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REVIEW

Footprints on water: the genetic wake of dispersal among reefs

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Abstract Analysis of genetic data can reveal past and ongoing demographic connections between reef populations. The history, extent, and geography of isolation and exchange help to determine which populations are evolutionarily distinct and how to manage threatened reefs. Here the genetic approaches undertaken to understand connectivity among reefs are reviewed, ranging from early allozyme studies on genetic subdivision, through the use of sequence data to infer population histories, to emerging analyses that pull the influences of the past connections away from the effects of ongoing dispersal. Critically, some of these new approaches can infer migration and isolation over recent generations, thus offering the opportunity to answer many questions about reef connectivity and to better collaborate with ecologists and oceanographers to address problems that remain.

Keywords Coral reef · Connectivity · Gene flow · Multi-locus genotyping

Introduction

Coral reefs have patchy spatial distributions. Habitats unsuitable for reef dwellers separate populations at spatial scales ranging from a few meters between coral heads within a lagoon to the thousands of kilometers separating reefs in the Central and Eastern Pacific. If isolated reefs harbor individuals of the same species, then those reefs were demographically connected at some point in history. When and by what route they were connected matters if we want to understand the evolution and ecology of those reef animals. For example, a single colonization event could bring a founding propagule from one reef to another, with no subsequent connection for thousands of generations. Such isolated populations should respond independently to local selective regimes, and their distinctiveness should mark them as targets for conservation efforts (Fraser and Bernatchez 2001). In contrast, many migrants may move between distant populations every generation, perhaps demographically sustaining a down-current population or swamping locally favored genotypes with more globally favored variants. Ideally, we would like to know not only the frequency of connections and the number or proportion of migrants moving between reefs, but also routes of dispersal (especially if intervening stepping stone populations are involved) and whether patterns of connectivity have changed over time, either prehistorically or in response to human activities. Patterns of connectivity as they exist today are especially important for designing management strategies to restore and conserve reef populations.

Answering these questions would be difficult anywhere, but the biology of most reef dwellers further complicates matters. Direct observations can help us follow dispersal by some larger marine animals directly (e.g., sea turtles, Nichols et al. 2000; tuna, Block et al. 2005), but most tropical marine fish (Sale 1980) and invertebrate (Thorson 1950) species disperse via tiny pelagic larvae. This small size, combined with the great

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distances between many reefs, restricts the application of direct monitoring as a means for studying the dispersal of most reef animals (although see Carlon and Olson 1993; Planes et al. 2002; Jones et al. 2005).

Alternatively, connectivity among reef populations can be estimated indirectly by genetically comparing samples from different populations. Populations may differ in the presence of alternate forms (alleles) at homologous loci, in the frequency of these alleles, and in associations between alleles at different loci (linkage). These differences accumulate and break down among populations at very different rates. A new point mutation may require millions of years to become fixed at a nuclear locus, yet only a handful of generations may suffice for recombination to break down linkage disequilibrium.

These rate differences present both problems and opportunities to the empirical biologist trying to understand connectivity among reefs. On the positive side, the diversity of analyses and markers now available can produce reliable answers to many (perhaps most) of the when, how much, and by what route questions about connectivity. In practice, this wealth of choice can lead to wasted efforts, as no single analysis or genetic marker is appropriate for every question, species, or spatial scale. What is more, even decisive studies can leave confusion in their wake, as differences in the operative time scales of different approaches can lead different readers to draw conflicting conclusions from the same results.

The purpose of this review is to match particular questions about reef connectivity to appropriate analyses and genetic markers. It will also be noted when these analyses can address conservation issues. There have been recent reviews concerning the genetic inferences that can be made about population isolation (Hellberg et al. 2002), and demography (Hellberg 2006a) in marine animals. Palumbi (2003) has discussed some of the ways that population genetic data can be applied to the design of marine reserves, and van Oppen and Gates (2006) have reviewed ways in which genetic research has informed the conservation of corals; little of the contents of those papers will be repeated here. Instead, this review will chart the progression of questions about connectivity among reef populations addressed over the last 20 years. The review starts with studies that ask whether populations are subdivided or not, and then moves to other studies that look at historical connections and barriers among populations, and finally to genetic analyses of migration in the time frame of the present day. Along the way, recurring problems will be pointed out, as well as promising techniques that have been underutilized. It is hoped that this format will make it easier for those planning genetic studies of reef connectivity to distinguish fruitful approaches from futile ones.

