Connectivity and stability of mesophotic coral reefs

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ABSTRACT

Mesophotic coral ecosystems (MCEs), occurring at depths of 30 to over 150 m, represents the deep continuum of adjacent shallow coral reefs about which little is known. These reefs are most developed, and most frequently studied, in areas where light penetration is high and photosymbiotic reef-builders (corals) can persist as common members of the benthic community. The upper mesophotic zone typically extends to 60 m and comprises communities that are generally similar to those found in shallow reef systems. Below 60 m, the lower mesophotic zone is dominated by sponges and algae that are uncommon or absent from shallower areas, and a fish fauna that is largely specialized to these intermediate depths. It is likely that these ecosystems are much more widespread and important than was previously recognized. MCEs have the potential to function as refugia for shallow reefs because many disturbances in the upper 30 m may leave MCEs largely intact. Ontogenetic movement and spawning migrations by reef fishes provide an important ecological component to connectivity between shallow and mesophotic reefs and may represent the effective range of larval dispersal. However, there is currently limited information on genetic connectivity between deep and shallow coral reef populations, and this is a critical gap in understanding the role of MCEs in coral reef resilience. Here we review the connectivity and trophic relationships between the shallow and mesophotic coral reefs, the potential role of MCEs as refugia, and the effects of a new biological invader that exposes critical gaps in our understanding of the stability of these ecosystems.

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1. Introduction

As shallow-water coral reef ecosystems worldwide continue to decline (Wilkinson, 2000), identifying and protecting areas where biodiversity is maintained and reef communities remain intact, have become an important conservation priority (Glynn, 1996; Pikitch et al., 2004). Resource managers and conservation scientists alike have embraced the creation of networks of marine protected areas (MPAs) as the best way to ensure the persistence of these ecosystems in the face of multiple interacting stressors. These networks rely on the assumption that protected areas will serve as sources of larval recruitment for denuded reef areas further downstream, and research on MPAs has therefore focused on the size and spacing of reserves, and on the hydrodynamic current patterns connecting them (Agardy, 1997; Ogden, 1997; Halpern and Warner, 2002; Palumbi, 2003; but see Sale et al., 2005; Baums et al., 2006). In its broadest sense, this connectivity emphasizes linkages across spatial scales and temporal scales (i.e., demographic vs. evolutionary dimensions), gene flow between populations, and trophic energy interactions. In the context of this review,

"connectivity" is defined to be inclusive of all of these considerations unless otherwise specified. Recent advances in our understanding of connectivity suggest that early estimates of potential dispersal are probably too large (Roberts, 1998). Although long distance dispersal has been documented (e.g., Lessios and Robertson, 2006; Newman and McConnaughey, 1987; Shulman and Birmingham, 1995; Victor, 1986), hydrodynamic models that incorporate larval behavior indicate that long-distance dispersal may not sustain broad open populations (Baums et al., 2006; Cowen et al., 2000, 2006), and recent studies have documented distinct subpopulations over spatial scales of less than 100 km (e.g., Barber et al., 2002; Brazeau et al., 2005; Purcell et al., 2006). An increased emphasis is now placed on closer and more frequent spacing of MPAs to accommodate lower effective connectivity.

Closely-spaced shallow-water coral reef MPAs may be equally exposed to broad-scale climatic events such as coral bleaching and ocean acidification (Hoegh-Guldberg, 1999; Hoegh-Guldberg et al., 2007; Hughes et al., 2003; Kleypas et al., 1999), as well as various anthropogenic stressors (Nowlis et al., 1997). Consequently, recovery of degraded shallow reefs may be significantly limited if it is solely dependent on recruitment from shallow reefs. To date, research on coral reef connectivity has emphasized two-dimensional connections between sources and sinks. Although biophysical models of connectivity do take depth and larval behavior into account, the notion that the

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deepest portion of a reef might serve as potential sources of recruits for adjacent shallow reefs has not yet been investigated. Even if relative vertical (deep-shallow) distances are greater, on a per-meter basis, than horizontal (shallow–shallow) distances, deep reefs may still be less constrained by physical barriers than other shallow reefs. Consequently, the connectivity of deep reefs and their adjacent shallow counterparts might be much greater than between relatively distant shallow reefs. In this review, we assess what is known of the genetic, and trophic interactions between deep and shallow reefs, and the potential role of stable deep reefs as refugia for shallow reef species. We also highlight critical gaps in our understanding, and show how linkages between these relatively understudied habitats and other important tropical ecosystems may improve the success of conservation strategies in the marine tropics.

1.1. Mesophotic coral ecosystems

Reef-building corals, and their associated benthic community, are primarily found in relatively shallow water (<30 m) throughout the tropics, due in part to light limitations of the symbiotic photosynthetic zooxanthellae. However, it now appears that some of these species may not be as depth-limited as previously thought (e.g., Lesser et al., 2010). The physiological constraints of SCUBA, and the high costs of submersible use, have forced most marine biologists to focus their research efforts on shallow coral reefs. The advent of technical diving has provided a glimpse into the deep reef communities (Lehnert and Fischer, 1999), now known as "mesophotic coral ecosystems" (MCEs: Lesser et al., 2009). Often these deeper reefs represent extensions of the nearby shallow reef communities with species-specific adaptations that result in a unique community structure (Khang and Kelley, 2007; Rützler and Macintyre, 1982). In other cases, geomorphology can form natural barriers resulting in well-defined species boundaries and unique biodiversity (Liddell et al., 1997). One of the most obvious abiotic differences on MCE reefs is the low irradiance of photosynthetically active radiation (e.g., PAR irradiance in the Bahamas is 2100 μmol - quanta m^{-2} sec^{-1} at the surface and only 45 μmol quanta m^{-2} sec^{-1} at 100 m: Lesser et al., 2009, 2010). A few deep-adapted zooxanthellate corals and algae exist in this community, but overall percent cover of photosynthetic organisms is significantly lower than on the nearby shallow reefs (Smith et al., 2004; Grigg, 2006; Lesser and Slattery, 2011). In the Caribbean, sponges dominate these deeper reefs, and their size typically exceeds that of shallow reef conspecifics (Reed and Pomponi, 1997). However, in some areas, especially where the bottom substrate is made up of calcareous cobble and sand, large macrophytes can dominate space (e.g. Leichter et al., 2008). MCE reef organisms, particularly filter feeders, may compensate for the lack of primary production through nutrients transported by internal waves (Leichter and Genovese, 2006) which fuels picoplankton production that, in turn, is consumed by sponges (Lesser, 2006). In addition, geomorphology and hydrodynamic processes can have a tremendous impact on deep reef ecology (e.g., Khang and Kelley, 2007; Liddell et al., 1997) and resilience (Bak et al., 2005). To date, the mesophotic zone remains relatively understudied compared to other reef habitats (Menza et al., 2008), although recent reviews document potentially important biodiversity at a number of MCE sites worldwide (Khang et al., 2010; McClain and Barry, 2010; Rooney et al., 2010).

