INVITED REVIEW
A restoration genetics guide for coral reef conservation

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Abstract

Worldwide degradation of coral reef communities has prompted a surge in restoration efforts. They proceed largely without considering genetic factors because traditionally, coral populations have been regarded as open over large areas with little potential for local adaptation. Since, biophysical and molecular studies indicated that most populations are closed over shorter time and smaller spatial scales. Thus, it is justified to re-examine the potential for site adaptation in corals. There is ample evidence for differentiated populations, inbreeding, asexual reproduction and the occurrence of ecotypes, factors that may facilitate local adaptation. Discovery of widespread local adaptation would influence coral restoration projects mainly with regard to the physical and evolutionary distance from the source wild and/or captive bred propagules may be moved without causing a loss of fitness in the restored population. Proposed causes for loss of fitness as a result of (plant) restoration efforts include founder effects, genetic swamping, inbreeding and/or outbreeding depression. Direct evidence for any of these processes is scarce in reef corals due to a lack of model species that allow for testing over multiple generations and the separation of the relative contributions of algal symbionts and their coral hosts to the overall performance of the coral colony. This gap in our knowledge may be closed by employing novel population genetic and genomics approaches. The use of molecular tools may aid managers in the selection of appropriate propagule sources, guide spatial arrangement of transplants, and help in assessing the success of coral restoration projects by tracking the performance of transplants, thereby generating important data for future coral reef conservation and restoration projects.

Keywords: ecotypes, genotypic diversity, inbreeding, outbreeding depression, transplant, zooxanthellae

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Introduction

Unsurprisingly, high human population densities on the world's tropical shores and changing environmental conditions have had a significant and detrimental impact on coral reef systems (Pandolfi *et al.* 2003). Yet, reefs deserve protection. They are highly diverse (Reaka-Kudla 1997) and provide important services to local and national economies (reviewed in Cesar 2000). Next to reducing fishing pressure, conservation efforts target hermatypic corals because of their role as structural species of reefs (*sensu* Connell *et al.* 1997) and their narrow tolerance to warming seawater temperatures (Glynn 1991; Graham *et al.* 2006).

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Corals resemble long-lived trees in many aspects: adults are site-attached yet species can be geographically widely distributed (Veron 1995), occur over steep elevation gradients (Sheppard 1982), be phenotypically variable (Smith *et al.* 2007), and they display a fascinating variety of reproductive and growth strategies (Table 1) (Harrison & Wallace 1990; Fautin 2002). Sexual larvae are produced by hermaphroditic or gonochoric parents via internal or external fertilization. Time larvae spent in the plankton ranges from minutes to several months and, as a result, dispersal distances extend from centimetres to thousands of kilometres (Carlon & Olson 1993; Ayre & Hughes 2000; Harii *et al.* 2002). Just as varied are the ways in which corals reproduce asexually including fragmentation and production of unfertilized larvae (Table 2) (Tunnicliffe 1981; Ayre & Resing 1986). Hence, clonal structure of local populations is often

Table 1 Contribution of inbreeding and asexual reproduction to population structure of scleractinian corals as assessed by molecular methods. The probability of identity (P_{ID}) gives an indication of how likely a novel genet was mistaken for a ramet of an existing genet: *A. palmata* = 1.4×10^{-7} (Baums *et al.* 2006a), *M. annularis* = 6.6×10^{-6} (Foster *et al.* 2007), *S. hystrix* = 2.1×10^{-6} (Ref 9). Alloz. = allozyme. Msat = microsatellite markers. MtDNA = mitochondrial DNA. F_{IS} = inbreeding coefficient. *Ds = Solander's Ds. F_{IS} w/out clones: F_{IS} was or was not estimated after excluding repetitive multilocus genotypes. Reproductive mode (M): BR = brooder, BC = Broadcaster. Pop = population, PR = Puerto Rico, FK = Florida Keys, MX = Mexico, OTI = One Tree Island. Sign. = significant. N/A = not available. $ = Standard Error

