



Ecology of mesophotic coral reefs

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ABSTRACT

Mesophotic coral reefs, reefs at depths of 30 m to 150 m, are receiving renewed interest from coral reef scientists and managers because they are linked physically and biologically to their shallow water counterparts, have the potential to be refugia for shallow coral reef taxa such as coral and sponges, and can be a source of larvae that could contribute to the resiliency of shallow water reefs. Here we review what is currently known about how mesophotic reef communities are structured and identify critical areas where new information is needed. The review covers two primary taxa, coral and sponges, where a majority of the ecological work on mesophotic coral reefs has been done, and physical processes (e.g., the attenuation of visible irradiance and internal waves) that exert significant abiotic control on the structure of these deep reef communities. Understanding the ecology of mesophotic coral reefs, and the connectivity between them and their shallow water counterparts, should be a primary focus of future reef studies as the worldwide degradation of shallow coral reefs, and the ecosystem services they provide, continues.

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Contents

1. Introduction	1
1.1. Coral reefs in decline worldwide	1
1.2. Mesophotic coral reefs	2
1.3. The underwater light environment	3
1.4. The importance of sponges on mesophotic coral reefs	4
1.5. Benthic–pelagic coupling	4
1.6. Refugia and connectivity	5
1.7. Conclusions and research directions	5
Acknowledgements	7
References	7

1. Introduction

1.1. Coral reefs in decline worldwide

Coral reefs worldwide are threatened with severe degradation owing to global climate change, and local impacts such as over-fishing and pollution (Hoegh-Guldberg, 1999; Hoegh-Guldberg et al., 2007; Carpenter et al., 2008). For tropical nations with coral reef ecosystems the loss of these habitats, and the ecological services they provide (i.e., tourism, fisheries, shoreline protection), directly diminishes their economic base and hampers the potential for sustainable develop-

ment (Knowlton, 2001). The most profound effects have occurred in the Caribbean where declines of shallow-water zooxanthellate scleractinian corals are closely linked to the loss of the sea urchin *Diadema antillarum*, increasing incidence of coral disease, recurring disturbance events such as hurricanes, and coral bleaching related to thermal stress (Gardner et al., 2003; Hughes et al., 2003; Lesser, 2004). The most profound changes have occurred on coral reefs <20 m deep whereas deeper reefs (>30 m) have been shown to be largely free from anthropogenic and natural impacts (Bak et al., 2005). There is evidence to support this; a study on the conservation status of 704 species of scleractinian corals worldwide revealed that 40% are found at depths <20 m, whereas the remaining 60% can survive at depths >20 m (Carpenter et al., 2008).

Coral reef zonation (Fig. 1) starting from land includes a low wave energy back reef zone dominated by lagoons with sea grasses and

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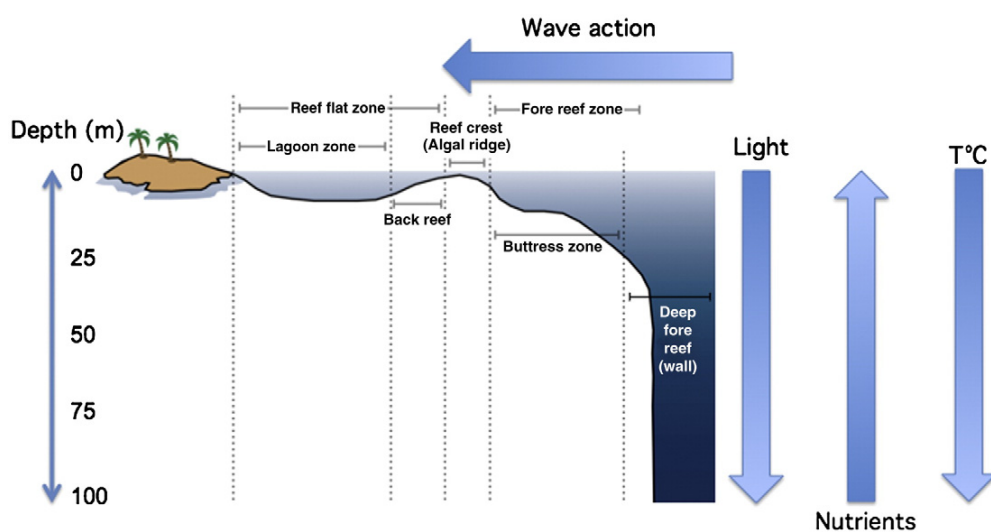


