequency of hybridization within biogeographic regions. Hybridization appears to be more frequent at the edges of some coral species' distributional ranges, for example, at the northern periphery of the distribution of the Caribbean genus *Montastraea* (Fukami et al. 2004). There is also limited evidence of intergeneric hybridization between *Pocillopora* and *Stylophora* at the southern extremity of their ranges on the GBR (Miller & Ayre 2004). In such peripheral locations, densities of mates are likely to be low, few species are present, and hybrids may be able to exploit nonparental niches, as shown for plant species (Lexer et al. 2003, Rieseberg et al. 2003).

The broad geographic scales over which corals interact through introgressive hybridization are unparalleled in terrestrial animal groups. The distribution of the coral hybrid *Acropora prolifera* throughout the Caribbean (Veron 2000, Wallace 1999) suggests that hybridization occurs over the entire biogeographic ranges of the two parental species, *A. palmata* and *A. cervicornis*. Similarly, species of Indo-Pacific *Acropora* are sympatric over hundreds to thousands of kilometers and have consistent patterns of low interspecific gene flow on both the eastern and western coasts of Australia (Márquez et al. 2002a). Other pairs of *Acropora* species have a reticulate evolutionary history on reefs in Japan (Hatta et al. 1999). Interbreeding on this scale differs radically from the norm for terrestrial animals, where hybrid zones are usually narrow and maintained by a balance between dispersal and selection (reviewed in Arnold 1997, Barton & Hewitt 1985). Although concepts of hybrid zones have

expanded to encompass mosaic hybrid zones and attention is now focusing on geographical distributions of genealogical lineages (reviewed in Hewitt 2001), in general, animal hybrids have been assumed to be limited to contact zones where neither parent species is particularly fit. The closest parallels to potential geographic scales of hybridization among corals are found in plants. For example, oak species in the genus *Quercus* in the eastern United States (Whittemore & Schaal 1991) and *Eucalyptus* species in Australia (Potts & Reid 1988) are accepted as syngameons of interbreeding species across broad distributional ranges. Recent evidence that hybridizing species of coral reef fish are also broadly sympatric but ecologically partitioned by reef habitat (van Herwerden et al. 2006) suggests that broad scales of interbreeding may not be uncommon among broadcast-spawning animals.

SPECIES CONCEPTS FOR HYBRIDIZING CORALS

Coral species are traditionally recognized on the basis of morphological characters, particularly skeletal structures, but evolutionary relationships implied by morphology are not always reflected in molecular phylogenies (Fukami et al. 2004, van Oppen et al. 2001, Wolstenholme et al. 2003). Different rates of evolution for morphological and molecular characters (Wolstenholme et al. 2003), phenotypic plasticity, and convergent evolution may partly explain these mismatches, but reticulate evolutionary relationships detected among mass-spawning corals of Indo-Pacific *Acropora* (Hatta et al. 1999; van Oppen et al. 2001, 2002) are also likely to have contributed, particularly in cases of closely related species that interbreed. Regardless of such mismatches, it is clear that discrete coral species with distinct ecological characteristics do exist and define stable and cohesive entities despite occasional interspecific gene flow (Márquez et al. 2002a, Miller & Babcock 1997, Wolstenholme et al. 2003, as described above for *A. millepora* and *A. pulchra*).

Examples of interspecific gene exchange occurring between corals that are nonetheless morphologically and ecologically distinct suggest that, just as in plants, cohesive mechanisms override occasional gene flow to maintain recognizable species boundaries. Spatial heterogeneity on reefs, particularly as caused by steep environmental gradients (e.g., light, hydrodynamic and exposure gradients with depth), leads to dramatically different habitats over scales measured in tens of meters and provides a mechanism by which disruptive selection could maintain morphologically discrete taxa with distinct physiological requirements over distances small enough to allow mixing of gametes. Thus, even when adults of mass-spawning species differ in their benthic habitats along depth-defined environmental gradients, gametes from these species are able to interact and fertilize at the sea surface, continually renewing the potential for interspecific gene flow. Disruptive selection combined with disjunction between the benthic habitat of adults and the sea surface location of fertilization may partly explain how well-defined morphological and ecological coral species persist while maintaining opportunities for some interspecific gene flow.