Species	Marker	# loci	Location	Pop	Samples (N)	Scale (km)	F_{IS}	Range (^ SD)	Sign.	F_{IS} w/out clones	N_g/N	Range	G_o/G_e	Range	M	Ref (N)
Caribbean																
Acropora cervicornis	Nuclear, mtDNA	4	Caribbean	22	276	2500	N/A				0.58	0.25–1.00	N/A		BC	1
Acropora palmata	Msat	5	Caribbean	20	1300	2500	–0.00	(–0.03)–0.03	No	Yes	0.52	0.05–1.00	0.34	0.05–1.00	BC	2,3
Montastraea annularis	Msat	10	PR, FK, MX	5	127	1200	0.26	0.15–0.37	Yes	N/A	0.90	0.84–1.00	N/A		BC	4
...	Msat, nuclear	4	Honduras	3	146	3	0.00	(–0.01)–0.03	No	Yes	0.82	0.67–0.92	N/A		BC	5
Montastraea faveolata	Msat, nuclear	10	PR, FK, MX	5	152	1200	0.24	0.15–0.40	Yes	N/A	0.95	0.93–1.00	N/A		BC	4
Indian																
Pocillopora verrucosa	Alloz.	5	S Africa	6	256	70	0.49	0.28–0.68	N/A	No	0.65	0.55–0.81	0.64	0.52–0.79	BR	6
Pacific																
Acropora aspera	Alloz.	6	W Australia	4	244	200	–0.46*	(–0.38)–(–0.54)	Yes		0.80	0.53–0.96	N/A		BC	7
Acropora cuneata	Alloz.	N/A	GBR	3	409	1200	0.27	0.07^	Yes	No	0.40	0.20–0.63	0.91	0.66–1.14	BR	8
Acropora cytherea	Alloz.	N/A	GBR	3	440	1200	0.13	0.05^	Yes	No	0.71	0.45–0.82	0.87	0.70–1.07	BC	8
Acropora digitifera	Alloz.	6	W Australia	6	341	200	–0.35*	(–0.28)–(–0.39)	Yes		0.77	0.56–0.91	N/A		BC	7
Acropora hyacinthus	Alloz.	N/A	GBR	3	438	1200	0.25	0.11^	Yes	No	0.49	0.36–0.63	0.94	0.78–1.20	BC	8
Acropora millepora	Alloz.	4	GBR	3	435	1200	0.37	0.11^	Yes	No	0.63	0.33–0.78	0.71	0.17–1.16	BC	8
Acropora nasuta	Msat, nuclear	3	GBR	4	216	500	0.31	0.02–0.48	N/A	N/A	0.82	0.69–1.00	N/A		BC	9
Acropora palifera	Alloz.	6	Australia	6	299	2	0.20	(–0.03)–0.41	Yes		0.47	0.40–0.64	0.93	0.68–1.15	BR	10
....	Alloz.	N/A	GBR	3	423	1200	0.22	0.05^	Yes	No	0.64	0.45–0.80	1.02	0.71–1.17	BR	8
Acropora valida	Alloz.	5	GBR	3	398	1200	0.35	0.16^	Yes	No	0.26	0.10–0.49	0.49	0.20–1.01	BC	8
Fungia fungites	Alloz	7	W Australia	2	120	5	0.57	0.018$	N/A	No	N/A	0.40–1.00	N/A	N/A		11
Goniastrea aspera	Alloz.	5	Japan	8	374	500	0.22	(–0.01)–0.46	N/A	No	0.90	0.82–1.00	0.84	0.68–1.00	BR/BC	12
Goniastrea favulus	Alloz.	2	GBR	2	N/A	N/A	0.13	0.11–0.14	No		N/A		N/A		BC	13
Mycedium elephantotus	Alloz.	7	Taiwan	3	90	370	0.23	0.16–0.33	N/A	No	0.98	0.96–1.00	0.94	0.90–1.00	BC	14
Pavona cactus	Alloz.	4	GBR	9	119	10	N/A		N/A	No	0.35	0.03–0.94	0.35	0.00–0.90	BC	15
Pocillopora damicornis	Alloz.	7	Australia, OTI	2	238	10 s	0.30	0.14–0.41	N/A	No	0.83	0.69–0.90	0.85	0.72–1.03	BR/BC	16
...	Alloz.	4	Hawaii	8	N/A	N/A	N/A				0.24	0.09–0.35	N/A		BR/BC	17
...	Alloz.	6	Australia	9	443	2	0.03	(–0.02)–0.15	No	No	0.89	0.81–0.96	0.91	0.72–1.03	BR/BC	10
...	Alloz.	4	W Australia	25	N/A	450	0.17*	0.15	No	Yes	0.40	0.15–0.75	0.27	0.09–0.61	BR/BC	18
...	Alloz.	N/A	GBR	3	407	1200	0.28	0.17^	Yes	No	0.80	0.54–0.96	0.88	0.63–1.10	BR	8
...	Alloz.	7	Australia, Lord Howe	7	285	20	0.16	(–0.03)–0.55	N/A	No	0.74	0.58–0.93	0.75	0.61–1.02	BR/BC	19
Pocillopora meandrina	Msat	4	S Pacific	32	1012	2000	0.17	0.07–0.23	N/A		1	N/A	N/A	N/A	BC	20
Porites compressa	Alloz.	7	Hawaii	6	269	300	N/A		N/A		0.85		0.79		BC	21
Seriatopora hystrix	Msat	9	NW Australia	6	284	60	0.22	0.14–0.29	Yes	Yes	0.99		N/A		BR	22
...	Alloz.	7	GBR	3	408	1200	0.51	0.1^	Yes	No	0.49	0.18–0.85	0.70	0.44–1.17	BR	8
...	Alloz.	9	GBR	12	2180	90	0.23	(–0.22)–0.59	Yes	No	0.60	0.14–0.98	0.75	0.18–1.21	BR	23
Styllophora pistillata	Alloz.	N/A	GBR	3	411	1200	0.17	0.03^	Yes	No	0.46	0.27–0.64	0.98	0.86–1.17	BR	8

References: (1) Vollmer & Palumbi 2007; (2) Baums *et al.* 2005; (3) Baums *et al.* 2006a; (4) Severance & Karl 2006; (5) Foster *et al.* 2007; (6) Ridgway *et al.* 2001; (7) Whitaker 2004; (8) Ayre & Hughes 2000; (9) Mackenzie *et al.* 2004; (10) Benzie *et al.* 1995; (11) Gilmour 2002; (12) Nishikawa & Sakai 2003; (13) Stoddart *et al.* 1988; (14) Dai *et al.* 2000; (15) Ayre & Willis 1988; (16) Ayre & Miller 2004; (17) Stoddart 1983; (18) Stoddart (1984b); (19) Miller & Ayre 2004; (20) Magalon *et al.* 2005; (21) Hunter 1993; (22) Underwood *et al.* 2007; (23) Ayre & Dufty (1994).

Table 2 Selfing estimates for tropical scleractinian corals obtained by comparing the genotype of the offspring to the parental genotypes through the use of molecular methods. Mode: reproductive mode. BC = broadcaster, BR = brooder

Species	Marker	# loci	Locations	Pops (N)	Samples (N)	% selfing	Range	Mode	Ref
Acropora palifera	Allozymes	3	GBR	2	124	Low		BR	24
Acropora palifera	Allozymes	2	GBR	1	N/A	Low		BR	25
Acropora palmata	Msat	5	Caribbean	1	2281	Low	0.003–0.007	BC	2,3
Favia fragum	RAPDs	30	Florida	1	332	48.7	8.0–94.4	BR	26
Goniastrea favulus	Allozymes	2	GBR	2	N/A	50	0.35–0.78	BC	12
Porites asteroides	RAPDs	33	Florida	2	229	49.2	0.0–78.9	BR	26
Seriatopora hystrix	Allozymes	2	GBR	1	N/A	Low		BR	25
Tubastrea coccinea	Allozymes	2	GBR	1	N/A	100		BR	25
Tubastrea diaphana	Allozymes	2	GBR	1	N/A	100		BR	25

References: as in Table 1, (24) Ayre & Miller (2006); (25) Ayre & Resing (1986); (26) Gleason *et al.* (2001).

unknown and hard to predict (Baums *et al.* 2006a). In contrast to trees, scleractinian corals derive their nutrition mostly from algal symbionts, and these have varying degrees of host specificity (LaJeunesse 2002; Baker 2003). The coral–symbiont genotype interaction adds an additional layer of complication to the study of population structure, dispersal and adaptation of reef-building corals.

The time frame over which corals may adapt to current global warming is debated (Lasker & Coffroth 1999; Baker 2001; Hoegh-Guldberg *et al.* 2002; Reshef *et al.* 2006). Over the short-term, corals may adapt to changing environmental conditions by changing their algal symbionts (Baker 2001), or by changing bacterial communities living in their mucus layer (Reshef *et al.* 2006). The coral host may also develop resistance towards adverse conditions (e.g. emerging diseases) (Potts 1984b). Regardless of the time frame considered, against some man-made disturbances, such as dynamite fishing and ship groundings, adaptation responses seem unlikely. Thus, however adaptable the coral holobiont (the coral animal and its pro- and eukaryotic symbionts) may be towards changing environmental conditions, there will be a need for active restoration of disturbed reefs.