Are reef populations subdivided?

Panmixia is the population genetic extreme in high connectivity among populations. If all sampled populations freely interbred, then global genotype frequencies can be predicted from global gene frequencies using the Hardy Weinberg Principle. Alternatively, restricted movement of genes among populations will cause an excess of homozygotes compared to Hardy–Weinberg predictions. The degree of homozygote excess (or heterozygote deficit) can provide a measure of population subdivision (F_{ST}, the proportion of total genetic variation partitioned among subpopulations) and can, in combination with certain assumptions, be used to calculate the average number of migrants moving among populations (see Neigel 1997; Waples 1998; Whitlock and McCauley 1999 for important caveats).

Such estimates have long been used to infer whether populations of reef animals are panmictic or subdivided. The earliest allozyme work confirmed that species with extended pelagic larval developments show little differentiation among populations, although the small F_{ST} values seen at trans-Pacific spatial scales were still surprising (Winans 1980; Nishida and Lucas 1988). Generally, an inverse relationship between larval development time and population subdivision was expected, and this held in reef fish (Doherty et al. 1995). Allozyme studies on reef corals (Ayre and Hughes 2000) found more subdivision among brooding corals than broadcasting species, although even the latter could show considerable differentiation. But not all patterns revealed by allozymes fit with conventional wisdom based on larval dispersal potential. Lacson et al. (1989) found a substantial change in allele frequencies at one of the eight loci they surveyed in bicolor damselfish from the Florida Keys, suggesting the possibility that selection might promote differentiation at this locus and thereby bias estimates of connectivity downwards. Selection can also homogenize allozyme frequencies, thereby inflating connectivity estimates. This seems to be the mechanism underlying the conflict between allozyme and DNA-based studies on the oyster *Crassostrea virginica.* Buroker's (1983) allozyme work suggested genetic uniformity over the range of this species. Surveys of presumably neutral DNA polymorphisms (Reeb and Avise 1990; Karl and Avise 1992), however, found a genetic discontinuity near Cape Canaveral in Florida, suggesting that the allozyme pattern had been influenced by stabilizing selection.

The threat of the confounding effects of selection on allozymes thus began to drive population geneticists, including reef scientists, to employ mtDNA as a marker. Aside from side stepping problems with selection on allozymes (although see Ballard and Rand 2005; Bazin et al. 2006; but also Berry 2006; Wares et al. 2006), mtDNA also promised greater sensitivity to reduced gene flow between populations due to its smaller effective population size (Birky et al. 1989). Indeed, a few early applications of mtDNA to reef animals found genetic breaks that had not been evident from allozyme surveys. Both Lavery et al. (1996) and Williams and Benzie (1997) reported a genetic discontinuity between East Indian and West Pacific populations (of coconut crabs and sea stars, respectively) that did not appear in their earlier allozyme work. Apart from recognizing these historical breaks, however, the picture of reef subdivision offered by mtDNA was largely similar to that inferred from allozymes; among populations to either side of the major barrier, mtDNA was no more sensitive to subdivision than allozymes had been. And while mtDNA did reveal extensive differentiation among populations of some brooding species of reef fish (Planes et al. 2001), a more general relationship between pelagic larval duration and degree of subdivision is not evident (Shulman and Bermingham 1995; Bay et al. 2006; Bowen et al. 2006). Only recently has mtDNA revealed surprising reef population subdivision at relatively small (<1,000 km) spatial scales, for example in blennies (Riginos and Nachman 2001), stomatopods (Barber et al. 2002), gobies (Taylor and Hellberg 2003), and snappers (Ovenden et al. 2004).