1.2. Genetic connectivity between deep- and shallow-reefs

Issues of connectivity are being vigorously debated, and have practical implications for the management and establishment of marine protected areas (Cowen and Sponaugle, 2009; Hedgecock et al., 2007; Hellberg et al., 2002). Long-distance dispersal and open populations had been accepted as the operating mode for most broadcast spawning populations but recent work has suggested that many populations of marine organisms experience more local larval retention than previ-

ously thought, while other populations receive significant subsidies from other populations (Cowen and Sponaugle, 2009; Hedgecock et al., 2007). We now have a better understanding that the ecological consequences of the variability in connectivity is a function of life history, dispersal mode, and oceanography and is highly variable both spatially and temporally (Gaines et al., 2007). Most of our understanding of connectivity comes from the genetic variability of geographically dispersed marine species over 10's to 1000's of km but understanding the variability in connectivity of populations over strong vertical gradients in the abiotic environment, such as occurs from shallow to mesophotic reef depths, would have profound effects on our understanding the genetic differentiation of populations over short spatial scales (Swearer et al., 2002). This would also have important implications for management and conservation strategies for mesophotic coral reefs. Additionally, corals and sponges exhibit both brooding and broadcasting reproductive strategies and these different life-history characteristics should have significant effects on gene flow, and therefore connectivity, between populations.

To understand the evolutionary underpinnings of mesophotic reef diversity, it is necessary to quantify dispersal among these habitats, and between the mesophotic and shallow reef ecosystems. At present there is limited data to evaluate genetic connectivity between shallow and MCE reefs; however, the high level of endemism in the lower mesophotic zone indicates a limited role in replenishing depleted near-shore reefs. Thresher and Colin (1986) observed that a high proportion of fish at 60–150 m did not inhabit shallower (30–60 m) or deeper (150+ m) realms. Porter (1973) observed that "these depths are occasionally visited by opportunistic species from above, but primarily they lie in a twilight zone belonging neither to the shallower water species nor the abyssal species, but to the intermediate dwellers themselves." Contrary to these observations at 60–150 m, the upper limit of the mesophotic zone (30–60 m) is inhabited by many shallow reef species, as indicated by the depth ranges reported for common reef fishes (Randall, 2007). Furthermore, many of the prominent fish families on coral reefs include species that span shallow and deep MCE zones, such as the Acanthuridae, Chaetodontidae, Pomacanthidae, Pomacentridae, Serranidae, Grammatidae, Scarridae, Holocentridae, Apogonidae, Sciaenidae, Muraenidae, and Carangidae. Biogeographic surveys of mesophotic reef fish have documented greater endemism and more restricted ranges than shallow reef fish. Pyle (2000) observed a 53% overlap in the shallow reef fish fauna of Palau and Papua New Guinea, but only a 5% similarity in the mesophotic reef fish fauna. Based on these considerations, it seems likely that the upper mesophotic zone (30–60 m) can function as a refuge for shallow reef organisms, whereas the reef below this zone has higher endemicity and fewer taxonomic links to shallow reefs. However, this conclusion suffers from a comparatively low number of studies on mesophotic reefs relative to shallow reefs (Menza et al., 2008).

Ontogenetic movements and spawning migrations by reef fishes, decapod crustaceans and gastropods provide a potentially important ecological component of connectivity between shallow and mesophotic coral reefs. The evidence for ontogenetic movements between shallow and mesophotic reefs is based on variability in abundances of life history stages (Nagelkerken and van der Velde, 2003). Typically juveniles are found in nearshore coastal habitats (e.g., seagrass beds, mangroves, or estuaries), while adults dominate the offshore deep reef habitats (Blaber et al., 1989; Blaber and Blaber, 1980; Sheaves, 1995). Spawning aggregations also provide an important mechanism of connectivity between shallow and mesophotic reefs. They can encompass hundreds to thousands of individuals that migrate short distances ("resident": <5 km) to daily spawning sites, or migrate over larger spatial scales ("transient": 5 to >200 km) for annual spawning events (reviewed by Domeier and Colin, 1997; Nemeth, 2009). In addition, these episodic spawning migrations may have a significant effect on local energetic transfer as biomass fluctuates over vertical depth gradients (Hamner et al., 2007; Meyer and Schultz, 1985).

Many reef-building corals host symbiotic dinoflagellates in the genus *Symbiodinium* whose autotrophic inputs contribute to the metabolic needs of their hosts and help them calcify fast enough for reefs to accumulate. Thus a change in symbiont structure/function with depth has the potential to significantly impact MCEs through their effects on the productivity of the holobiont. Diekmann et al. (2003) and Frade et al. (2008) examined the community structure of *Symbiodinium* in the scleractinian genus *Madracis* at one site in Curaçao and found a novel symbiont taxon (B15) that appears to be specialized to deep environments (>25 m). Similarly, Bongaerts et al. (2010a) identified a *Symbiodinium* type (C33) that was particularly abundant in *Seriotopera hystrix* on mesophotic reefs of the Great Barrier Reef. Lesser et al. (2010) examined zooxanthellae genotypes within the broadcast spawning coral *Montastraea cavernosa* over a depth gradient of 3 to 91 m in the Bahamas. A total of sixteen *Symbiodinium* ITS2 sequences were recovered, including eight novel sequences and seven haplotypes specific to MCE depths. Based on a multidimensional scaling (MDS) analysis there were significant differences in *Symbiodinium* genetic diversity between shallow (3–45 m) and mesophotic (61–91 m) samples of *M. cavernosa* (Lesser et al., 2010). Taken together, these results suggest that the degree of connectivity among symbiont populations may depend on the mode and timing of symbiont acquisition for the coral host in question.