Because many coral species share genetic variation with closely related species, phylogenetic species concepts based on species monophyly (e.g., Baum & Shaw 1995, Cracraft 1989) should not be applied to corals, especially because genes can have

different histories of separation and gene flow (e.g., within the Caribbean *Acropora*; Vollmer & Palumbi 2002). A more appropriate species concept for corals is one that embodies the spirit of the biological species concept (sensu Dobzansky 1937, Mayr 1963) in which species are viewed as entities that are effectively reproductively isolated from other such groups (i.e., the cohesion species concept of Templeton 1989), but acknowledges that complete reproductive isolation among species does not reflect biological reality. The approach of plant biologists, who have always tolerated a degree of hybridization among well-defined species (sensu Grant 1981, Rieseberg 1997), is particularly relevant to coral species. Similarly, the botanically derived concept of a syngameon (Grant 1981), which links species that are capable of interbreeding and exchanging genes in a reproductive community, usefully describes many groups of closely related coral species. The possession of a mating system that tolerates and potentially takes advantage of a degree of interspecific gene exchange adds a new dimension to the similarities between the life histories of corals and plants. In view of this, delimiting good coral species requires multiple lines of evidence (e.g., as for the Caribbean *Montastraea* and Indo-Pacific *Acropora*) to interpret how sometimes contradictory morphological, ecological, reproductive, and genetic characters best characterize cohesive coral species (Wallace & Willis 1994). Although the extent to which the consequences of gene flow are potentially adaptive versus negative requires further exploration, this propensity of corals adds to current understanding of the role of hybridization in animal speciation.

SIGNIFICANCE OF HYBRIDIZATION FOR TROPICAL CORAL SPECIES AND THE RESILIENCE OF CORAL REEFS

Tropical reef corals are facing a suite of challenges, the cumulative impact of which may jeopardize the persistence of some (e.g., Caribbean) coral reef ecosystems as they have been known in recent geological times. The threat of ocean warming is potentially catastrophic to animals that live within 1–2°C of their upper thermal limits (Hoegh-Guldberg 1999, Hughes et al. 2003). Moreover, exploitation of coral reef communities has disturbed their trophic balance, in some cases causing community phase shifts from coral- to algal-dominated reefs (Hughes et al. 2003). The unprecedented rise of coral disease on Caribbean reefs has decimated populations of the dominant framework-building corals in the genera *Acropora* and *Montastraea*, as well as major gorgonian species (Harvell et al. 2002). To respond to these challenges, coral species need a variety of mechanisms for rapid evolutionary change.

Hybridization events are an important source of raw material for rapid evolutionary change in a variety of plant and animal groups and also have the potential to facilitate adaptive radiation when new adaptive zones are invaded (Seehausen 2004). A study of Darwin's finches in the Galapagos Islands highlights the ability of hybrids to provide a rapid response to environmental change, in this case through novel beak morphologies when climatological changes abruptly reduced the seed types available (Grant & Grant 1996). Moreover, backcrossing facilitated the persistence of the parental species' genetic diversity when finches failed to breed successfully in pure-bred matings. Hybridization may also significantly increase resilience to novel disease

challenges. For example, hybrids of frog species arising through allopolyploid speciation had increased disease resistance to two different parasites that each infected one of the parent species (Jackson & Tinsley 2003). Similarly, hybrid parakeets had significantly higher measures of immune function than inbred parental species, through enrichment of depauperate gene pools (Tompkins et al. 2006). Such evidence that hybridization can mediate the response of species to rapid climatological change and the development of disease resistance highlights the potential significance hybridization may hold for the persistence of coral species, which face similar environmental challenges.