Reef restoration efforts are ongoing worldwide. Examples include securing fragments in place stemming from injured colonies (Bruckner & Bruckner 2001), rearing fragmented coral pieces in mid-water nurseries for outplanting on reefs (Amar & Rinkevich 2007), and 'rescuing' colonies from threatened inshore habitats by outplanting them to offshore sites (University of Florida 2007). How likely is it that these activities will achieve their goal of restoring reefs? Clearly, if the initial cause of population decline is not removed (e.g. rising temperatures, infectious disease outbreak), restored populations may meet the same fate as their predecessors. After cessation of short-lived physical disturbance (ship groundings, anchor damage), restoration is a sensible option. However, restoration monies could be wasted because transplanted colonies may be maladapted

to their new surroundings, sexual reproduction in restored stands may be compromised due to gametic incompatibility of genets, or diversity of associated fauna may be depressed due to low genotypic diversity of restored coral stands. To date, such genetic factors have received little attention during design and monitoring of reef restoration projects.

In contrast, during design of marine reserves, population genetic surveys of reef connectivity are routinely consulted. They are meant to inform the size and spacing of protected reefs to ensure that they are self-sustaining and possibly export propagules to neighbouring (fished) sites (Palumbi 2003). Why then do genetic considerations play a minor role in coral restoration projects?

Traditionally, coral populations have been regarded as open: their planktonic larvae seemed to convey high gene flow throughout their ranges (reviewed in Hellberg 2007) and opportunities for small-scale adaptation appeared to be limited (Warner 1997). The phenotypic plasticity of many coral species expressed over small spatial scales (sometimes metres) (e.g. Bruno & Edmunds 1997) reinforced the view of large, mixed populations and this was further substantiated by a lack of population structure in mitochondrial DNA surveys of coral populations (Hellberg 2006). Hence, there seemed to be a low risk of complications arising from site-adaptation during restoration projects.

Since, evidence for predominantly local recruitment of propagules over ecological time-scales has accumulated based on individual-based oceanographic dispersal models (e.g. Cowen *et al.* 2000, 2006). The development of nuclear genetic markers (allozymes, microsatellites and single-copy nuclear markers) revealed that variability of scleractinian nuclear DNA is on par with that found in sponges, coelenterates and plants (Table 3) (Solecava & Thorpe 1991; Cole 2003; Hellberg 2006). Even though these studies likely reflect past connectivity patterns (Pleistocene) rather then ongoing gene flow (reviewed in Benzie 1999; Hellberg 2007), evidence points towards closed populations over

Marker	Species	Ref	Loci	H_O	SD	H_E	SD
Alloz	*A. palifera*	10	5	0.26	0.03	0.29	0.02
	G. aspera	12	5	0.29	0.05	0.37	0.05
	M. elephantotus	14	7	0.25	0.08	0.34	0.11
	P. damicornis	10	5	0.47	0.02	0.49	0.03
	P. damicornis	19	8	0.23	0.04	0.27	0.03
	P. verrucosa	6	5	0.14	0.02	N/A	
	Mean		5.8	**0.27**	0.04	**0.35**	0.05
	Sponges and coelenterates (44 species)	27	15.5	**0.22**	0.10	**0.21**	0.10
	Plants (247 species)	28	17.8	**0.12**		**0.13**	
Msat	*A. palmata*	2	5	0.76	0.05	0.76	0.03
	M. annularis	5	4	0.54	0.10	0.54	0.10
	M. annularis	4	7	0.65	0.04	0.79	0.03
	M. faveolata	4	7	0.61	0.06	0.72	0.03
	P. meandrina	20	4	0.63	0.03	N/A	
	S. hystrix	22	9	0.30	0.09	0.42	0.12
	Mean		6.0	**0.58**	0.06	**0.65**	0.06
SCN	*M. annularis*	4	3	0.18	0.17	0.33	0.19
	M. faveolata	4	3	0.28	0.10	0.40	0.06
	Median		3.0	**0.23**		**0.37**	

Table 3 Heterozygosity of tropical scleractinian corals as estimated by allozymes (alloz), microsatellite (msat) and single copy nuclear (SCN) markers. Only studies that reported or allowed for calculation of observed (H_O) and expected heterozygosity (H_E) averaged over populations and markers are included. See Table 1 for sample sizes and study locations. SD = standard deviation.

References (Ref): as in Table 1, (27) Solecava & Thorpe (1991); (28) Cole (2003).

greatly reduced spatial scales from what was previously thought. It thus seems justified to reconsider the assumption of a general lack of local adaptation in reef-building corals, and evaluate potential consequences for the design of restoration studies.

Studies on adaptive genetic variation and studies of inbreeding and outbreeding depression in corals are lacking entirely mainly due to technical difficulties in developing molecular resources for corals. Instead, I examine the evidence for factors that may increase the potential for local adaptation including population structure and mating system of corals and suggest that site-adaptation in corals may be more common then previously thought. I then review possible consequences of this hypothesis on the design of restoration projects. Because plants show frequent site-adaptation (ecotypes) and share similar life-styles with corals, guidelines may be borrowed from plant restoration genetics although application of such recommendations is less than straightforward. While many plants have been domesticated, only a few coral species complete a full life cycle in captivity resulting in a lack of model species on which to test restoration strategies. Recommendations for plant restoration include the delineation of seed transfer zones within which propagules can be moved safely without resulting in a loss of fitness of the population or species. I review suggested causes for loss of fitness including founder effects, genetic swamping, inbreeding and/or outbreeding depression and then outline the limitation and benefits of utilizing molecular approaches in designing, implementing and assessing coral restoration projects.

Adaptation in scleractinian corals

Traditionally, common garden and reciprocal transplanting experiments have been employed to test for site adaptation in plants (Hufford & Mazer 2003) and corals (Potts 1984b; Edmunds 1994; Bruno *et al.* 1997; Baird *et al.* 2003; D'Croz & Mate 2004; Smith *et al.* 2007). Genets from environmentally different sites (e.g. shallow vs. deep or inshore vs. offshore) are reciprocally transplanted to test whether they perform equally well, worse than, or better than the genotypes found at that site. In parallel, genets may be transplanted to a third, novel environment to test how they perform relative to each other in a common environment.

As one might expect, studies on reef-building corals have found species with generalist genotypes (Smith *et al.* 2007), species that show site-adaptation (D'Croz & Mate 2004), and species that harbour both generalist and specialist genotypes (Potts 1984a; Vermeij *et al.* 2007). Several studies show local dominance of certain genets (Box 1, Hunter 1993; Baums *et al.* 2006a). For example, in wild *Pavona cactus* stands, some clones dominated intraspecific competitive interactions, better survived fragmentation and were more widespread than subordinate clones (Willis & Ayre 1985). Such studies have produced information on the performance of the specific combination of coral and zooxanthellate genotype present in the experimental units.