Fig. 1. Coral reef zonation showing gradients of light, nutrients and temperature with changes in depth from shallow reefs to mesophotic depths. Coral zonation image courtesy of Cayman Islands Twilight Zone 2007 Ocean Exploration Expedition and Kyle Carothers, NOAA-Ocean Exploration.

patch reefs at depths from 2 to 10 m. The next zone is the reef flat leading to the reef crest or algal ridge composed of consolidated calcareous material, corals and crustose coralline algae where high energy waves break and lose their energy before entering the back reef. The fore reef zone extends from 1 to ~30 m and can include spur and groove as well as a deep buttress zones of well developed, coral dominated, communities. These fore reef communities then slope steeply down into low energy deep fore reef zones where steep gradients of light dominate the habitat and where upwelling or internal wave induced delivery of nutrients and particulate organic material to shallower depths occurs. Temperature also decreases from the surface to mesophotic depths. Generally, speaking this will be less than 5 °C lower than surface temperature down to depths of ~100 m for coral reefs (Fig. 3B, Lesser et al., in review) and is probably not a significant abiotic factor influencing the community structure of mesophotic reefs in tropical zones. It is within the deep fore reef zone that mesophotic coral reef communities develop and generally range from 30 m to 150 m. Mesophotic coral reefs have been understudied because of technological limitations and the excessive costs of using submersibles that normally dive to depths in excess of 900 m. However, the depths where mesophotic coral reefs occur can now be reached safely by remotely operated vehicles, autonomous underwater vehicles, and increasingly by the use of technical diving technologies. In particular, the continued use and development of technical diving such as closed circuit rebreathers in combination with mixed gas (e.g., TRIMIX) will facilitate new research on mesophotic coral reefs and has already resulted in several interdisciplinary studies on the ecology and biology of light-dependent mesophotic coral reefs in deep-water habitats (Pyle, 1996; Lehnert and Fischer, 1999; Leichter and Genovese, 2006; Leichter et al., 2007, 2008; Lesser et al., in review).

Mesophotic coral ecosystems are deep fore reef communities where low light is a dominant abiotic feature and are comprised largely of light-dependent zooxanthellate corals, azooxanthellate scleractinian corals, macroalgae and sponges. The number of ecological studies in these settings is extremely limited especially compared with the number of studies in shallow water (Menza et al., 2008). The study of deep coral reefs goes back as far as the United States Exploring Expedition (1838–1842) where more than 200 species of coral were reported by Dana (1846) including dozens of species that occur at deep depths (Dana, 1846). One of many notable

discoveries was that photosynthetic reef building corals could live in habitats at deeper depths (>30 m) than previously believed possible. The lack of knowledge about mesophotic coral reef environments has impacted our broader understanding of the ecology, biodiversity, and connectivity of all coral reef communities. Additionally, the potential of mesophotic coral reefs to serve as important refugia and nursery habitats for crucial fish populations; potential sources and sinks of shallow coral larvae; their physical-biological interactions and trophic structure, and the causes and significance of increased biodiversity on deep coral reefs compared to their shallow counterparts represent critical gaps in our knowledge of these systems (Leichter et al., 1998; Pyle, 2000; Diaz and Rützler, 2001; Riegel and Piller, 2003; Feitoza et al., 2005; Grigg, 2006; Leichter and Genovese, 2006; Lesser, 2006; Kahng and Kelly, 2007). Here we review our current knowledge of mesophotic coral reef communities, including our inherent biases, and identify crucial scientific questions that we believe should be addressed to understand and protect these novel ecosystems.