Corals themselves have been notably absent from population studies on mtDNA. It turns out that rates of nucleotide substitution are extremely slow for the mitochondrial DNA of corals, along with other anthozoans and sponges (Shearer et al. 2002; Hellberg 2006b; Wörheide 2006). These slow rates (about 100 times slower than those for most animals, Hellberg 2006b) have stalled efforts to infer historical connections between reef corals. Sequence variation at nuclear ITS regions has sometimes been employed as substitute marker in taxa with slow mtDNA, but intra-individual variation (sometimes exceeding that among populations) can blur any picture of connectivity that might arise otherwise from their interpretation (Wörheide et al. 2004; Vollmer and Palumbi 2004; note that the genus *Acropora* may be exceptionally troublesome in this regard, Wei et al. 2006). To date, most population genetic studies on corals have still been based on allozymes (see Table 1 in van Oppen and Gates 2006). However, single copy nuclear sequences (van Oppen et al. 2000; Mackenzie et al. 2004; Severance and Karl 2006) are now available for a growing number of coral species.

Other genetic markers, microsatellites (Selkoe and Toonen 2006) have also been developed for corals (e.g., Shearer and Coffroth 2004; Baums et al. 2005a, b; Maier et al. 2005) and have been used more generally to expose subdivision among reef inhabitants with broad pelagic larval dispersal. For example, Rhodes et al. (2003) used cluster analysis to identify three differentiated regions within western and central Pacific populations of the grouper *Epinephelus polyphekadion*. Microsatellites have also proven adept at distinguishing populations at smaller spatial scales (<100 km) in reef species whose life histories suggest more limited dispersal potential (e.g., the gorgonian *Pseudopterogorgia elisabethae*, Gutierrez-Rodriguez and Lasker 2004, and the cardinalfish *Pterapogon kauderni*, Hoffman et al 2005).

Notably, subdivision studies employing microsatellites (and any other highly heterozygous markers) often produce very low values of F_{ST}. Purcell et al. (2006), for example, found a Caribbean-wide F_{ST} of just 0.003 in the French grunt *Haemulon flavolineatum*. Such small values result from the extremely high heterozygosity of microsatellite loci. High polymorphism within populations will deflate values of F_{ST} (because so much variation *within* populations leaves little to be apportioned *among* populations), even if populations share no alleles. This has a couple of important implications. First, F_{ST} values obtained from markers with different heterozygosities cannot be compared directly. Hedrick (2005) suggested a simple way to standardize F_{ST} that would allow for such comparisons (see also Meirmans 2006 for software that implements an improved way to do this). Second, if highly variable markers are to be used in any test for subdivision among reef populations, then population sample sizes must be adequately large (around 50 as a rule of thumb, see Ruzzante 1998; Ryman et al. 2006) to capture this high genetic diversity or else the tests will have low power. Microsatellites are not the only marker to exhibit high variation in reef animals; regions of the mitochondrial genome can as well (e.g., in spiny lobsters, Silberman et al. 1994; urchins, Lessios et al. 1998). In fact, if every individual in a study has a unique mtDNA haplotype, the maximum possible F_{ST} is zero, despite the fact that no alleles are shared among populations. Such high levels of variation are probably tied to the large effective populations sizes of some marine populations, a factor that should also boost the frequency of deleterious alleles (Launey and Hedgecock 2001), including null alleles (alleles that fail

to amplify and can thereby lead to apparently high levels of homozygosity).

Do stepping stones connect reefs?

Finding significant subdivision among populations is only a start, providing just a gross idea that dispersal among populations is sufficiently limited so that they accrue some degree of genetic differentiation. But if all populations are not freely exchanging genes, then there are some populations more closely connected than others? The simplest model for geographic bias in gene flow is the stepping stone model, in which dispersal takes place only between adjacent populations. Slatkin (1993) devised a test for whether populations obeyed such a pattern of connectivity: plot the log of inferred gene flow against the log of geographic distance of separation for all pairwise combination of populations. For a one-dimensional array of populations, as along a linear coastline, the slope should be −1. For a two-dimensional array, the slope should be −0.5 (see also Rousset 1997).