Adaptation response of the holobiont to changing conditions, specifically rising seawater temperatures, has mostly been attributed to the zooxanthellate partner. Functional differences exist among taxa of zooxanthellae (Chang *et al.* 1983; Warner *et al.* 1996; Iglesias-Prieto & Trench

1997; Loram *et al*. 2007) and host–symbiont associations change predictably over depth gradients (mostly in the Caribbean; Frade *et al*. 2008; LaJeunesse 2002; Warner *et al*. 2006). For example, *Montastraea* sp. colonies harbour A-, B- and D-type zooxanthellae in shallow water (< 6 m) and C-types in deeper water (Rowan & Knowlton 1995; Rowan *et al*. 1997). The level of specificity between host corals and dinoflagellate endosymbionts varies greatly (reviewed in Baker 2003). Some hosts associate with more than one clade, some choose specific symbionts. Conversely, some symbionts are specific to certain hosts while others are widely distributed. When environmental conditions change (most notably temperature), the symbiosis can break down (bleaching), sometimes causing widespread coral mortality (reviewed in Glynn 1991; Coles & Brown 2003). Bleaching threshold and severity depends on the specific partners involved (Lasker *et al*. 1984; Rowan *et al*. 1997; Glynn *et al*. 2001) and, after bleaching has occurred, different taxa of zooxanthellae might dominate the intracolonial symbiont community than before the disturbance (Baker 2001; Glynn *et al*. 2001). There has been considerable debate whether such changes in symbiont composition are adaptive (Baker 2001; Kinzie *et al*. 2001) and how long these changes persist after the disturbance had ended (Thornhill *et al*. 2006).

In principal, selection by higher water temperatures on the symbiosis could have several effects by favouring (i) already resistant strains of zooxanthellae; (ii) corals that harbour resistant strains; (iii) corals that can associate with new (to them) types of zooxanthellae; and/or (iv) coral colonies that are temperature resistant themselves. Synergistic effects are expected but the relative contribution of each partner to holobiont performance has never been measured.

Symbiont-free larvae often provide the only means of evaluating genet performance of the coral host alone (but see Grottoli *et al*. 2006). Experiments during the 2007 *Montastraea faveolata* spawning event in the Florida Keys revealed that azooxanthellate larvae from controlled crosses differed in their ability to survive captive rearing (Baums *et al*. unpublished data, Fig. 1) and settle in response
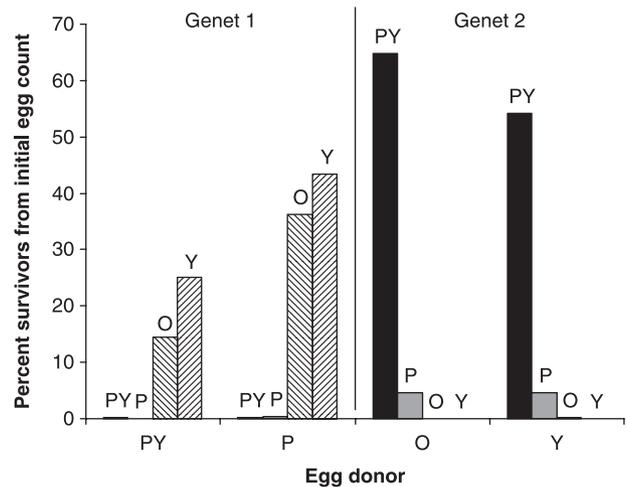

Fig. 1 Survivorship of *M. faveolata* larvae at day 4 from reciprocal crosses among four parent colonies belonging to two genets (genet 1: colonies PY and P, genet 2: colonies O and Y). Genet identity was confirmed by genotyping using published methods (Foster *et al*. 2007; Severance *et al*. 2004). Gametes were collected from hermaphroditic colonies on September 27, 2007 in the Florida Keys. Sperm and eggs were separated, washed repeatedly and their amounts adjusted to $6.1 \times 10^7 \pm 2 \times 10^7$ (SD) and $17\,358 \pm 3987$ (SD), respectively. After fertilization (one hour), embryos were raised in the laboratory where they underwent normal development. Selfing did not produce viable larvae beyond day 3 (e.g. PY × PY and PY × P). Survivorship of eggs depended on the genet (genet 2 produced more viable larvae) as well as on the colony (genet 2 eggs fertilized by sperm from colony P did not survive as well as genet 2 eggs fertilized by colony PY even though PY and P are clonemates). Further experiments are needed to confirm this surprising apparent differential investment in the sexes on the colony level (Baums and Miller, unpublished Data).

to settlement cues (algal extract, Miller *et al*. unpublished data). Furthermore, offspring from certain crosses outperformed larvae from a mix of all crosses (batch culture). This preliminary evidence justifies further study of adaptive variation attributable to the host alone.

Differential performance of coral colonies in varied environments implies that there may be sufficient inherited variability in advantageous traits (either of the host or symbionts) for selective breeding programs to improve the performance of the species in changing environmental conditions. While common in animal husbandry such a strategy seems unadvisable for wild species where the goal is to restore and conserve, not to improve (but see Harris *et al.* 2006 for the opposing argument). Conversely, this indicates that some genets may be maladapted for environments they may be transplanted to during restoration efforts.

Population structure and gene flow

Range-wide surveys of neutral genetic diversity in scleractinian corals provide evidence for the existence of subdivided populations that have experienced sufficiently restricted gene flow to accumulate differences. The scale over which population differentiation is observed ranges from 25 km to 7000 km and is not easily predictable. In general, evidence is mounting that substantial population differentiation exists for the majority of scleractinian corals (Van Oppen & Gates 2006). The reader is referred to recent thorough reviews on this subject (Van Oppen & Gates 2006; Hellberg 2007).

The above illustrates that there is at least some chance that local adaptation occurs in certain coral species. Plants, like corals, are site-attached, widely distributed, occur over steep environmental gradients and local adaptation is common. The similarities justify a closer look at plant restoration guidelines. These seek to minimize factors that could cause loss of fitness in restored populations such as founder effects, genetic swamping, inbreeding and outbreeding.

