

REPLY COMMENT

Discernment of sexual recruits is not critical for assessing population recovery of *Acropora palmata*

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ABSTRACT: Miller et al. (2007; Mar Ecol Prog Ser 335:227–231, this volume) dispute the ability of visual surveys to distinguish between colonies of *Acropora palmata* formed by sexual and asexual processes. They argue that approaches that do not consider genetic diversity are not appropriate for assessing population recovery. Visual surveys are clearly not reliable for distinguishing colony origin; however, the significance of the findings in Miller et al. (2007) for assessment of population recovery is not clear. While genetic diversity may indeed be important for population survival and species persistence, our study (Grober-Dunsmore et al. 2006; Mar Ecol Prog Ser 321:123–132) assessed population recovery by temporally sampling demographic attributes which are critical for ecosystem function (e.g. topographic complexity) over shorter ecological timescales. Ideally, genetic studies should be contextualized with demographic and other environmental and ecological data to improve our understanding of processes that lead to population persistence. However, without having historical genetic data from *A. palmata* populations, or being able to distinguish which genets are more or less resilient, or being able to identify source–sink dynamics, genetic tools presently offer limited information for assessing population recovery of *A. palmata*.

KEY WORDS: Acroporid · Caribbean Sea · Clones · Microsatellites · Recruitment

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Assessing coral community recovery

Recovery of coral communities has been assessed historically by quantifying changes in coral cover, colony abundance, population densities, and size class distribution (Colgan 1987, Connell et al. 1997). An increase in one or more of these attributes generally indicates a trajectory toward demographic recovery (Hughes & Tanner 2000). Numerous field studies (e.g. Jordan-Dahlgren 1992, Edmunds & Carpenter 2001, Rogers et al. 2003, Grober-Dunsmore et al. 2006) have used demographic measures as indicators of potential recovery of Caribbean *Acropora palmata* populations from the mass mortality of the 1980s, in part because these measures are cost-effective, easy to sample,

informative, and comparable to historical data. For example, long-term studies of quadrats in Jamaica documented loss of corals, followed by recent increases in recruits and coral cover (creating 3D structure) (Woodley 1999, Woodley et al. 1999, Edmunds & Carpenter 2001). These measures were related to changes in the environment, e.g. densities of echinoid grazers, and used as indicators of the recovery trajectory of the coral communities.

Miller et al. (2007, this volume) have critiqued this approach, suggesting that demographic measures are necessary, but not sufficient to assess recovery of clonal invertebrates; they argue that some measure of genetic diversity is 'quintessential'. We agree that genetic diversity is indeed important for long-term

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survival and persistence of populations in general, and that the suite of emerging molecular tools to characterize the genetic structure of coral populations will help us understand genetic variation within and among local populations. However, such molecular studies are in their infancy. Consequently, 'normal' levels of genetic diversity are not understood for any coral population or species over ecologically relevant scales of space or time. Furthermore, little is known about the importance of genetic diversity of residual populations as it relates to persistence and, in this case, recovery of *Acropora palmata* around the island of St. John, US Virgin Islands.

Miller et al. (2007) raise an excellent point: visual sampling cannot reliably distinguish between recruits arising from sexual propagules and those arising from asexual propagules. It should be noted, however, that the term 'recruitment' in our study refers to the addition of new members to a population (Richmond 1997), without implication of sexual or asexual origin. We and others (e.g. Jordan-Dahlgren 1992, Rogers et al. 2003; also see Bruckner 2003) have only suggested that new recruits (<15 cm in maximum dimension) were likely to be of sexual origin based on the absence of colonies in prior sampling, previous population abundance and size distribution, colony appearance, and existing genetic data. We acknowledge that colony origin cannot be ascertained without appropriate genetic tools.