Exact matches to these expectations have been few in the marine setting. Hellberg (1995) found the expected slope in a brooding temperate coral at a spatial scale of 1–50 km, but the slopes at both larger (100–1,000 km) and smaller (1–10 m) spatial scales (Hellberg 1994) were shallower than expected for a strict stepping stone model. At the smaller scale, high levels of gene flow resulted in similar levels of gene flow among all populations regardless of separation. At the larger spatial scale, low levels of ongoing gene flow meant that genetic drift dominated population structure, and drift takes many generations (see below) to reflect just how isolated populations are. Under such conditions, the match between genetic differentiation and physical isolation will be poor (Slatkin 1993; Hellberg 1995; Hutchinson and Templeton 1999). Consistent with this, several reef species show a weak relationship between gene flow and distance at small and large spatial scales, with a tighter match in-between the extremes (Lavery et al. 1995; Planes et al. 1996; Planes and Fauvelot 2002). The geographic scale at which these relationships shift varies among species, probably with larval dispersal potential.

Significant correlations between genetic differentiation and geographic distance are commonly reported as "isolation-by-distance", even though the system studied may bear little resemblance to the continuous populations for which Wright (1943) coined this term and the relationship between the two variables falls shy of Slatkin's (1993) explicit predictions. Without such a match, the strong conclusion that gene flow is limited to immediately neighboring populations cannot be drawn. Such weak relationships can still prove useful however. Palumbi (2003) used simulations to show that plots of F_{ST} estimates against distance can be used to distinguish the signal of limited dispersal from noise, as Purcell et al. (2006) were able to do for French grunts even though only 0.3% of their microsatellite variation was partitioned among populations.

Barriers and byways

Few reef biologists familiar with their organisms and where they live would believe that geographic isolation alone determines the degree of connectivity among populations. Currents may shower downstream populations with larval rain from upstream sources, or parch isolated populations that lie off their course. Intervening unfavorable habitats may also act as barriers that disconnect populations. Barring a complete migration matrix among populations, some rules of thumb regarding whether particular current paths are effective routes of dispersal and which barriers hinder gene flow would allow for informed predictions about connectivity.

Barriers that isolate populations of several species can be identified by comparing the gene genealogies of co-distributed taxa. Co-occurring genetic breaks in these taxa should indicate general barriers to connectivity and also reduce the chances that a genetic break observed in just one species results from demographic artifact (Irwin 2002). For marine species, the best known such phylogeographic break occurs at Cape Canaveral (Avise 2000), where an offshore jet divides the tropical waters of south Florida from more temperate northern ones. Amongst Caribbean reef species, the Mona Passage region (between the islands of Hispaniola and Puerto Rico) is emerging as a similar shared barrier. Taylor and Hellberg (2003) found the first genetic break here in a parasite-cleaning goby, confirming earlier biogeographical observations (Colin 1975; Starck and Colin 1978). That initial mtDNA work has since been expanded by nuclear gene sequences from the same species and from a congeneric goby complex with a different (sponge-dwelling) ecological habit (Taylor and Hellberg 2006). Moreover, a coincident genetic break also occurs in *Acropora palmata* (Baums et al. 2005a) and oceanographic models point to the Mona Passage region as a special barrier to larval transport (Baums et al. 2006a; Galindo et al. 2006). Still, the Mona barrier is by no means universal: some bivalves (Lee and O'Foighil 2005) and

wrasses (Rocha et al. 2005b) show a Caribbean/Floridian break further north instead.

Differences among closely related sympatric species can be informative as well. Rocha et al. (2002) examined the co-phylogeography of three surgeonfishes, all of whose ranges extended from Brazil north into the Caribbean. The single species that could inhabit the soft-bottomed habitat under the intervening Amazon River outflow showed no genetic break, while the two other species with more restrictive habitat requirements did. Thacker (2004) similarly observed the impact of adult habitat, finding greater subdivision among populations of the lagoon-dwelling goby *Gantholepis anjerensis* than its more generalist congener *G. scapulostigma*, despite the longer pelagic larval period of the former. Bird et al. (in press) have likewise found an important role for differences between microhabitats in structuring populations of Hawaiian limpets. Reid et al. (2006) pointed to a major caveat, in that some patterns interpreted as phylogeographic breaks may actually mark abutting distributions of cryptic species specific to different habitats. Specifically, they found that the geographic distributions of closely related littorine gastropods traced continental and oceanic habitats, a pattern that may help explain other phylogeographic breaks in the central Indo-West Pacific (Barber et al. 2000; Lourie and Vincent 2004). These studies show that differences in adult habitats may help explain some of variance in levels of connectivity after only larval dispersal potential has been considered. Despite some common patterns, however, closely related co-occurring species with similar biologies may still differ in population structure (Severance and Karl 2006) and in where phylogeographic breaks lie within their ranges (e.g., Reid et al. 2006).