Founder effects, genetic swamping, inbreeding and outbreeding

Founder effect

Founder effects may occur in natural and captive populations when these populations are descendent from a limited number of individuals (bottleneck) (Wares *et al.* 2005). This may result from initial colonization of a new site in the wild, or the initiation of a breeding program with individuals that capture only a small portion of the natural diversity of the source population. The severity of a genetic bottleneck depends on population growth, the mating system, frequency of immigration and the initial genetic diversity (Hedrick 2000). Of these factors, coral restoration programs can directly influence initial genetic and genotypic diversity of repopulated areas, mostly through propagule selection. In seagrasses, poor initial genotypic diversity resulted in reduced population growth of

transplanted eelgrass (*Zostera marina*), prompting the recommendation that initial collections of eelgrass shoots should include a higher diversity of genotypes (Williams 2001).

Evidence for founder effects in marine organisms is equivocal but no studies on corals have been published (McQuaid 1996; Williams & Davis 1996; Andrew & Ward 1997; Planes & Lecaillon 1998; Rhode & Duffy 2004). Marginal habitats such as the Eastern Pacific (Glynn & Colgan 1992) and newly created habitat (e.g. volcanic islands, artificial reefs) provide opportunities for study.

Genetic swamping and asexual reproduction

Genetic swamping may occur as a result of translocation of individuals into remnant natural populations (Anttila *et al.* 2000). This involves the increase in frequency of introduced genotypes or alleles either because they have a fitness advantage or they outnumber natives (Hufford & Mazer 2003). If the numerical advantage of the introduced variant is large enough, swamping can occur without hybridization of introduced and native individuals. For example, an introduced haplotype of the common reed, *Phragmites australis*, has largely replaced native types in New England (Saltonstall 2002).

Coral species frequently reproduce via asexual reproduction, e.g. by fragmentation, budding, pedal laceration and production of asexual larvae (Table 1) (Tunnicliffe 1981; Highsmith 1982; Bruno 1998). Asexually reproducing coral species display varying degrees of genotypic diversity over their range (Box 1). Fragmentation is caused by external physical disturbance. It is common in branching acroporids (Baums *et al.* 2006a; Tunnicliffe 1981), *Madracis* (Vermeij *et al.* 2007), *Porites* (Hunter 1993) and *Pavona* (Willis & Ayre 1985) but has also been reported for massive *Montastraea* species (Foster *et al.* 2007). Fragments have a higher chance of survival when they are large (Lirman 2000) so that dispersal is limited but, over time, genets can extend over tens of metres (Neigel & Avise 1983; Baums *et al.* 2006a; Foster *et al.* 2007).

Several brooding species release asexually produced planulae as evidenced by having multilocus genotypes identical to their mothers' (Stoddart 1983; Stoddart *et al.* 1988; Brazeau *et al.* 1998; Sherman *et al.* 2006). Asexually produced planulae have, theoretically, the same dispersal potential as their sexually produced counterparts and thus could be transported further than fragments (Stoddart 1983). Several clones of *Pocillopora damicornis* in Hawaii were found distributed over eight reefs (Stoddart 1983).

Considerable variability in genotypic evenness and richness on small spatial scales is common within and across species, ranging from minimal clonal replication to reefs dominated by just one genet (Hunter 1993; Ayre & Hughes 2000; Miller & Ayre 2004; Baums *et al.* 2006a).

Genetic swamping of local genotypes by translocated colonies is a possibility in corals however, for genetic swamping to occur, local adaptation of genotypes must be small. As argued above, local adaptation may be more common in corals than previously thought, thus swamping may not be of major concern in most coral populations. Regardless, the propensity of corals to reproduce asexually must be considered in restoration projects. Local dominance of one or a few genets may decrease their likelihood of sexual reproduction due to genet-specific fertilization success (Baums and Miller, unpublished data, Fig. 1) and dilution of gametes (Allee effect) in self-incompatible species. In addition, the genotypic diversity of foundation species may influence their growth rates and the recovery and diversity of associated ecosystems (Crawford *et al.* 2007; Reusch *et al.* 2005; Crutsinger *et al.* 2006). As mentioned earlier, limited initial genotypic diversity translated into reduced population growth of transplanted eelgrass (*Zostera marina*) (Williams 2001). Genotypic diversity of seagrass also had a positive effect on the biodiversity of associated invertebrate fauna (Reusch *et al.* 2005). The interplay between genotypic diversity of foundation corals and diversity of the reef ecosystem is an exciting area for future research.

Inbreeding

Inbreeding depression commonly results from mating of close relatives. Mating among relatives increases in frequency in small, closed populations and thus is of concern in threatened natural populations as well as in captive breeding programs (reviewed in Frankham 2005). All populations carry a genetic load of lethal or disadvantageous alleles that are not usually purged by selection because they are recessive and, while at low frequency, occur only as heterozygotes (Wang *et al.* 1999). Mating among relatives increases the chance that offspring inherit lethal or disadvantageous alleles from both parents in which case the recessive allele is exposed.

In plants, inbreeding depression is negatively correlated with selfing rate, thus supporting theoretical expectations (Charlesworth & Charlesworth 1990) that selfing reduces the magnitude of inbreeding depression (Husband & Schemske 1996). Similarly, ancestral inbreeding reduced the magnitude of inbreeding depression in experimental *Drosophila* populations (Swindell & Bouzat 2006). Inbreeding depression may be reduced in selfing species through selection acting on selfed offspring that are homozygous for the recessive lethal allele resulting in a purging of the genetic load. Husband & Schemske (1996) showed that the purging of inbreeding depression caused by early onset lethal recessive alleles is more effective than purging of mildly deleterious traits expressed late in the life cycle. Thus, while naturally inbreeding species showed lower inbreeding depression in early life cycle stages compared to outcrossing species, inbreeding depression was of equal magnitude late in the life cycle for both mating systems.

Two cases studies illustrate the complexity of stage-specific selection on inbred individuals. In two ascidian species, the natural outcrosser showed more inbreeding depression during embryo survival in experimental inbreeding trials compared to its naturally selfing congener, while survival rates were similar during later life-stages (Cohen 1992). In a long-lived Australian *Eucalyptus* with mixed mating, survival of inbred and outbred progeny was similar until about 4 years when intense competition due to closure of the canopy set in and led to higher survival of outbred progeny (Hardner & Potts 1997). The authors argue that inbreeding is retained despite intense inbreeding depression to ensure reproduction in times of reduced adult density (when forests are mature). Sessile cnidarians often compete for growing space and thus inbreeding may be favoured to decrease costs of cooperation among close kin (Grosberg & Hart 2000). These and other studies (Hammerli & Reusch 2003; Ishida 2006) provide evidence that inbreeding depression may still affect naturally inbreeding species and thus could occur in naturally inbreeding marine invertebrates.