1.2. Mesophotic coral reefs

The physical environment of these deep fore reef communities includes strong gradients in downwelling solar irradiance and protection from strong wave action compared to their shallow counterparts (Fig. 1). Under normal circumstances there are modest changes in seawater temperature from the surface to deeper waters (up to 150 m) and mesophotic reefs are not regularly affected by high temperature stress associated with surface waters (Hoegh-Guldberg, 1999; Lesser, 2004; Hoegh-Guldberg et al., 2007). There are several descriptive studies of mesophotic coral reef communities from Carrie Bow Cay, Belize (Rützler and Macintyre, 1982), Reunion Island (Bouchon, 1981), Bermuda (Fricke and Meischner, 1985), St Croix, US Virgin Islands (Kühlman, 1983), the Red Sea (Kühlman, 1983; Fricke and Knauer, 1986), French Polynesia (Kühlman, 1983), and Jamaica (Goreau and Wells, 1967; Lehnert and Fischer, 1999) but very few long-term, or process oriented, ecological studies. One long-term study from the Caribbean (i.e. Bonaire and Curacao) does show consistent coral cover of up to 60% at depths greater than 30 m on decadal time scales which demonstrates long-term stability and protection against both natural and anthropogenic changes associated with shallow reefs (Bak et al., 2005). This study also showed

variable temperatures from >28 °C to less than 24 °C at 50 m suggesting that internal waves are occurring on these reefs (Bak et al., 2005). In the Bahamas, Liddell et al. (1997) reported on the percent cover and species diversity of coral reef communities down to a depth of 250 m. Their results showed a distinct bathymetric zonation pattern consisting of coral cover of 3–23% above 50 m and significant declines with increasing depth whereas the percent cover of sponges increased with increasing depth. The authors suggested that sedimentation and the decrease of solar radiation with increasing depth were the two most important factors regulating the zonation patterns of mesophotic coral reefs. While the disturbance provided by sedimentation is an important factor affecting the structure and stability of mesophotic communities, the decrease in solar radiation with depth is the most profound abiotic factor affecting these ecosystems (see below).

Zooxanthellate scleractinian corals, as important members of the mesophotic reef community, exhibit specific depth distributions and have been the subject of many studies. A study in the Indian Ocean showed that *Leptoseris fragilis*, *L. hawaiiensis* and *L. incrustans*, were the only corals out of 120 species described whose abundance increased with depth and decreasing solar radiation (Bouchon, 1981), and this genus has been described from mesophotic coral reefs in clear oceanic waters worldwide. *Leptoseris* sp. has been observed at 153 m near the island of Hawaii (Kahng and Maragos, 2006), *L. fragilis* has been found at 145 m in the Gulf of Aqaba (Fricke and Knauer, 1986) and *L. hawaiiensis* from Johnston Atoll is the deepest reported photosynthetic coral, to date, at 165 m (Maragos and Jokiel, 1986). In the Caribbean and the Bahamas, *Montastraea cavernosa*, *Agaricia lamarki*, *A. grahamae* and *Leptoseris cucullata* can all be found at depths >100 m (Reed, 1985). The presence of these zooxanthellate scleractinian corals at depths >30 m has prompted a significant amount of research into photophysiological adaptations of corals to provide insight into the physical and biological factors controlling the lower depth limits of photosynthetic corals and therefore coral reefs (Dustan, 1982; Wyman, 1987; Falkowski et al., 1990; Lesser, 2000; Frade et al., 2008a; Lesser et al., in review).

1.3. The underwater light environment

The light environment is an important factor controlling the productivity, physiology, and ecology of corals (Dustan, 1982;