In conclusion, hybridization has contributed in diverse and significant ways to the evolution of coral species in the ecologically prominent Indo-Pacific *Acropora*, as well as to the major Caribbean framework-building genera *Montastraea* and *Acropora*. We assert that the evolutionary potential of hybridization is important to conserve, thus hybrids like *A. prolifera* represent important reservoirs of novel genetic diversity that may facilitate adaptive radiation under changed environmental circumstances. In addition, their ability to pass genes between species represents a potentially significant mechanism for rapid evolutionary change of parental species. As advocated by Ennos et al. (2005) in a recent review of conservation principles for taxonomically complex groups, efforts should be directed toward the conservation of evolutionary processes that generate such biodiversity rather than the current focus on the conservation of species, which are ambiguous entities in taxonomically complex groups. Recommendations against the need to protect hybridizing species because they fall outside the framework of conventional species definitions or are interpreted as jeopardizing the persistence of pure native species (e.g., Allendorf et al. 2001) ignore the dynamic nature of species and the potentially integral role that hybridization may play in the founding of lineages. Given the implications of ocean warming for increasing frequency and severity of mass bleaching events and emerging coral diseases, it is important to realize that hybridization has contributed to the evolutionary diversification of corals and that it has the potential to contribute significantly to the resilience of coral species and the coral reef ecosystem into the future. Conservation strategies that protect the evolutionary processes that have given rise to modern reef corals and are likely to contribute to their future resilience should be paramount.

SUMMARY POINTS

1. Hybridization has contributed to the evolution of many ecologically dominant and structurally important corals in diverse and significant ways.

2. Interspecific gamete compatibility in no-choice crosses and developmental competence of hybrids suggest there may be few absolute pre- or postzygotic barriers to interspecific breeding among many mass-spawning species of Indo-Pacific *Acropora*. However, in sperm choice experiments, conspecific matings take precedence, providing a mechanism for maintaining morphospecies boundaries when prezygotic barriers are semi-permeable.

3. Although decoupling of adult (benthic) and natal (sea surface) habitats in mass-spawning corals continually renews opportunities for hybridization, spatial heterogeneity and steep, depth-related environmental gradients on reefs provide a mechanism by which disruptive selection could also contribute to the maintainance of morphologically and ecologically discrete taxa despite occasional gene flow.

4. Juvenile coral hybrids are not less fit than purebreds, as indicated by comparative survival and growth in a large-scale grow-out program. Greater growth and survival of juvenile hybrids in environmentally variable and extreme habitats suggest a role for hybrids in adaptation to new environments.

5. In the Indo-Pacific, molecular phylogenies of mass-spawning species in the genus *Acropora* are consistent with reticulate evolutionary pathways. Although population genetic studies indicate hybridization events are rare on ecological timescales, on evolutionary timescales, they are likely to have facilitated adaptive radiations leading to their current high diversity.

6. In the comparatively depauperate Caribbean, molecular studies reveal that one of only three exant Atlantic *Acropora* species is a hybrid, providing a conduit for one-way gene flow from *A. palmata* to *A. cervicornis* and a mechanism for the introduction of novel genetic material.

7. The capacity of the hybrid *A. prolifera* to colonize marginal habitats distinct from its parent species and evidence of hybridization at geographical boundaries of the Caribbean *Montastraea* support an evolutionary role for hybridization in range expansion and adaptation to changing environments.

8. The distribution of the hybrid *A. prolifera* throughout the entire Caribbean ranges of its parent species highlights the broad geographic scales of hybridization possible in marine environments when the location of gamete interactions is spatially segregated from adult habitats. Such scales differ from the narrow hybrid zones typical of most animals and provide new insights into the process of hybridization in animal species evolution.

9. In combination, outcomes of hybridization are likely to be significant for the future resilience of reef corals, for example, by providing options for rapid response to changing environments and climatologies as well as increasing resilience to novel disease challenges. Hybridization warrants consideration when developing conservation strategies for reef corals.

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