Within species, the relationship between present day current patterns and inferred patterns of gene flow is generally poor (Shulman and Bermingham 1995; Benzie and Williams 1997; Palumbi et al. 1997; Benzie 1999; Lessios et al. 2003; Reid et al. 2006). To date, most studies looking for relationships between currents and genetic similarity have been based on frequencies (for both allozymes or mtDNA) or sequence similarity (primarily for mtDNA). For both of these types of data, the time required for the influence of migration to equilibrate with genetic drift is long: approximately $(\ln 2)/(2\,m + 1/2N_e)$ generations (where m is the migration rate and N_e the effective population size) to go just half way to equilibrium values in case of F_{ST} (Crow and Aoki 1984; Neigel 1997), or twice the number of generations as number of copies of genes to coalesce in an isolated population (Rosenberg 2003). Thus, patterns of connectivity inferred by these means should reflect only present-day currents that have remained constant for long periods (many thousands of generations or longer). Indeed, some of the few data that seem consistent with present current patterns (Baums et al. 2005a, 2006a) are based on linkage disequilibrum, which should build up and break down at far shorter time scales (see below).

The shadows of history

The history of connectivity is not merely a nuisance that prevents us from seeing patterns of present-day migration. Knowledge of past patterns of connectivity and isolation are necessary for reconstructing the geographic context of species formation (Marko 1998; Meyer et al. 2005), for understanding the assembly of marine communities (Wares and Cunningham 2001), and for designating evolutionary significant units for conservation (Bowen 1999).

Relationships among populations can be inferred from the topologies of genes sampled from those populations. Rocha et al. (2005a), for example, reconstructed the direction of a natural colonization of the tropical Atlantic by the goby *Gnatholepis thompsoni* from ancestors in the Indian Ocean. Coalescent analyses placed a date on the initial invasion as well as expansions within the Atlantic. Such analyses can also put a minimum time of isolation on populations where sampled genes are monophyletic. Taylor and Hellberg (2003) found reciprocal monophyly of mitochondrial sequences between gobies (*E. evelynae*) sampled from Barbados and Curacao; coalescent analyses (Kuhner et al. 1998) suggested these had been isolated for >75,000 years, despite a geographical separation of about 1,000 km and larvae with a 3-week pelagic duration. Populations of a congener (*E. oceanops*) in Belize and Florida had been separated even longer (800,000 years, Taylor and Hellberg 2006).

Interpretation of these analyses warrants some caveats however (see Arbogast et al. 2002). First, using a single locus to infer population history entails the possibility that selection (Ballard and Rand 2005) or other forces acting on this marker (including stochasticity necessarily associated with coalescent processes, Hudson and Turelli 2003) may mislead and the certainty that confidence intervals will be broad. Second, placing dates on events using genetic data entails calibrating a molecular clock, which necessarily adds the variance associated with a Poisson mutational process to the vagaries of figuring just when two populations or species diverged.

Inferences about past changes in population size can be made by considering the distribution of pairwise

differences between sampled sequences (Rogers and Harpending 1992). Lessios et al. (2001) used this approach to test whether the urchin *Diadema antillarum* had expanded its population size recently (perhaps due to anthropogenic disturbances) before its demographic crash in 1983. Inspection of the pairwise distribution plots showed that any expansion of *D. antillarum* greatly preceded expansions inferred for two Pacific *Diadema* species, neither of which attain the densities once seen in *D. antillarum*. Fauvelot et al. (2003) found evidence for past demographic expansions in several co-occurring reef fish they surveyed, which was especially pronounced for lagoon species. They attributed this to the impacts of Holocene sea level changes and subsequent recolonizations.