Wyman, 1987; Falkowski et al., 1990; Lesser, 2000; Frade et al., 2008a), and it restricts the distribution of most species to depths of 60 m or less (Fig. 2). In the optically clear waters of the tropics the attenuation of solar radiation, both the ultraviolet (UVR: 290–400 nm) and photosynthetically active radiation (PAR: 400–700 nm) components with increasing depth is largely a function of the optical properties of the water itself since there is very little dissolved or particulate matter to absorb these wavelengths (Fig. 2). While the absolute amount of downwelling irradiance (E_d) decreases with depth, so does the spectral composition of the underwater light field as depth increases with the ultraviolet/blue and red wavelengths exhibiting the greatest decreases with increasing depth. To illustrate this we modeled the underwater light field using spectral irradiance data collected adjacent to a mesophotic coral reef in the Bahamas and calculating a spectral attenuation coefficient (K_d m^{-1}) for both downwelling UVR and PAR to model depths greater than 20 m. Using this data we then calculated an average vertical K_d m^{-1} of 0.06 m^{-1} for PAR that is consistent with Case 1 or Case 2 waters with chlorophyll concentrations of <0.5 μg l^{-1} . From this data we then calculated the midpoint of the euphotic zone ($2.3/K_d$ PAR) which occurs at ~ 38 m and is more commonly referred to as the 10% light level whereas the bottom of the euphotic zone, or the 1% light level ($4.6/K_d$ PAR), occurs at ~ 77 m. The 1% light level is generally believed to be where photosynthesis equals respiration (i.e. compensation point) and above this depth there is net photosynthesis and production of organic matter and below this respiration exceeds photosynthesis and there is net consumption of organic material. As an apparent optical property of the water column, the vertical K_d used for these calculations assumes the optical properties of the water are homogeneous from top to bottom for these calculations. The irradiance of PAR for these data spans from 2100 μmol quanta $m^{-2} s^{-1}$ at the surface to ~ 45 μmol quanta $m^{-2} s^{-1}$ at 100 m where most corals saturate their photosynthetic rates at around 300 μmol quanta $m^{-2} s^{-1}$ (Falkowski et al., 1990). These data are essential to quantitatively relate the irradiance reaching the sea surface to the underwater solar spectral irradiance reaching the surface of a coral reef and individual corals, and also suggest that where corals occur at depths deeper than the 1% light level other trophic processes (e.g., heterotrophy) must be in play to offset the net loss of productivity through photoautotrophy.

The photosynthetic apparatus of zooxanthellate scleractinian corals, macroalgae, and sponges harboring photosynthetic cyanobacteria must

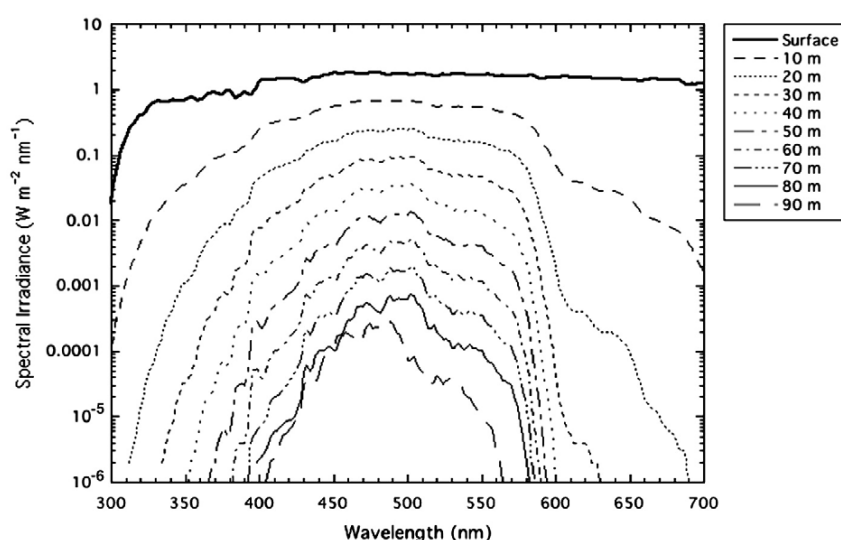


Fig. 2. Spectral irradiance curves from 300–700 nm modeled from the surface to 90 m depth. We modeled the underwater light field using spectral irradiance data collected adjacent to a mesophotic coral reef in the Bahamas and then calculated a spectral attenuation coefficient for downwelling irradiances to model depths deeper than 20 m.

adjust to both the attenuation, or decrease, in PAR as well as changes in the spectral composition of light with depth (Fig. 2). Both the decrease in light with depth, and changes in the spectral composition, can affect the productivity and species diversity of corals, macroalgae, and sponges over a depth gradient (Huston, 1985; Falkowski et al., 1990; Gattuso et al., 2006). In addition to the effects of the attenuation of light on the photophysiology of corals with depth there are additional decreases in light specific to corals growing on steep and vertical surfaces that dominate many mesophotic coral reef ecosystems. Despite the fact that these corals often project flat surfaces from the substrate they receive less than 25% of the total downwelling irradiance at any particular depth (Falkowski et al., 1990). There are also small-scale differences in the light environment over the entire fore reef, including the mesophotic zone, which can result in additional and unanticipated patterns of zooxanthellate scleractinian coral species distribution (Vermeij and Bak, 2002). In Hawaii a comprehensive survey of the Au'ua Channel (Kahng and Kelly, 2007) revealed that *Leptoseris* sp. were rare in shallow water (<50 m) but dominated in areas of hard and stable substrate between 60 and 120 m. Its decline below 90 m was attributed to a combination of changes in irradiance with depth, daily temperature fluctuations (± 2 –4 °C) associated with changes in the depth of the seasonal thermocline, and lack of stable substrate to attach to (Kahng and Kelly, 2007).