So, is there genetic connectivity between mesophotic- and shallow-reefs? To date there have been few studies that have specifically attempted to address this question. Even between shallow reef habitats the question of genetic exchange is still equivocal (Bowen et al., 2006; Cowen et al., 2000; Mora and Sale, 2002; Taylor and Hellberg, 2005). For example, pygmy angelfishes (genus *Centropyge*) are characterized by a broad depth distribution, but many species occur primarily or exclusively in depths greater than 30 m (Pyle, 2003). An analysis of mtDNA cytochrome *b* in the Pacific flame angelfish (*Centropyge loriculus*) revealed no population structure across 5700 km of the central–west Pacific (Schultz et al., 2007). Slower water movement at depth may diminish the potential for long distance dispersal and provide a greater opportunity for allopatric speciation. However, this hypothesis remains untested and there is implicit data to suggest that internal waves and/or upwelling might still provide a mechanism to transport progeny between mesophotic- and shallow-reef depths (Leichter et al., 1998, 2008; Leichter and Genovese, 2006).

At mesophotic reef depths fish dispersal may be rather limited. The goldband snapper (*Pristipomoides multidens*) that occurs in rocky habitats from 40 to 245 m throughout the Indo-Pacific has a strong population structure across 1500 km of ocean between Australia and Indonesia (Ovenden et al., 2002). Likewise, the endemic Hawaiian grouper (*Epinephelus quernus*) that occurs from shallow depths to at least 350 m throughout the 2000 km length of the entire archipelago (Randall, 2007) also exhibits significant population structure based on mtDNA control region sequences (Rivera et al., 2004). This site-specific genetic structure is likely due to low dispersal as larvae and adults, and possible loss of larval cohorts by prevailing currents (Ovenden et al., 2004; Rivera et al., 2004). Benthic species also exhibit distinct genetic populations within deep reef communities. For example, the black coral *Antipathes fiordensis*, an endemic to fiords of SW New Zealand, produces weak swimming pelagic larvae with limited ability to disperse. Accordingly, this antipatharian exhibits significant overall population structure, and genetic partitioning between fiords separated by as little as 15 km (Miller, 1997). The azooxanthellate scleractinian coral, *Lophelia pertusa*, is thought to have a global distribution at a depth range of 200 to 1000 m. At 10 sites across the northeast Atlantic, Le Goff-Vitry et al. (2004) observed significant overall population structure, a modest genetic partitioning between coastal (fiord) sites, and a strong genetic break between coastal and offshore habitats. While these cold-water deep reef systems are physically disconnected from tropical reefs (Roberts et al., 2006), they share similar community-structuring abiotic conditions with MCEs (see Lesser et al., 2009 for review).

More recently the genetic structure of the Caribbean coral, *Montastraea cavernosa*, from Little Cayman Island, Lee Stocking Island Bahamas, and San Salvador Bahamas, at Shallow (3–10 m), Medium (15–25 m), Deep (30–50 m) and Very Deep (60–90 m) depths was examined using amplified fragment length polymorphisms (AFLP) (Brazeau et al., in review). The AFLP technique is one of a number of DNA fingerprinting procedures that takes advantage of the polymerase chain reaction (PCR) to amplify a limited set of DNA fragments from a specific DNA sample (Blears et al., 1998). AFLP fingerprints can be used to distinguish very closely related organisms, and the dependence on sequence knowledge of the target genome is eliminated. Most importantly, AFLPs have been shown to be reproducible and reliable. This is at least partially due to the fact that limited sets of generic primers are used and these are annealed to the target under stringent hybridization conditions. The large number of bands generated gives an estimate of variation across the entire genome, thus giving an excellent picture of the level of genetic variation. This is an especially powerful technique to ask questions about gene flow and larval dispersal over spatial scales of meters to kilometers (Amar et al., 2008; Brazeau et al., 2005). Using discriminant function analysis (DFA), two statistically significant discriminant functions were computed. A scatter plot of the canonical scores for each individual shows clear discrimination between all locations (Fig. 1A). The scatter plot for groups based upon depth also exhibit clear differences with some overlap among the shallow and medium depth populations suggesting greater genetic similarity between samples collected from these two groups which are significantly different from the deep and very deep populations (Fig. 1B). These data suggest limited dispersal of this broadcast spawning coral over large spatial scales and possible movement of individuals in a stepping stone pattern from shallow to deep depths. Mechanistically, this type of pattern could be due to larval dispersal patterns forced by oceanographic conditions, or to local selection. Since we have sampled only adults to date we cannot differentiate between the direction of connectivity or the mechanisms (Brazeau et al., in review). However, these results are similar to those of Bongaerts et al. (2010a), on the Great Barrier Reef Australia, where local selection local selection for specific symbiont genotypes was the most parsimonious explanation for host genetic patterns. Interestingly, the pattern of AFLP genotypes between shallow and mesophotic corals described above matches very well with the depth distribution of the corresponding *Symbiodinium* genotypes from the same exact coral samples (Lesser et al., 2010).

1.3. Trophic connectivity between deep- and shallow-reefs

Despite the fact that coral reefs occur exclusively in oligotrophic waters, they are considered to be one of the most productive ecosystems in the world (Muscatine 1990; Sorokin, 1990). The productivity and main source of energy for a particular part of the reef largely depends on the availability of solar irradiance, nutrients and suspended organic matter; each of these factors may change with depth (Lesser et al., 2009). For sponges, transplant experiments showed that deeper habitats are more conducive to higher growth rates than shallow habitats (Trussell et al., 2006). The applicability of this pattern for mesophotic depths is supported by observations in Florida, Belize and the Bahamas, where the size distribution and growth rates of the sponges *Callyspongia vaginalis*, *Agelas conifera*, and *Aplysina fistularis*, and their particulate food supply, increases with increasing depth (Lesser, 2006). Additionally, the biomass and biodiversity of sponge species increase with depth in the mesophotic zone throughout the Caribbean (Reed and Pomponi, 1997; Slattery, personal observation).