Pairwise mismatch distributions can also be used to infer past range expansions; genetic evidence for a population expansion should be clear in recently colonized parts of the range, but inferred expansions should not exist in source regions or predate those in other places (Hellberg et al. 2001). Even simpler comparisons can also hint at past range expansions. Gene diversity is relatively low in some Indian Ocean populations relative to their Western Pacific sisters (Reid et al. 2006) and also in some Central Pacific populations of mutualistic shrimp and gobies compared to Okinawa further west (Thompson et al. 2005), suggesting that the less genetically diverse regions may have been founded by propagules from progenitors in more diverse refugia. Such potential colonization events have also been inferred at far smaller spatial scales, as for a single population of *Pocillopora meandrina* differentiated from two others also sampled from Moorea (Magalon et al. 2005). Differences in genetic variation where the less variable population is not a subset of a larger source may indicate population isolation, as for several disparate species of coral on Lord Howe Island, at the southern end of the Great Barrier Reef (Ayre and Hughes 2004).

Present-day patterns of connectivity

The exchange of migrants in the present day does not draw a genetic picture of reef connectivity on a clean canvas. The image rests on top of, and may bleed into, earlier genetic traces. Separating these can become critical, as when trying to determine whether two genetically similar populations are exchanging a few migrants in the present or have become isolated in the recent past.

Nielsen and Wakeley (2001) developed a Markov chain Monte Carlo approach (IM, isolation with migration) to address this problem. IM simultaneously estimates divergence times and asymmetrical migration rates between pairs of populations, along with effective population sizes for the two populations and their common ancestral population (see also Hey and Nielsen 2004). This approach can be used to distinguish whether two populations are isolated, presently exchanging migrants, or some combination of the two. Lessios and Robertson (2006) applied this method to the longest standing question in reef connectivity: whether there is ongoing exchange across the Eastern Pacific Barrier first noted by Darwin (1859) in *The Origin of Species*. Not only was ongoing gene flow evident for many of the reef fish they examined, but the direction of dispersal was sometimes opposite the west-to-east direction generally predicted. Despite the apparent success of this application of IM, however, this approach may not find broad utility in reef connectivity studies due to some limiting assumptions. Among them, the model is based on a single population that has split into two (and only two) isolated daughter populations.

An alternative way of simultaneously analyzing population size and pairwise migration rates is provided by the program MIGRATE. Earlier versions of this program (Beerli and Felsenstein 2001) were based on maximum likelihood estimates, and could prove computationally intensive. The most recent version uses a Bayesian framework, which is faster and more accurate (Beerli 2006). Richards et al. (2007) used new version of MIGRATE to infer levels and direction of gene flow in three Caribbean sponge-dwelling invertebrates (two gammarids and an ophiuroid), and found evidence countercurrent dispersal in the Florida Keys in one of their study species.

To this point, the genetic approaches discussed have been reducible to variation in either state or frequency at individual loci. Combining results from different loci may increase precision, but provides no synergistic effect. Exciting new analyses simultaneously utilize information derived from the allelic states of different loci (collectively called the multi-locus genotype) from the same individual (see Manel et al. 2005). One family of approaches identifies recent immigrants (those that have arrived in the last few generations) by the mismatch between their multi-locus genotypes and the range of genotypes expected for the population from which they were sampled (Paetkau et al. 1995; Rannala and Mountain 1997; Cornuet et al. 1999; Wilson and Rannala 2003). These techniques offer the genetic means to evaluate migration between populations in ecological terms (as m, the migration rate) over ecological time, not as a number of individuals (Nm) averaged

over thousands of generations (and subject to many unrealistic assumptions) produced by F_{ST}-based estimators. The power of these analyses has been demonstrated empirically by comparison to mark-recapture data for lizards (Berry et al. 2004). For *A. palmata*, this approach suggested patterns of migration among populations that are consistent with known current patterns during the spawning season (Baums et al. 2005a, 2006a).