Most of the zooxanthellate scleractinian corals endemic to mesophotic communities have a fixed plate-like morphology or change shape with depth to a plate-like morphology as a result of phenotypic plasticity. One example of this is the mounding coral, *M. cavernosa*, which develops a flattened, plate-like, morphology with depth to increase its surface area for light capture (Reed, 1985; Lesser et al., in review). Other unique adaptations have also been observed in several species of coral. For example, *L. fragilis* expresses a host derived light-harvesting pigment system that is believed to enhance the photosynthetic performance of their symbiotic zooxanthellae in low light environments by transforming shorter wavelengths of light to longer wavelengths that can then be absorbed by the photosynthetic pigments of the zooxanthellae. This adaptation suggests a co-evolutionary process has occurred between the host and symbiont to benefit the symbiosis at these depths (Schlichter et al., 1986; Schlichter and Fricke, 1991; Kaiser et al., 1993). Although *L. fragilis* exhibits maximum rates of photosynthesis at depths of 70–90 m, the unique host pigment adaptation is hypothesized to allow it to survive as deep as 145 m in the Red Sea (Fricke et al., 1987).

The ability of any coral species to photoacclimatize to the low irradiances at depths >30 m is largely a function of the organization of the photosynthetic apparatus in their symbiotic zooxanthellae (Wyman, 1987; Falkowski et al., 1990; Lesser, 2000). However, it also involves changes in the trophic strategies that support the growth of corals. In the Red Sea, the coral *Stylophora pistillata* photoacclimatizes down to a depth of 65 m by increasing its chlorophyll concentration, and by changing to a more plate-like morphology to capture as much light as possible (Mass et al., 2007). Despite these changes, and with decreases in energetic costs measured as a decrease in respiration, rates of photosynthesis and calcification still 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). 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). The nutrient or food resources for this switch could be supplied by upwelling or internal waves that could then help support the growth of corals in these low light habitats (Leichter and Genovese, 2006). One approach to assess whether a switch from autotrophy to heterotrophy has occurred is to measure changes in the carbon stable isotope signal of the host, zooxanthellae and skeleton of corals with increasing depth (Muscatine et al., 1989).

This provides a signal integrated over time that can reliably show shifts from autotrophy to heterotrophy with depth in corals (Muscatine et al., 1989; Maier et al., 2003; Lesser et al., in review). Understanding the reliance of these mesophotic corals on mixotrophy, and at what depths this occurs, will require studies employing photophysiological, energetic, feeding, and stable isotope approaches.