The sponge *A. conifera* changes significantly in $\delta^{15}N$ and $\delta^{13}N$ stable isotope signatures over the depth range of 9–91 m with a significant depletion in the carbon signature, and enrichment in the nitrogen signature, over the depth range (Fig. 2). Both isotopic signals are a combination of several sources; the sponge tissue signal, the signal of the resident microbial communities, and the signal of the picoplankton
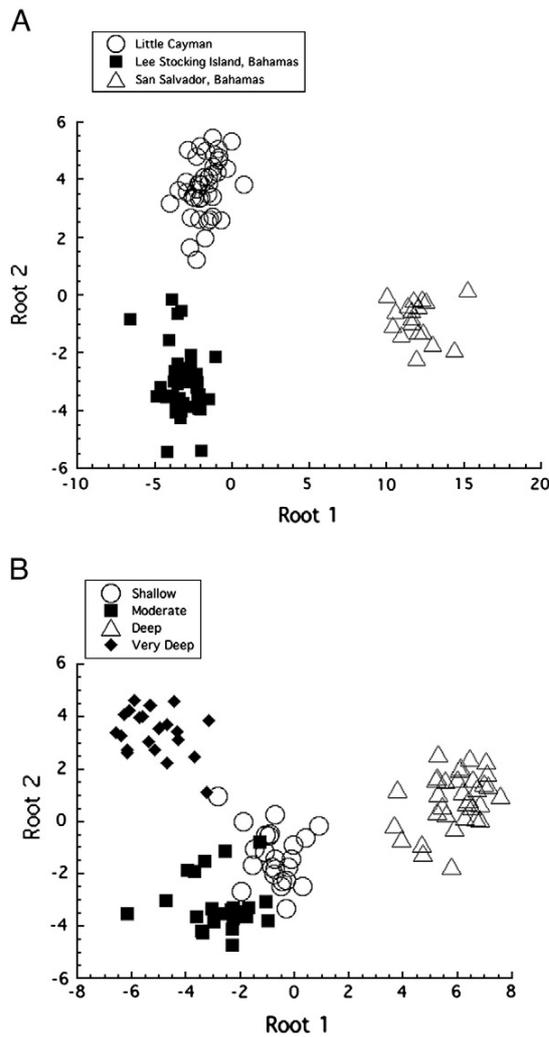
A

B

Fig. 1. AFLP analysis using three sets of selective AFLP primers for host tissues of *Montastraea* cavernosa (see Brazeau et al., 2005 for details). A total of 105 coral samples were analyzed from three locations, Cayman Islands, Lee Stocking Island and San Salvador. At each of these locations samples were grouped into four depth categories; Shallow (3–10 m), Medium (15–25 m), Deep (30–50 m) and Very Deep (60–90 m). Using DFA analysis two statistically significant discriminant functions were computed and plotted. A) The scatter plot of the canonical scores for each individual shows clear discrimination between all locations. B) The scatter plot for groups based upon depth as described above also exhibit clear differences with some overlap among the shallow and medium populations.

Fig. 2. δ^{15}N and δ^{13}C signatures of whole tissues for *Agelas conifera* from Little Cayman Island. Changes with depth for both isotopic signatures are significant (ANOVA: P<0.05) and common superscripts from multiple comparison testing (Tukey's HSD) represent depths not significantly different from each other. Fiore and Lesser, unpublished.

isotopic fractionations of inorganic nitrogen (Fiore and Lesser, unpublished data). Carbon and nitrogen isotopic signatures of macroalgae can also vary over relatively small depth gradients. Leichter et al. (2003) showed increasing δ^{15}N enrichment with depth on a Florida reef and attributed the changes to increased exposure to deep-water sources of nitrate with a δ^{15}N signature close to $+5.0$‰ (Leichter et al., 2007).

A few studies have identified specific mechanisms that would facilitate the transfer of energy or resources in the form of nutrients to deep coral reefs (e.g., internal waves: Leichter et al., 2003). Deep oceanic water is rich in dissolved nutrients and suspended particles, and has been shown to provide important resources from deep to shallow depths (Leichter et al., 1996, 2003; Leichter and Genovese, 2006). A potential limitation to these resources may be that water motion generally decreases with depth, reducing the ability of passive benthic suspension feeders to capture suspended particles. Some organisms, however, are more efficient at exploiting heterotrophic resources at depth. Sponges circulate water through choanocyte feeding chambers and as such are able to use particulate heterotrophic resources effectively. As a result of increasing concentrations of particulate matter, sponges experience increased growth rates and greater biomass with increasing depth (Lesser, 2006), and a similar pattern of increasing growth rates with depth has been observed for the coral *Madracis mirabilis* at mesophotic depths in Jamaica (Leichter and Genovese, 2006).

Light availability is generally not limited within shallow reef zones so many of the most conspicuous benthic organisms found there are autotrophic. Macroalgae are autotrophic and therefore restricted to depths where light availability can sustain photosynthesis, although low-light tolerance has been reported (e.g., Aponte and Ballantine, 2001; Littler et al., 1985; Runcie et al., 2008). The development of large algal beds in MCEs directly adjacent to shallow reefs is not very common as reef-associated grazing fishes, such as parrotfish, normally play an important role in reducing fast growing algal species (Leichter et al., 2008). Some algae, however, such as *Halimeda* sp. and *Lobophora variegata*, which are less preferred by herbivores (Arnold et al., 1995; Duffy and Hay, 1990), may occur on MCEs in relatively high abundances (Hillis-Colinvaux, 1986; Herzlieb et al., 2006; Khang and Kelley, 2007; Smith et al., 2008; Lesser and Slattery, 2011). Not only does irradiance decrease with depth, but MCEs also see a reduction of spectral quality (i.e., primarily blue and green wavelengths reach mesophotic depths).

Sessile benthic organisms have adopted specific strategies to deal with poor light conditions. For example, small-scale differences in the