Selfing in corals. Selfing contributes to inbreeding in at least some coral species. Hermaphroditic coral species are capable of selfing under laboratory conditions (Table 2) in the absence of nonself sperm. Non-self sperm may be preferred under natural conditions (Willis et al. 1997; Hatta et al. 1999; van Oppen et al. 2002) so that the contribution of selfing to reproduction in wild populations of broadcast spawning corals is mostly unknown. Only two studies on brooding corals report selfing rates based on progeny array analysis and compared them to heterozygosity deficits of adult populations (Stoddart et al. 1988; Ayre & Miller 2006). In both studies, adult populations were more inbred than expected based on brood selfing rates, suggesting the presence of additional selective or structuring processes. Note that no data exist on fitness of inbred vs. outbred individuals during different life stages of scleractinian corals. Such data is needed to assess if inbreeding can be ignored as a concern for these species.

Multiple reproductive strategies in corals. Inbreeding and mixed asexual/sexual reproduction appear to be a ubiquitous feature of sessile marine invertebrate populations (Grosberg 1991; Coffroth & Lasker 1998; Carlon 1999) though experimental artefacts (null alleles) may inflate the incidence of inbreeding (Addison & Hart 2005). Genetic studies on corals examining their reproductive strategies and their influence on local population genetic structure have been conducted for over 20 years (Refs in Table 1) but have not been summarized. Tables 1 and 2 list

Box 2 Genetic and genotypic diversity

Genetic diversity can be defined on several levels in organisms that have sexual and asexual reproductive modes such as corals and plants (reviewed in Toro & Caballero 2005). Genetic diversity *sensu stricto* (or gene diversity) refers to the amount of variation on the level of individual genes in a population. Genetic diversity may be expressed as heterozygosity or allelic richness. Genetic diversity can differ among the genomes within a cell. Mitochondrial DNA has proven nearly invariable within coral species, maybe due to the presence of an ancestral, effective repair mechanism that has been lost subsequently in several other metazoan lineages (Shearer *et al.* 2002; Hellberg 2006). This low genetic diversity of the mitochondrial genome does not extend to the nuclear genome (Hellberg 2006; Solecava *et al.* 1991). In fact, observed and expected heterozygosity as measured by allozyme markers, microsatellites and single copy nuclear genes are comparable to if not higher than values obtained for other metazoans (Table 3).

In contrast to genetic diversity, genotypic diversity is defined as the number of unique multilocus genotypes and varies on the level of whole organisms. A multi-locus genotype (genet) may occur several times (ramets) in a population only as a result of asexual replication (identity by descent). The number and relative abundance of ramets from different genets determine the genotypic richness and genotypic evenness, respectively (reviewed in Arnaud-Haond *et al.* 2007). Genotypic and genetic diversity describe processes that have to be managed separately.

Differentiating between inbreeding and asexual reproduction can be difficult when using markers with limited power to resolve genotypic diversity as commonly used in the coral literature (Table 1) and confidence levels vary among published clonal reproduction indices (N_g/N and G_o/G_e) (Table 1). Statistical methods can asses the likelihood that shared genotypes in a dataset are due to low variation of markers (Valiere 2002; Stenberg *et al.* 2003) and should be reported (Table 1). Furthermore, the basis for calculating the inbreeding coefficients (Wright's *f* or Solander's Ds) differed between coral studies: some included all genotypes while others only considered unique multilocus genotypes to avoid inflation of *F*-statistics (Halkett *et al.* 2005). Detection of asexual reproduction and inbreeding is a function of sampling effort and scale (because one might expect physically close colonies to also be more closely related or the result of fragmentation). Again, studies differ widely in sampling protocols and spatial scales considered, thus only general trends can be gleaned.

studies that used molecular methods to assess the contribution of inbreeding and asexual reproduction in tropical scleractinian corals (references obtained from searches in the Web of Science and ReefBase). Due to differences in statistical power and treatment of the data, it is problematic to compare absolute values of F_{IS} (the inbreeding coefficient) and clonal reproduction among studies (Box 2). Instead, the authors' interpretations of their data are discussed here. Recruits are produced by outcrossing, self-fertilization and asexual processes to varying degrees (Refs in Table 1). Of the 41 studies that report on population genetic structure and/or selfing in tropical scleractinian corals, only five concluded that coral populations were largely outcrossed. Authors judged populations to be inbred 13 times and not inbred 15 times (16 did not comment). There was no apparent difference between brooders and broadcasters in contrast to earlier expectations that brooders should show higher levels of inbreeding (Carlon 1999).

Reproduction via asexually produced planulae or fragmentation was reported to be important 16 times, not important 21 times and 7 studies did not comment. Authors favoured either inbreeding or asexual reproduction in their interpretation of local population genetic structure, but never both. It is not clear whether this finding has a biological basis or is due to problems with data interpretation. In either case, this was true across and within species: depending on habitat and geographical location, *Pocillopora damicornis* was reported to be either inbred (Ayre & Hughes 2000) or have significant asexual reproduction (Stoddart 1984b). Similarly, based on F_{IS}, two studies concluded that *Seriatopora hystrix* had inbred populations (Ayre *et al.* 1994; Ayre & Hughes 2000) and one did not (Underwood *et al.* 2007). Asexual reproduction was more prevalent in marginal than central habitats in at least two species: *Acropora palmata* (Baums *et al.* 2006a) and *Pocillopora damicornis* (Stoddart 1984a, b; Miller & Ayre 2004). This variability in mating strategies within and across species prevents a one-size fits all approach to the design of restoration projects.

Outbreeding

Hybrids stemming from intraspecific mating may show fitness advantages or disadvantages compared to their parents when grown in their parent's habitat. Fitness advantages of F_1 hybrids (hybrid vigor or heterosis) may result from mating between parents from diverged populations (Johansen-Morris & Latta 2006). Such mating

can mask recessive deleterious alleles or confer a fitness advantage through superior performance of heterozygotes (overdominance) (Pujolar *et al.* 2005; Pace *et al.* 2006). Hybrids may harbour novel allele combinations that result in new favourable multilocus genotypes (epistasis).

Outbreeding depression describes the loss of fitness resulting from intra or interspecific hybridization caused by the disruption of either intrinsic gene interactions (epistasis) or interactions of genes and environment. Disruption of locally adapted genotypes may occur in F_1 or later generations. Recombination in the first generation dilutes locally adapted genotypes (dilution) because only one half of the adapted alleles are present so that the hybrid may be less fit than the parents. Epistatic interactions may not be seen until the F_2 or later generations: in F_1 large blocks of interacting genes are still intact and will only by broken up during later recombination events (hybrid breakdown) (reviewed in Willi *et al.* 2006). For example, crosses between two ecotypes (moist and dry soil) of an annual grass produced a range of outcomes from hybrid vigor in the F_2 generation to hybrid breakdown in the F_6 compared to the midparent (Johansen-Morris & Latta 2006). Similarly, F_2 hybrids from crosses of two runs of pink salmon showed lower survival than F_2 controls (Gharrett *et al.* 1999).