1.4. The importance of sponges on mesophotic coral reefs

After corals, sponges are the most abundant benthic fauna on many coral reefs (Diaz and Rützler, 2001). For example, >80 sponge species have been recorded on reefs in the Florida Keys (Schmahl, 1990) and ~300 species on Bahamian reefs (Reed and Pomponi, 1997). Sponge biomass on Caribbean reefs is five–six times greater than on the Great Barrier Reef where there are more species dependent on heterotrophy than on the Great Barrier Reef where sponges with photosynthetic symbionts are more common (Wilkinson, 1987; Schmahl, 1990). However, many aspects of sponge biology and ecology are still poorly understood, particularly in mesophotic reef communities. Caribbean sponges such as *Callyspongia vaginalis*, *Agelas conifera*, and *Aplysina fistularis* acquire their food heterotrophically, but might also contain symbiotic autotrophic and heterotrophic bacteria as symbionts. Both picoplankton (cyanobacteria and prochlorophytes) and heterotrophic bacteria, the primary food used by sponges, increases with depth to at least 92 m (Lesser, 2006), and the sponges filter these bacteria efficiently with clearance rates of 83–90%. The differences in the amount, and composition of picoplankton appear to have significant effects on the distribution and abundance of many species of sponge across the Caribbean and the Bahamas (Lesser, 2006). Even for shallow sponge communities (<20 m) transplant experiments show that deeper populations of sponges have higher growth rates than do shallower populations as a result of the greater availability of food at the deeper depths (Trussell et al., 2006). This also occurs over broader depth ranges including both shallow and mesophotic reefs where changing energy budgets with depth in the sponge *Plakortis angulus-piculatis* from the Bahamas and Caribbean show that deep reef individuals grow faster and invest more in protein than shallow reef conspecifics. This pattern switches when deep sponges are transplanted into the shallow reef suggesting that it is a phenotypically plastic character that shifts with changes in food availability (Slattery et al., in review). We believe there is broader generality for this pattern that can be extended to mesophotic sponge communities in Florida, Belize, the Bahamas and the Cayman Islands where the species diversity, percent bottom coverage, size distribution and growth of many species of sponge increases with increasing depth, as does their particulate food supply (Lesser, 2006; Lesser et al., in review; Slattery and Lesser, unpublished). Additionally, the biomass and number of species of sponges increases in the Bahamas at depths greater than 50 m (Liddell et al., 1997; Reed and Pomponi, 1997) suggesting that food is not limiting for sponges at these depths (Lesser, 2006). Sponges are crucial components of mesophotic coral reef communities that couple water column productivity to the benthos, are a major component of coral reef biodiversity, and create essential habitat for many species of invertebrates and fish (Diaz and Rützler, 2001; Rebiro et al., 2003).

1.5. Benthic–pelagic coupling

On coral reefs the physical processes associated with nutrient delivery are increasingly recognized as important contributors to coral reef community structure. For instance, the largest pools of biologically available inorganic nitrogen and phosphorus in the oceans are associated with water masses below the thermocline (typically depths >30–50 m) and the dynamics in the upwelling of these water masses strongly influence patterns of marine primary production. The variability in primary productivity, in turn, can strongly affect the

community structure of benthic consumers, especially suspension feeders such as corals and sponges (Menge et al., 1997; Gili and Coma, 1998; Lesser, 2006). Shallow (10–15 m) patch reef communities are comprised of varying percentages of scleractinian corals, soft corals, sponges and other macro-invertebrates. By contrast mesophotic reef communities in the Caribbean occur at depths >30 m and where sponges increase in the percent cover and light dependent corals are rare and less diverse than at shallower depths (Liddell et al., 1997). Light becomes limiting at these depths and food availability in the form of heterotrophic bacterioplankton provides the resources that these sponge-dominated communities consume (Lesser, 2006). There is, of course, some variability in this as a profile of water column temperature (black), density (red) and chlorophyll *a* concentration (green) from a vertical cast of a continuously recording profiler and nitrate concentration (blue + symbols) from samples collected seaward of the Florida Keys, USA in summer demonstrates (Fig. 3A). In this case a deep chlorophyll maximum exists at ~60–70 m and it has been demonstrated that pulses of food and nutrients from deeper depths can be delivered to shallower portions of mesophotic reefs (as shallow as 30 m) or even onto shallow reefs by a variety of mechanisms that produce upwelling at local to regional spatial scales and on time scales of hours to days and weeks (Fig. 3B). These mechanisms range from large-scale alongshore winds, to divergences associated with coastal currents and the interaction of currents with topographic features such as headlands and islands, to the interaction of internal waves with seafloor features including ridges, pinnacles and the shelf break, and finally hurricanes which can mix the overlying waters of coral reefs down to a depth of over 200 m (Fig. 3B). However, at several sites in the Caribbean basin relict pleistocene ridges at about 65 m constrain upwelled nutrients to the mesophotic zone and encourage sponge growth in this region (Slattery et al., in review).

From a comparative perspective it has recently been shown that deep tropical kelp communities at 30–200 m in the Galapagos are the result of local oceanographic processes such as upwelling events that provide essential nutrients close to the surface where sufficient light is available to drive photosynthesis (Graham et al., 2007). Similarly, a zone of deep primary productivity associated with abundant macroalgal communities at 40–60 m depth has been described on the shelf seaward of the Florida Keys (Leichter et al., 2008) which are very similar to the macroalgal communities described above (Graham et al., 2007). In coastal settings internal waves can cause vertical displacements (on the order of tens of meters to perhaps as much as 200 m) of deep water masses, and non-linear and breaking internal waves can cause both the vertical and horizontal net transport of dissolved nutrients (Fig. 3A) and suspended particles including phytoplankton (composed mostly of picocyanobacteria) and zooplankton (Leichter et al., 1998, 2003).