being consumed. Taking this into consideration, the carbon signature is consistent with consumption of a mixed community of heterotrophic and photoautotrophic picoplankton (Boschker and Middleburg, 2002), with more heterotrophic picoplankton occurring in deeper water. This is consistent with work on the feeding biology of sponges and the food available to them as depth increases (Lesser, 2006). The differences observed in the δ^{15}N signature with depth are small (Fig. 2), and less than what is normally interpreted as trophic enrichment (~3–4‰ per trophic level: Kieckbusch et al., 2004). One possible reason for the observed isotopic signatures is that sponges at all depths are consuming picoplankton (Lesser, 2006) that are isotopically lighter (e.g., nitrogen fixers). Another possibility is that sponges from different depths contain different microbial communities. Therefore, the "bulk" signal we observe could be a function of changes in the symbiotic microbial community and the nitrogen transformations carried out by those microbes because different microbial populations can exhibit different
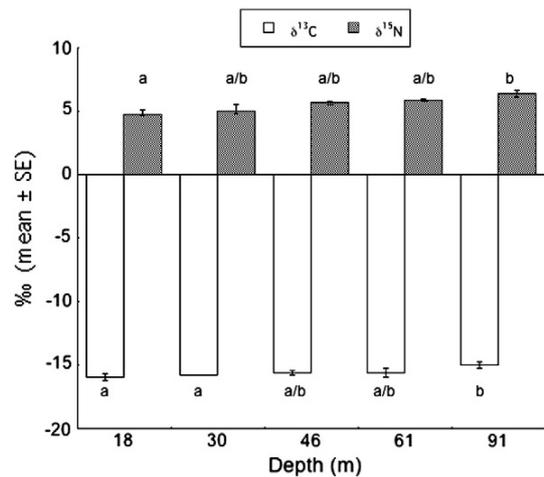
light environment along the deep fore reef may result in unanticipated patterns of distribution for some cryptic species of zooxanthellate corals (Vermeij and Bak, 2002). Autotrophic performance is enhanced through changes in photosynthetic pigment concentrations that increase the ability to capture light, and by changes in morphology to increase surface area (i.e., plating) (Lesser et al., 2010). Supplementary pigments in the host can change photosynthetically inactive wavelengths to photosynthetically active radiation (Schlichter et al., 1985). Nonetheless, light availability in MCEs becomes too low at certain depths for photosynthesis to contribute significantly to the process of calcification in reef building corals (Mass et al., 2007; McCloskey and Muscatine, 1984). At least one scleractinian coral has been shown to complement the reduction of symbiotic photosynthetic activity after bleaching by increasing heterotrophic feeding (Grottoli et al., 2006), and there is a continuing debate on the relative contribution of photoautotrophy versus heterotrophy based on characteristics such as polyp size (Porter, 1976; Sebens, 1997).

So what is the evidence for a transition from autotrophic to heterotrophic feeding strategies in deep reefs? In the mesophotic zone the attenuation of light is the most significant change in the abiotic environment affecting the physiology of corals (Lesser et al., 2009, 2010). It follows then that the decreased ability of a coral to photosynthesize in the mesophotic zone will increase the reliance of corals on other trophic strategies, such as heterotrophy, to meet their overall metabolic costs for growth and ultimately their distribution and abundance (Falkowski et al., 1990; Muscatine et al., 1989). Khang et al. (2010) have suggested that the evidence for a transition to heterotrophy with increasing depth is sparse, but their argument confuses this issue with food limitation and many, if not most, scleractinian corals depend on heterotrophy for varying amounts of required carbon and nitrogen that is both species-specific, and environment-dependent (Alamaru et al., 2009; Grottoli et al., 2006; Houlbreque and Ferrier-Pages, 2009). Additionally, it has been shown that corals can shift their trophic reliance from being primarily autotrophic to a greater dependence on heterotrophy for their carbon requirements as light decreases with increasing depth by using a mixotrophic strategy (Muscatine et al., 1989). This seminal paper solidified the use of stable isotopic data as a marker of trophic status in corals and suggested that the increasingly depleted $\delta^{13}C$ signature of the animal tissue of corals, and its divergence from the $\delta^{13}C$ of their zooxanthellae, were evidence of increasing heterotrophy in the presence of continued translocation of photosynthate down to a depth of 50 m, clearly demonstrating a mixotrophic strategy. Muscatine et al. (1989) simply stated that other $\delta^{13}C$ depleted sources of carbon were being acquired by many Caribbean corals at deeper depths and this could be explained by a larger reliance on feeding upon zooplankton with a $\delta^{13}C$ of −18.9 to −19.8‰ (Land et al., 1977), or feeding on oceanic particulate organic matter (POM) with a $\delta^{13}C$ of −18.4 to 24.4‰ (Rau et al., 1982). Other reported $\delta^{13}C$ isotopic values for zooplankton or POM are from −14 to −25‰ (Land et al., 1975; Owens, 1987; Peterson and Fry, 1987), and mean values of −19.9‰ for POM $\delta^{13}C$ from waters adjacent to the Florida Keys have recently been reported (Lamb and Swart, 2008). The values for animal tissue in some of the corals examined by Muscatine et al. (1989) at 50 m are consistent with these zooplankton or POM values.

More recently, the Red Sea coral *Stylophora pistillata* has been shown to photoacclimatize down to a depth of 65 m by increasing its chlorophyll concentration, and by changing to a more plate-like morphology maximizing light capture (Mass et al., 2007). Despite these changes, and with decreases in energetic costs measured as a decrease in respiration, rates of photosynthesis and calcification declined significantly with increasing depth (Mass et al., 2007). It was concluded that corals at the deeper end of their vertical distribution were probably surviving as a result of heterotrophic feeding on zooplankton (Mass et al., 2007). This study was then followed by Einbinder et al. (2009) who used stable isotopic signatures on *S. pistillata*

from the same location and depth range to discern the trophic status (i.e., photoautotrophy versus heterotrophy) of these corals. They observed significant differences in both zooxanthellae and animal tissue $\delta^{13}C$ values with increasing depth, and the animal tissue signal was significantly more depleted than the zooxanthellae signal at 30 m and deeper. Einbinder et al. (2009) conclude that because the change in $\delta^{13}C$ values "remain constant" with depth in the mesophotic zone that this is evidence for dependence on the same source of carbon by both the animal tissues and zooxanthellae, and not an increase in heterotrophy. But in Table 1 of their results section they report a significant functional relationship between the $\delta^{13}C$ signatures of the animal tissue and zooxanthellae of *S. pistillata* and depth using values from over the entire depth range. Rather than remaining constant, this argues strongly for change with depth in both coral compartments. Additionally, the $\delta^{13}C$ signals of the animal compartment at depths of 50 m and 65 m are consistent with $\delta^{13}C$ values reported for zooplankton and POM (see above).