Challenges for assessing recovery of *Acropora palmata*

The broad suite of reproductive tactics employed by *Acropora palmata* presents some interesting challenges for assessing recovery. Foremost, *A. palmata* is able to generate asexual larvae, either by parthenogenesis or self-fertilization. The prevalence of this may be more common than previously thought (e.g. Baums et al. 2005a). In their study, 51 of 304 (17%) of the larvae resulting from attempted sexual crosses contained only maternal genotypes, and an additional 12 larvae were generated from self crosses. Polyp bail-out is an additional mode of asexual reproduction where polyps detach themselves from their parent colony, drift to disperse, and re-settle if they encounter suitable substrate (Sammarco 1982). While rarely documented in any coral (Richmond 1997, Domart-Coulon 2004), polyp bail-out may occur in *A. palmata*. Such asexually-produced larvae and propagules may have dispersal potential similar to sexually-generated larvae, making determination of larval origin difficult without comprehensive sampling of populations across broad spatial scales. Unless a sampling scheme captures the genetic diversity across a potentially interconnected popula-

tion (by fragmentation, or asexual or sexually derived propagules), genetic methods (e.g. Miller et al. 2007) will overestimate the proportion of 'sexually'-derived individuals and underestimate the number of asexually-derived individuals.

Partial mortality of colonies and resheeting of relict framework further complicate assessment of recovery. Partial mortality can divide larger colonies into smaller die-back colonies (Hughes & Jackson 1980), or remnants, which may be difficult to distinguish from framework that is being re-sheeted and/or colonized by new recruits (Bonito & Grober-Dunsmore 2006). To minimize misclassification of remnant colonies as new recruits, Grober-Dunsmore et al. (2006) underestimated potential new recruits by placing remnant/resheeting colonies in a separate class based on the maximum dimension of living tissue. Loose fragments and encrusting colonies not on relict framework were recorded separately. In spite of this conservative approach, we still found considerable increases in colony abundance, and we suggested that recovery may be occurring based on changes in size class distributions over time. Miller et al. (2007) critiqued our use of size class information to infer recovery, based on their sampling of 2 patches of *Acropora palmata* with similar size class distributions that differed to extremes in clonality. We agree that size frequency distribution data may be misleading, since colony size may not be directly related to age or origin, and the formation of die-backs can increase the number of individual colonies. However, size class data provide reliable estimates of habitat complexity and ecosystem services provided by the corals (e.g. refuge and foraging habitat for fishes and invertebrates), and combined with long-term monitoring size class data are useful for assessing colony survivorship.

Genetic diversity and recovery

Miller et al. (2007, p. 4 of Comment) argue that genetic diversity is a 'quintessential component of recovery'; we challenge this statement and propose that the jury is still out on whether genetic diversity is a necessary precursor for *Acropora palmata* recovery. While high genetic diversity may promote species resilience, scientists have little understanding of the genetic diversity of *A. palmata* populations prior to the die-off. Perhaps populations were represented by a relatively homogeneous genetic pool, which contributed to their widespread susceptibility to disease, or certain areas (e.g. continental reefs of Florida) may have been more clonal, and other areas (e.g. oceanic reefs such as Navassa) may have had more sexual recruits, due to more differences in current patterns and water quality

conditions, factors which affect larval supply and recruitment potential. To what extent genetic diversity was reduced during the mass mortality remains unclear. White-band disease may have served as a strong selective agent, killing a large number of non-resistant genotypes. If so, genetic diversity throughout the region may have been depressed, potentially inhibiting the adaptive response ability of surviving populations. Conversely, those genotypes that survived in the remnant stands may be those that are best suited to existing conditions, and thus apt to thrive. What remains to be seen is whether genetic diversity in surviving populations allows *A. palmata* to persist over short (ecological) and longer (evolutionary) time scales.

Scientists have yet to ascertain the importance of genetic diversity in *Acropora palmata* populations, in part because of the high variability found between locations (100s km), between reefs within locations (1 to 10 km), and within individual reef patches (meters). Baums et al. (2005b) sampled *A. palmata* at 11 locations (1300 colonies across 48 reefs) and found that the incidence of unique genets ranged from 15% (Florida) to 100% (Navassa) among locations. Within locations, the percent of unique genets also varied highly (e.g. 25 to 96% among reefs in Mona). Furthermore, there is considerable variability in genetic diversity within distinct reef patches (Baums et al. 2005b, 2006). In Panama, adjacent patches (15 m radius) separated by just 1.5 m had 24 and 65% unique genets (Baums et al. 2006). Around the island of St. John, high genetic variability among reefs was also found (Baums et al. 2005b, 2006). At Hawksnest, a sample reef common to both the Baums et al. (2006) and Grober-Dunsmore et al. (2006) studies, 37% of the colonies sampled were unique genets, despite the high potential for fragmentation at this site. Just 2 km offshore from Hawksnest at Johnson's Reef, 70% of sampled colonies were unique genets (Baums et al. 2006).