While these techniques promise to reveal some of the patterns of connectivity we seek, some important caveats must be considered. One is the problem of unsampled "ghost" populations that exchange migrants with sampled populations and can potentially alter inferred patterns of dispersal. Slatkin (2005) found that ghost populations could create the appearance of connectivity between populations not directly exchanging migrants. This is a special concern for broadly distributed reef taxa, where exhaustive sampling is logistically unfeasible (unlike for Berry et al. 2004's lizards). Perhaps, more worrisome is the implicit assumption of high levels of self-recruitment made by some of the software implementing these approaches. BAYESASS (Wilson and Rannala 2003), for example, sets maximum total immigration at 30% (as noted by Baums et al. 2005a), meaning that populations cannot drop below 70% self-recruitment; fair enough for skinks in rock piles, but a consequential assumption for potentially open marine populations where we need genetic approaches to delineate patterns of connectivity. A randomization of genotypes with respect to population of origin quickly reveals this constraint, and is worth doing for any analysis.

Multi-locus genotyping can also be used to identify and define populations that have been isolated for only a modest number of generations. Classical measures of population structure (e.g., F_{ST}) require a priori designation of populations. Pritchard et al. (2000) developed clustering methods that use multi-locus genotypes from highly variable loci (usually microsatellites) to circumvent this problem. These analyses (implemented by the program STRUCTURE) work by assuming that loci are not physically linked and show no linkage disequilibrium (nonrandom associations between alleles at different loci) within freely interbreeding clusters. Individual genotypes are assigned to different clusters to minimize linkage disequilibrium within clusters, and the number of clusters can be estimated. Because linkage disequilibrium can build up and break down quickly, this approach can discriminate between groups genetically isolated for just a short time (as few as 20 generations; see Rosenberg et al. 2001; Wang et al. 2003 for empirical examples; Waples and Gaggiotti 2006 for simulations). Baums et al. (2005a) used STRUCTURE to reveal a surprising pattern of population differentiation in *A. palmata*. Despite subtle allele frequency differences among localities (F_{ST} ranged from 0.012 to 0.094 for the five loci), STRUCTURE distinguished genotypes to the west and east of the Mona Passage (with Puerto Rican individuals showing mixed ancestry), a region where coupled biophysical models indicate that eddies steered by the steep topography may reduce cross-passage flow (Baums et al. 2006a) during the spawning season. Thus, the few marine applications of new genetic approaches targeted at ecological times scales appear to agree with observed current patterns more often than do genetic approaches that integrate over longer time scales. These clusters also seem to constitute biologically different units for conservation purposes: *A. palmata* populations in the two regions differ in their clonal structure, suggesting different strategies for their management (Baums et al. 2006b).

Future

New genetic analyses should deliver some of the patterns of connectivity long promised to reef biologists. For one thing, new analyses hold promise for disentangling the influences of past isolation from present day migration (Nielsen and Wakeley 2001). This approach also may help distinguish recently diverged sister taxa from older species pairs that have continued to hybridize (especially among mass spawning *Acropora*; e.g., Márquez et al. 2002).

Second, multi-locus genotyping approaches that employ linkage disequilibrium as the currency of differentiation among populations (e.g., STRUCTURE, Pritchard et al. 2000; BAYESASS, Wilson and Rannala 2003) offer the possibility of detecting the build up and break down of isolation on short time scales, perhaps down to a single generation. Populations delineated by STRUCTURE might also serve as objective input for other analyses (such as MIGRATE and IM) that require populations to be defined a priori. The short times over which these linkage-based methods operate also offer opportunities to infer the impact of recent anthropogenic changes on connectivity (e.g., Zartman et al. 2006). Such changes might include the breakdown of corridors to dispersal, the imposition of artificial stepping stones (e.g., oil rigs), or the restoration of previously damaged ones.

New analyses, combined with the rising rate at which genetic data can be generated, will no doubt lead to novel insights about reef connectivity. Still, some questions about reef connectivity will not be answered

by genetic means alone because critical values of dispersal, such as the tipping point between demographically self-sustaining and dependent populations, may occur at relatively high levels of gene flow where the power of genetic inference is lowest (Waples and Gaggiotti 2006). Resolving such connectivity issues in these cases will require greater integration of genetic data with oceanographic (James et al. 2002; Baums et al. 2006a; Cowen et al. 2006; Galindo et al. 2006) and ecological approaches (Planes et al. 2002; Jones et al. 2005). Together, these analyses should provide a sharper picture of the movements past and present that connect reef populations.

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