In another study of stable isotopic signatures on *S. pistillata* and *Favia favus* from the Red Sea (Alamaru et al., 2009), the $\delta^{13}C$ values of both corals changed significantly with depth, especially deeper than 15 m. The difference between the animal and zooxanthellae compartments was significantly different in *S. pistillata* as previously reported (i.e., Einbinder et al., 2009), but not in the case of *F. favus* (Alamaru et al., 2009). In this study the authors use a $\delta^{13}C$ value of −21‰ for POM that is in the range for reported values (see above), and more depleted than the animal tissue of either coral at any depth in their study. This argues against the use of POM or zooplankton by the corals, which is in contrast to the results reported by Einbinder et al. (2009). Additionally, these authors make the case that the $\delta^{15}N$ values of these corals over their depth range do not reflect the commonly observed metabolic enrichment in stable nitrogen isotopes (Owens, 1987; Peterson and Fry, 1987). But they do not report the $\delta^{15}N$ values of POM for the Gulf of Aqaba. The $\delta^{15}N$ values for nitrate/ammonium in the world's oceans are ~4–6‰, and deviations from this value are often the result of a system dominated by nitrogen fixers which produce POM that is isotopically depleted. The continued sinking and re-mineralization of this isotopically depleted material will produce nitrate and ammonium with depleted isotopic signatures that along with the POM could then be used by corals. But the rates of nitrogen fixation in the Gulf of Aqaba are generally low (Foster et al., 2009). In fact, low $\delta^{15}N$ values from nitrate in the Gulf of Aqaba are caused primarily by atmospheric deposition of isotopically depleted nitrate (Wankel et al., 2009). This isotopically depleted new nitrogen is then utilized by primary producers and could find its way into higher trophic levels (Aberle et al., 2010). It is clear that the nitrogen isotope dynamics in the Gulf of Aqaba are very different from other tropical regions that support coral reef ecosystems. Thus using $\delta^{15}N$ signals of corals to discern whether heterotrophy is occurring requires significantly more research in general, and in the Gulf of Aqaba specifically, with a particular focus on direct measurement of $\delta^{15}N$ signatures for potential sources across the entire depth gradient. While logistically difficult to accomplish in the field, depth-specific sampling of the isotopic composition of dissolved and particulate nutrient sources over a range of depths could lead to significant insight into the causes of variation in tissue isotopic composition for MCE organisms.

Lastly, a recent study on the Caribbean coral *Montastraea cavernosa* provides evidence of heterotrophy using stable isotopes of the host, symbiont, and skeletal compartments (Lesser et al., 2010). In this study the coral tissue, zooxanthellae and skeleton $\delta^{13}C$ become progressively more depleted with depth. The slight enrichment observed in the coral versus zooxanthellae $\delta^{13}C$ signatures is probably due to the translocation of fixed carbon to the host (Muscatine et al., 1989), and the difference in the host $\delta^{13}C$ isotopic signature at 91 m compared to its zooxanthellae is consistent with decreased translocation and an increased dependence on heterotrophy as discussed above. The $\delta^{13}C$ value for corals at 91 m is −19.3‰, also consistent with consumption of zooplankton or POM (see above). But this does not mean that all of the

carbon requirements of the corals at these depths were met by heterotrophy; estimated gross primary productivity was still positive, and productivity to respiration ratios (P/R) were highly variable with mean values just below unity (0.98 ± 0.89). These data suggest that photosynthesis is still occurring, but that other sources of carbon are being utilized as originally described by Muscatine et al. (1989). Additionally, skeletal $\delta^{13}C$ values show a significant depletion with increasing depth. Changes in skeletal $\delta^{13}C$ values reflect long-term integrated changes in coral metabolism, specifically photosynthesis and respiration, which are affected by the availability of light and heterotrophic food sources such as zooplankton (Grottoli, 2002; Grottoli and Wellington, 1999). In a well planned experiment it was shown that for the Hawaiian coral *Porites compressa*, a decrease in irradiance, and therefore photosynthesis, decreased the $\delta^{13}C$ values of the skeleton, while increases in the availability and feeding on zooplankton (= brine shrimp with a constant, known isotopic composition) caused an increase in skeletal $\delta^{13}C$ values (Grottoli, 2002). Grottoli (2002) described this observation as a result of increased availability of nitrogen through heterotrophy that increased photosynthesis and $\delta^{13}C$ values. This is consistent with many studies on heterotrophy in scleractinian corals (reviewed by Houlbreque and Ferrier-Pages, 2009); these showed significant increases in photosynthesis and calcification in corals that are feeding on zooplankton or POM. In the study by Lesser et al. (2010), the increase in $\delta^{13}C$ values for *M. cavernosa* at 61 m and 91 m was originally attributed to a decrease in metabolic fractionation but an increase in heterotrophy at these depths is just as viable an explanation since photosynthesis appears to be occurring, albeit at very low rates, at these mesophotic depths.

Thus, the relative contribution of autotrophic versus heterotrophic nutrition gradually changes over depth and causes distinct changes in benthic assemblages between shallow and deeper reefs. However, directionality of energy translocation between the shallow and deep reef zones is largely unexplored. Energy translocation from the deep to the shallow reef may occur in the form of picoplankton that originates from the influx of nutrient-rich sub-thermocline water (Lesser, 2006). Local hydrodynamic processes may transport these primary producers onto the shallow reef (Leichter et al., 1996, 2005). Similarly, the fixed carbon in deep macroalgal communities may be transported as detritus or drift algae to shallower reef zones (Leichter et al., 2008). Although largely unexplored, it also seems likely that energy and nutrients may move from shallow to deep reef zones (e.g., Harrold et al., 1996). Mobile predators, such as fish feeding on benthic flora and fauna, might potentially play a role in the translocation of fixed energy; however, predation on corals, sponges and algae in MCEs seems very limited. With our understanding of coral trophic biology, it is clear that species to species and site-to-site, specific effects will determine the degree of dependence on heterotrophy for mesophotic corals. It is also clear that multiple types of measurements will need to be employed to provide an indication of this transition to a greater dependency on heterotrophy. This is because of the complex nature of changes in physiology with increasing depth and the relationship between the multiple compartments of the coral holobiont.

1.4. MCE stability

Central to the hypothesis that mesophotic coral ecosystems might act as a refuge for species from connected shallow coral reefs (Bongaerts et al., 2010b; Glynn, 1996), is the issue of deep reef stability. If these MCEs are to act as a "seed-bank" for increasingly degraded shallow coral reefs then the source population must be in better condition than the sink population (Hanski, 1999). However, few deep reef studies have re-examined these communities over environmentally-relevant temporal scales, and those that have provide inconsistent results. Specifically, Lehnert and Fischer (1999) conducted transect surveys in Jamaica to a depth of 107 m using open circuit technical diving (TRIMIX); they concluded that the percent cover and species compo-

sition of specific reef zones had changed significantly since surveys conducted four decades earlier by Goreau (1959). In contrast, a long-term study of coral cover at three sites in Curacao and at one site in Bonaire suggested relatively consistent cover (about 60%) at 30 and 40 m over a time scale of three decades (Bak et al., 2005). Intuitively, the site-specific differences in environmental gradients of abiotic and biotic factors could explain variations within and among sites. This begs the question of what mechanistic changes have occurred to the MCEs of Jamaica, and whether these factors are in play at other sites throughout the Caribbean and/or Indo-Pacific.