Sampling scale is critical, as is the scale at which critical genetic processes occur, since this has important implications for the management of *Acropora palmata* populations. The high variability in genetic data suggests that caution is warranted when attempting to extrapolate results from small to large spatial scales. Many field studies assessing *A. palmata* population recovery, including ours, collected data across entire reef areas on spatial scales of kilometers to 10s of km. Miller et al. (2007) and Baums et al. (2005a,b, 2006) sampled reefs on a much finer scale (<50 m) and less thoroughly across island localities. Unfortunately, genetic tools developed to date cannot reveal the source of specific genets, thus providing little insight into source-sink dynamics. Determining the origin of larvae, directionality of genetic exchange and the

identity of 'successful' genets are crucial questions that molecular tools may help answer in the future. Toward this end, genetic studies should be contextualized with demographic information to determine which phenotypic traits make specific genotypes more or less successful under different reef conditions.

Potential mechanisms of recovery

The number of *Acropora palmata* colonies has increased in multiple locations around the Caribbean region (Bruckner 2003), though the mechanisms driving this are not understood. Demographic recovery, whether primarily sexually- or asexually-driven, appears to be occurring in many locations, undoubtedly providing key ecosystem services for thousands of species (Knowlton 2001). Spawning has been observed throughout the region, including St. John (R. Grober-Dunsmore & V. Bonito pers. obs.). In places with surviving dense patches of *A. palmata*, fragmentation may be a dominant mode of reproduction (Highsmith 1982). Dormancy and emergence could represent another potential source of recruits, although there is no published evidence that living tissue survived in apparently dead frameworks since the 1980s. The rapid appearance of new colonies in places where no or few surviving colonies remained suggests that larval recruitment (of sexual or asexual origin) may play a prominent role in the recent increase in colonies (Bruckner 2003). Interestingly, this increase coincides with the appearance of large numbers of *Diadema antillarum* throughout the region (e.g. Edmunds & Carpenter 2001).

Management implications

The ability to distinguish individual genotypes of corals will allow the opportunity to address a large number of research questions, though the application to current management decisions is debatable. Historically, management of *Acropora palmata* has been concerned with increasing or replacing colonies (albeit indirectly). In general, management actions focus on a reduction of stresses that may inhibit such recovery, rather than on an increase in genetic diversity. Demographic surveys (e.g. Grober-Dunsmore et al. 2006) provide critical data on abundances and size frequency distributions that can be used to evaluate the effectiveness of specific management actions. With limited resources available for management efforts, managers need to weigh the costs and benefits of different approaches for assessing recovery, and for identifying alternative management actions.

The long-term prognosis for *Acropora palmata* recovery is unclear. The definition of a point in time when recovery might be considered 'complete' varies (Brown 1997). Historically, recovery has been defined as a restoration of pre-disturbance levels of coral cover, colony abundance, population densities, and/or size class distribution (Colgan 1987, Done 1992, Connell et al. 1997, Hughes & Tanner 2000). However, there is little current consensus within the scientific community on the definition of 'recovery', and whether or not recovery should include a genetic component, in part because of a lack of historical baselines for the now highly perturbed populations. Molecular tools that are able to identify source–sink dynamics and distinguish which genets are more or less resilient to various stresses would be invaluable for management decisions. However, at present, visual surveys provide an integrated approach for acquiring cost-effective and relevant ecological information about *A. palmata* populations. Ideally, demographic and genetic information on these populations should be coupled across a range of spatial and temporal scales to fully understand population level processes, in order to make informed resource management decisions.

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