Detection of outbreeding (and inbreeding) depression requires careful experimentation including breeding studies, common garden experiments and reciprocal transplants of hybrid individuals (Hufford & Mazer 2003). Infrequent sexual reproduction in scleractinian corals (Harrison *et al.* 1990), difficulties in raising coral larvae in captivity and long maturation times render breeding studies extremely difficult. Thus, there is a lack of data on quantitative genetic variation in corals that could help predict the consequences of hybridization. Creative solutions may involve the use of model organisms (short lived nonzooxanthellate corals), improving coral husbandry to enable sexual reproduction in captivity (Petersen *et al.* 2006), and long-term field studies (Hardner *et al.* 1997). However, one may evaluate the potential for outbreeding depression in corals based on certain parameters that were found to be important in plants. These include the already discussed potential for occurrence of site-adaptation (ecotypes) and subdivided populations as well as the potential of interspecies hybridization.

Interspecies hybridization. In some coral lineages (*Acropora* and *Platygyra*), interspecies hybridization may have played an important role in the evolutionary history of the species (reviewed in Willis *et al.* 2006). Within morphospecies complexes of the Caribbean (*Montastraea annularis* sp. complex, *Madracis* spp.), morphological and reproductive divergence of sister species differs over the range of the species (Fukami *et al.* 2004; Levitan *et al.* 2004; Vermeij *et al.* 2007). Acroporid species that naturally spawn simultaneously are also capable of producing viable offspring in no-choice laboratory crosses (Willis *et al.* 1997), although conspecific gametes are preferred in multiple-choice experiments (Willis *et al.* 1997; Hatta *et al.* 1999; van Oppen *et al.* 2002). F_1 hybrids from *A. palmata* × *A. cervicornis* crosses, though rare, are found throughout the range of the parent species (see also van Oppen *et al.* 2002; Vollmer & Palumbi 2002) indicating that interspecies hybridization occurs naturally with some frequency.

Alteration of gene flow patterns among species through hybridization could be facilitated through transplantation projects, although it is unclear if that is an undesirable outcome. Only anecdotal reports of heterosis exist, where coral hybrids (e.g. *A. prolifera*) are fitter than both parent species and thus may outcompete them locally.

It is apparent that the diversity of population structures, mating systems and symbiont choices found in hermatypic corals is enormous and yet results on natural levels of inbreeding and outbreeding depression, site-adaptation and genotype–environment interactions are scarce. Detecting selection and adaptation in phenotypically plastic, long-lived species that reproduce rarely, recruit infrequently and contain intracellular symbionts like corals is not straightforward because quantitative genetic (quantitative trait loci, QTL) approaches cannot be used. However, population genomic approaches promise to provide the tools needed to address these questions.

Current limitations of molecular tools and future needs

Neutral genetic variation among populations as assessed by most coral studies may not parallel quantitative genetic differences that would indicate adaptation to local conditions (Box 2, Milligan *et al.* 1994; Hedrick 2001). Yet, the preservation of adaptive variation in wild species is an important goal of conservation efforts and the need for the development of techniques to study adaptive variation in wild species has been recognized for some time (Luikart *et al.* 2003; Stinchcombe & Hoekstra 2007). The advent of microarray technology made it possible to explore differences in gene expression among individuals, populations and species (Stoughton 2005) and has been applied to corals to identify stressed individuals (Edge *et al.* 2005) and genes involved in initiation of the coral-zooxanthellae symbiosis (Rodriguez-Lanetty *et al.* 2006). In parallel, technical and statistical advances in population genomics provided tools to study genome wide signatures of adaptation in thousands of samples (Wilding *et al.* 2001; Akey *et al.* 2002). Next generation sequencing methods continue to reduce the development cost of genomic tools for nonmodel organisms and have yielded promising results in wild species (Toth *et al.* 2007; Vera *et al.* 2008).

Population genomic approaches can be divided into several steps (Luikart *et al*. 2003): (i) sample many individuals; (ii) genotype many loci (single nucleotide polymorphisms or SNPs); and (iii) identify the outliers among those loci. Once outliers have been identified, they are removed to estimate demographic parameters such as population structure and expansion. The dataset with outliers included is then used to investigate the cause for outlier behaviour such as selection (Luikart *et al*. 2003). One needs large sample sizes to detect the signature of selection (the selection coefficient *s*) over other effects such as drift and demography, so that (Ne * s) > 1. Outlier loci behave differently from the majority of markers, e.g. they have large F_{ST} values (a measure of genetic differentiation) or show linkage disequilibrium. Several statistical methods have been developed for outlier detection (Stinchcombe & Hoekstra 2007). The usefulness of F_{ST} for this approach was reviewed and supported by Beaumont (2005). The patterns observed at outlier loci are then correlated with evolutionary, phenotypic, ecological, and environmental observations such as divergence between varieties (Tsumura *et al*. 2007), temperature gradients (Wilding *et al*. 2001), tidal exposure (Oetjen & Reusch 2007) and poison exposure (Storz & Nachman 2003). Oetjen & Reusch were able to identify a nodulin gene involved in water channelling as being under selection in periodically exposed and permanently subtidal seagrass populations using relatively few amplified fragment length polymorphism markers. It is likely that not all loci under selection can be identified using current statistical methods and some outliers may in fact be neutral (Teshima *et al*. 2006). After outliers are identified, experimental characterization of the proteins/signals involved, albeit difficult and costly, strengthens the inferences that can be drawn.

The study of adaptation (rather then the more common approach to survey neutral genetic variation) is informative for restoration projects mainly because it may help identify rare adaptations that deserve protection, match populations with similar adaptations (Hufford & Mazer 2003), avoid transplantation of maladapted genets (McKay *et al*. 2005; Edmands 2007) and reduce the risk of inbreeding and outbreeding depression (Lofflin & Kephart 2005; Marshall & Spalton 2000).

Restoration of reefs

Conducting a genetically sound restoration project involves four phases: (i) identification of goals; (ii) design; (iii) implementation; and (iv) assessment.