Shallow Caribbean reefs have seen a significant decline in coral cover, and an increase in macrofoliose algae since the 1980s (Hughes, 1994). These "phase shifts" are potentially mediated by a variety of natural and anthropogenic stressors (Gardner et al., 2003; Mumby, 2009) including: overfishing, severe storm damage, sedimentation, eutrophication, toxic discharge, disease, and thermal stress. With the exception of fisheries, which often have pronounced effects on deep coral habitat (Roberts et al., 2006), these disturbances are thought to be buffered by depth (= distance from stress: Bak et al., 2005; Graham et al., 2007; Lesser et al., 2009). For example, coral damage related to hurricanes, and the indirect effects of storm-mediated sedimentation, are limited to shallow reefs (Aronson et al., 1994; Bak et al., 2005; Woodley et al., 1981). Disease is also believed to be increasing worldwide and many of these are species-specific (Aronson and Precht, 2001; Harvell et al., 1999); given the depth distributions of coral species across shallow and mesophotic reefs (reviewed by Bongaerts et al., 2010b), it is not surprising that few deep reef diseases have been identified (Smith et al., 2008). In addition, non-point source discharge of nutrients and/or toxins into the marine environment can be particularly problematic near large centers of population but typically are diluted below threshold levels at MCE depths (LaPointe, 1997; Nowlis et al., 1997). However, point-source outfalls have the potential to increase levels of these anthropogenic compounds near MCEs (Proni et al., 1994). That said, there are few quantitative data to assess the impacts of these disturbances on the stability of deep coral reef environments.

Climate change effects, including thermal stress and ocean acidification, are a major concern for coral reefs (Hoegh-Guldberg, 1999; Hoegh-Guldberg et al., 2007; Kleypas et al., 1999). Temperature-induced bleaching has increased in recent years on shallow reefs (Donner et al., 2005), but the cooler temperatures at MCE depths (average 2 °C) may provide a refuge from thermal stress (Glynn, 1996). In fact, the few observations of coral bleaching on deeper reefs are typically attributed to "cold-water" bleaching (Kobluk and Lysenko, 1994; Bak et al., 2005; but see Lang et al., 1988). Likewise, shallow reefs will be affected directly by ocean acidification in the coming decades while cold-water coral reef ecosystems are predicted to experience a decrease in habitat availability as the aragonite saturation horizon becomes shallower (Roberts et al., 2006; Veron, 2008). It is not known whether the deep thermocline will isolate mesophotic reefs from the upward mixing of lower saturation state deep-water, but the upwelling of undersaturated (i.e., acidified) water from depths as shallow as 40–120 m has been shown to occur off the West coast of North America (Feely et al., 2008). It seems likely that sea-water pH and aragonite saturation are likely to be highly variable over even short temporal scales on deep coral reefs. However, this "physical isolation" of MCEs may drive some of the potential genetic variability and divergence in the MCE discussed above. It is now widely recognized that shallow reef ecosystems were severely disrupted by sea level changes associated with Pleistocene glacial cycles (Paulay, 1996; Shulman, 1998; Voris, 2000). Bellwood and Wainwright (2002) estimate that 90% of shallow reef habitats were lost in some areas. Sea level decreases of over 100 m are disruptive to many shallow reefs that are perched atop steep vertical slopes of oceanic islands. It seems likely that the lower mesophotic zone must have functioned in part as a refuge for corals and coral genetic material during the large sea-level changes in the Pleistocene.

On the whole, available data seem to support the hypothesis of MCE stability, although quantitative evidence indicates that the lower mesophotic community (60–100 m) includes about 20 to 50% endemics (Bongaerts et al., 2010b; Reed and Pomponi, 1997). Thus the "seed-bank" potential may be less promising than hoped and is further diminished by the presence of a unique genetic sub-population structure of corals (e.g., *M. cavernosa*, see above) across this depth gradient. If this pattern is consistent across a broad range of taxa then the expectation that mesophotic reefs may be refugia (Glynn, 1996) for any shallow water taxa is significantly reduced. Additionally, and more importantly, conditions may change unexpectedly. As mentioned above, following a thirty-year record of coral stability at three sites in Curacao and one site in Bonaire in the southern Caribbean (Bak et al., 2005), recent surveys by Stokes et al. (2010) have demonstrated a clear reversal in coral cover (see Fig. 3). The 2008 data point to large scale declines in coral cover across depths at all sites (Stokes et al., 2010). At 30 to 60 m the coral cover ranged from <10% to ~ 40%. Cover of macroalgae and dead coral and turf algae ranged from 10 to 45%. This is in direct contrast to results from Bak et al. (2005) in which the coral population abundances at 30 and 40 m were higher than abundances of shallower coral populations at 10 and 20 m, and suggests declines in coral abundance are not limited to shallow water. At these reefs the temperature and current patterns were dynamic with strong and variable flows and clear signs of intermittent upwelling of cool water in the deeper portions of the reef. The dynamic physical environment at the deeper sites doesn't, however, appear to confer protection from the factors causing widespread decline in corals in shallow water in Bonaire.

Similarly, recent work by Lesser and Slattery (2011), has documented a relatively rapid phase shift on the mesophotic reefs of the Bahamas that is attributable to an invasive species. The Indo-Pacific lionfish, *Pterois volitans*, has invaded virtually every "corner" of the Caribbean in the past decade, and they have caused significant damage to shallow reef fish populations (Albins and Hixon, 2008; Côté and Maljkovic, 2010). In 2006, the deep reefs surrounding Lee Stocking Island, Bahamas, were lionfish-free although several individuals were captured on nearby shallow-reefs. At that time, the percent sponge cover at depths of 46 and 61 m exceeded 30% and 70%, respectively. Coral cover at these same depths accounted for about 20% and 7.5%, respectively. Sponge and coral cover in 2009 decreased at these depths to less than 5% cover, while algae increased to approximately 90% cover. The only demonstrable causal changes to these MCEs, when hurricanes, coral bleaching and diseases were ruled out, were significant declines in the fish diversity and abundance over depth and time coincident with the arrival of lionfish on these mesophotic reefs. Since the decrease in fish biomass and diversity included many species that directly and indirectly affect algal abundance, it appears that predation by lionfish has generated a trophic cascade with implications for benthic community structure (Pace et al., 1999). These lionfish were present on the MCEs at levels comparable to the shallow reefs (Green and Côté, 2009; Lesser and Slattery, 2011). Although these data lack mechanistic detail the effects are unequivocal, and these results indicate that certain disturbances, especially introduction of exotic and invasive species, have the potential to significantly impact MCE stability.

1.5. Conclusions

In the face of overwhelming evidence for deterioration of shallow reef ecosystems (Hughes et al., 2003, 2010; Jackson et al., 2001), the management concerns for mesophotic ecosystems are heightened on several fronts. First, the upper mesophotic zone (30–60 m) apparently serves as a refuge for shallow reef organisms, as indicated by the many shallow reef species that also inhabit this depth stratum (Bak et al., 2005; Bongaerts et al., 2010b; Randall, 2007). Field observations and population genetic studies should be useful to test and potentially confirm this observation. Second, the lower end of the mesophotic zone (60–150 m) may have higher endemism and fewer links to shallow reef habitats (Lesser and Slattery, 2011; Porter, 1973; Reed and Pomponi, 1997; Thresher and Colin, 1986), and a fauna that depends more on heterotrophy than autotrophy. Phylogenetic studies will be useful in resolving the affiliations of these fauna. Third, while MCEs may have greater stability than shallow reefs across glacial sea level changes, they may be sensitive to disturbances in the upper water column that reduce light penetration. In this respect, they are probably even more vulnerable to stress than shallow reef counterparts, especially near human population centers (Lesser and Slattery, 2011). This mechanism could play a large role in explaining the recent changes observed in deep reefs at sites such as the north shore of Jamaica and the leeward shore of Bonaire where development has accelerated in the past decade. The high biodiversity and endemism in MCEs relative to shallow counterparts can be attributed to 1) restricted dispersal relative to shallow reef fauna, or 2) greater stability across Pleistocene glacial epochs. This in turn invokes questions about the origin of mesophotic reef fauna: are deep reef fauna derived from 1) other MCE reefs, or 2) adjacent shallow reefs? The former explanation would conform to a conventional allopatric speciation model with restricted dispersal, in which rare colonization events between mesophotic ecosystems are followed by
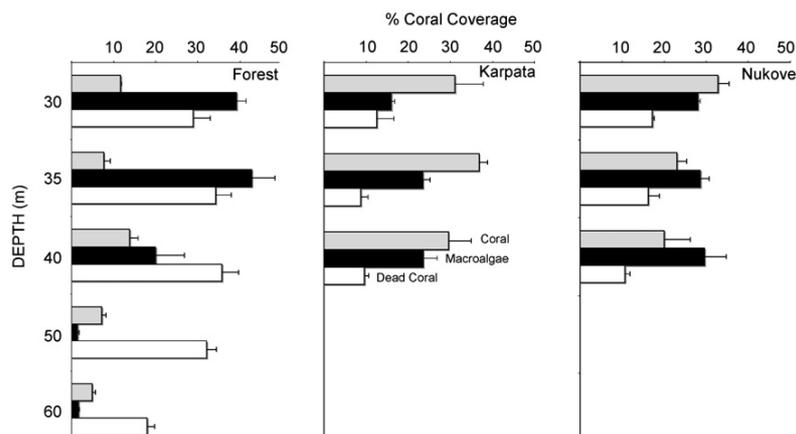

Fig. 3. Benthic photo sampling and analysis of community composition at reef sites around Bonaire, Netherlands Antilles in January 2008. Sampling of benthic community composition was conducted from 5 to 40 m depth at 6 sites and included sampling in the mesophotic zone down to 80 at two sites. At each depth and each site 15 photo quadrats were sampled along each of three 50 m transects for a total of 45 1 m² photos per depth per site. The resulting images were analyzed via standardized random dot procedures to estimate percent cover of all hard corals (identified to species) as well as macroalgae, turf algae, dead coral, and other invertebrates (mostly sponges and ascidians).

long-term isolation and divergence. The latter explanation would require divergence along stable ecological boundaries rather than geographic isolation. This ecological component to speciation (parapatric divergence) has been invoked recently to explain speciation in shallow reef fauna in the absence of geographic isolation (reviewed in Rocha and Bowen, 2008). It is likely that the deep reef forms a sink as organic material, detritus and sediment fluxes move downward with gravity. However, little is known about the frequency of occurrence of these processes and future research should focus on quantifying these energy fluxes in order to assess the role of MCEs in the trophic energy budgets, and possible source/sink relationships.

Future research into the foundations of mesophotic reef biodiversity should include studies of dispersal and larval retention, ontogenetic movements, as well as phylogenetic studies to resolve the age and origin of deep mesophotic reef fauna. The two factors identified above, restricted dispersal (with allopatry) and stable ecosystem conditions (with parapatry) need not be exclusive processes, and together could act in concert to produce the remarkable diversity in mesophotic ecosystems. Resolving the question of whether mesophotic/shallow systems are refuges requires parallel and contemporaneous studies in both systems. However, logistical difficulties in community-level investigations in these systems will be imposing. We recommend selecting 'model species' based on abundance and (presumed) functional importance in both systems. Research should involve coordinated efforts in the laboratory (e.g., genetic analyses) and the field (e.g., surveys, monitoring, transplant experiments, etc.). Although the 'pattern-generating' aspects of research (e.g., species lists, DNA analyses) are essential, the ultimate objective should focus on causal mechanisms structuring shallow and mesophotic ecosystems. In addition, preliminary comparative surveys of Atlantic and Indo-Pacific MCEs (Slattery unpublished) suggest that biogeographic patterns and processes may be very different across ocean basins; studies that provide information relative to a universal model of MCE function are clearly requisite. Research requirements related to working in MCEs include further developments in technical diving and/or in situ instrument packages. Finally, we must continue to address genetic, energetic, biochemical, and reproductive adaptations; these facets must be placed within the context of MCE biodiversity, ecology, and management.

Acknowledgments

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