Identification of goals

It has been suggested recently that rather than restoring ecosystems to their past states, ecosystems should be designed to withstand future change (Harris *et al*. 2006), a goal that seems elusive for most systems. While coral reefs are threatened as ecosystems, few member species are as yet critically endangered. The Caribbean acroporid species, *Acropora palmata* and *A. cervicornis* are the only scleractinian corals listed under the US Endangered Species Act in the 'threatened' category (Anonymous 2006) and under Mexican law as 'endangered'. Thus, reef restoration goals are mostly directed toward re-establishing communities and preserving biodiversity rather than ensuring the survival of any one species. No guidelines exist on how to create self-sustaining populations that resemble native reefs in their genetic composition and complexity (Box 1).

Specific goals of coral restoration projects include repairing physical damage from ship groundings (Lirman & Miller 2003) and anchor damage (Jameson *et al*. 1999), increasing the population size of target coral species of particular concern (Bruckner & Bruckner 2001) and increasing the three-dimensional structure of reefs to attract or retain reef fish after adult coral colonies have been diminished (reviewed in Seaman 2007).

Design and Implementation

During the design stages of restoration projects, the most immediate question is the source of the coral propagules. Because of the prevalence of population subdivision, inbreeding and potentially ecotypes in corals, source and recipient sites should be physically close and similar in environmental conditions (i.e. depth, sediment load). Fragments generated by disturbances such as hurricanes or ship groundings maybe secured in place to enhance survivorship (Bruckner & Bruckner 2001). However, when restoring devastated areas, it is sometimes necessary to introduce individuals from outside populations. Coral husbandry promises to provide a source for coral colonies that eliminates the need to collect fragments from neighbouring reefs, apparently solving the old problem of robbing Peter to pay Paul (Petersen *et al*. 2006). Coral reef restoration efforts with coral stock that has been nursed either *in situ* or *ex situ* are well underway (Shafir *et al*. 2006; Amar & Rinkevich 2007). The source of the transplantation stock varies but usually a few animals from nearby reefs are brought into nursery facilities where they are extensively fragmented, mounted on stalks, grown out, and then outplanted. Captive environments are likely selective and this may extend to *in situ* nurseries (Shafir *et al*. 2006). Few genotypes capable of survival in aquaria are able to reproduce sexually. Some genets, however, are producing large numbers of offspring in mid-water nurseries (Amar & Rinkevich 2007). Such recruits (asexual or sexual in origin) may represent genetically novel or depauperate material either because they are not adapted to local environments (Ammar *et al*. 2000) or they capture only a small amount of the total genetic variation. Differential

performance of genotypes in captive environments can be assessed using molecular tools to differentiate among genotypes and track them and their offspring over time. When spacing sexual and asexual propagules, the mating system of the coral species should be taken into account so that stands of only one sex in gonochoric species or stands of only one genet in self-incompatible hermaphrodites are avoided.

Assessment

A successful coral restoration project is determined by the increase in biomass of corals, their reproductive rates (sexual and asexual) and their associated fauna. Molecular tools can track individual corals (see references in Table 1), track their reproductive success through assignment of recruits to parents (Gleason *et al.* 2001; Ayre & Miller 2004; Jones *et al.* 2005) and track health status by use of stress markers (Edge *et al.* 2005; Forêt *et al.* 2007). The recent publication of a cnidarian genome (Putnam *et al.* 2007) will facilitate the development of diagnostic stress and population markers (Hofmann *et al.* 2005; Rodriguez-Lanetty *et al.* 2006; Forêt *et al.* 2007). Diversity and distribution of fauna supported by (plant) foundation species in ecosystems is influenced by the genetic and genotypic composition of that foundation species (Crawford *et al.* 2007; Reusch *et al.* 2005). This is an easily testable hypothesis for coral systems by conducting pre- and postsurveys of fauna associated with restored coral populations of known genotypic diversity. For example, genotypically and/or genetically poor coral stands may attract fish populations equally well. If true, and if enriching fish populations is the main goal of the restoration project, genetic composition of the coral stock could be ignored, at least over the short-term. When a good taxonomic reference database exists (Meyer & Paulay 2005; Rubinoff & Holland 2005), DNA barcoding approaches enable the inclusion of difficult to identify noncoral invertebrate fauna (Hellberg 2006) in these surveys in addition to the traditionally assessed mobile macro-fauna (Neigel *et al.* 2007).

Recommendations

Given the competing demands on monetary resources by a multitude of threats and the scarcity of tools and data available, should reef restoration efforts take genetic considerations into account? The genetic and genotypic diversity of coral populations is unpredictable and varied, yet knowledge of these factors would improve the design of ecologically and evolutionarily sound restoration strategies. Indirect evidence suggests that local adaptation may be important in shaping coral community structure but further studies are needed to understand the

contribution of symbionts vs. host to heritable genetic variation. Potential risks that small remnant, restored, or captive populations face, include inbreeding depression, outbreeding depression and genetic swamping. If results from long-lived, mixed-mating plant species are applicable to corals, inbreeding depression cannot be discounted as a potential outcome of restoration efforts even in naturally inbred species such as most scleractinian coral species. Outbreeding depression over small spatial scales, though historically regarded as rare, has received much attention lately in plant species that exhibit strong local adaptation (Edmands 2007). Careful experimentation in the field and laboratory is necessary to address this concern. Genetic swamping may not affect most coral species given the generally low survival of transplants and the hypothesized advantage of local genotypes. However, in the absence of detailed knowledge on the genotypic, neutral and adaptive genetic variation of most coral species, these statements are hypotheses rather than conclusions that require urgent testing. The dire state of reefs does not allow for postponement of projects until critical data are collected. Thus, following general IUCN guidelines (IUCN 2002), restoration efforts should, at the very least, carefully track ramets and genets used in transplantation efforts to further assess performance of genets and the consequences of transplantation on survival of coral communities. This data is fairly easy to collect and will improve our ability to design successful restoration projects substantially.

Future research should aim to separate the heritable contributions of all partners to the performance of the holobiont (Grottoli *et al.* 2006). To this end, experiments on performance of symbiont-free larvae are a promising avenue. In addition, I suggest a revival of common garden and transplanting studies combined with novel population genetic and genomics approaches for nonmodel organisms (Hofmann *et al.* 2005; Rodriguez-Lanetty *et al.* 2006; Toth *et al.* 2007; Vera *et al.* 2008) to address crucial gaps in knowledge. Results from the plant literature indicate that long-term success of restoration efforts may be influenced by genetic and genotypic diversity of restored populations (Hughes & Stachowicz 2004; Reusch *et al.* 2005; Crutsinger *et al.* 2006; Crawford *et al.* 2007). Thus, research is needed to determine the effect of genotypic diversity of coral populations on the reef ecosystems they support. Though incomplete, the data reviewed here underlines the need to consider genetic factors in coral restoration efforts.

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