Leichter et al. (1996, 1998, 2003) have demonstrated that internal waves deliver nutrients to coral reefs in the Florida Keys using direct measurements of both nutrient and particle transport and indirect evidence from stable isotope measurements of deep-water nitrate pools and the tissues of benthic macroalgae (Leichter et al., 2007). They also showed enhanced growth of the coral, *Madracis mirabilis*, in shallow mesophotic (30 m) reef zones where internal wave exposure was greatest and where heterotrophic suspension feeding by the coral occurred, and similar results for *M. mirabilis* were obtained in mesophotic zones (30–45 m) of Discovery Bay, Jamaica (Leichter and Genovese, 2006). In most cases where internal waves occur it has significant ramifications for water column productivity and the availability of food for sponges, corals feeding heterotrophically and the primary productivity of corals at deep, mesophotic, depths. There are, however, cases where internal waves limit the growth of important mesophotic taxa such as corals. In Palau, cold water (<18 °C) and thermal fluctuations of as much as 20 °C appear to limit coral growth in the mesophotic zone between 60 m and 120 m (Wolanski et al., 2004).

1.6. Refugia and connectivity

The issue of connectivity in the marine environment has been debated extensively owing to the implications for management, and for the establishment of successful marine protected areas (MPAs) (Hellberg, 2007). Corals and sponges exhibit both brooding and broadcasting reproductive strategies, and these different life-history characteristics have significant effects on gene flow and therefore genetic connectivity between populations (Wolanski et al., 2004). Previous research has identified the potential benefits of “upstream” sources of pelagic larvae being delivered to downstream coral reefs through prevailing oceanographic patterns that can improve the resiliency of these coral reefs (Roberts, 1997). Since then combined research by physical oceanographers, coral reef biologists and molecular biologists at various spatial and temporal scales has helped address questions related to population connectivity, and the evolutionary ecology of coral reef organisms. Probably the most complete studies have been conducted on fish and corals (Paris and Cowen, 2004; Baums et al., 2006; Cowen et al., 2006) and these studies show distinct population structure and limited larval dispersal over very large spatial scales, thus challenging the idea that coral reefs are “open systems” (Cowen et al., 2006). The degree of larval dispersal can vary significantly depending on the reproductive strategy (i.e. broadcast or brood) employed by corals or sponges. In the case of corals that brood their larvae the genetic differentiation of populations sampled over hundreds of kilometers showed limited dispersal ability of the brooded larvae at spatial scales as small as 12 km using molecular genetic techniques (Brazeau et al., 2005).

Whereas progress is being made on understanding population connectivity both within and between shallow reefs (van Oppen and Gates, 2006) the degree of connectivity between shallow and mesophotic coral reefs is largely unknown. Mesophotic reefs usually represent an extension of the adjacent shallow reef communities with some overlap in species composition but they also harbor unique species not found in the shallow community. Because mesophotic reefs are usually part of a shallow-reef continuum, it seems likely that conspecifics from both of these habitats are in fact part of a larger metapopulation as illustrated by reproductively mature fish (e.g. groupers *Epinephelus* spp.) migrating to mesophotic depths for spawning (Nemeth, 2005). The depth-dependent distribution of subpopulations might exhibit physical connectivity through hydrodynamic processes such as upwelling and internal waves (Leichter et al., 1998; Leichter and Genovese, 2006) or vertical migration by motile species such as fish (Feitoza et al., 2005). However, on Pacific mesophotic coral reefs many fish appear to be endemic to mesophotic depths (Pyle, 2000). Studies of the population genetics and connectivity of mesophotic populations should incorporate molecular approaches that provide multiple markers per individual, as a genomic fingerprint, such as the amplified fragment length polymorphism (AFLP) technique on taxa such as corals where population differences using mitochondrial markers cannot be adequately resolved (Cowen et al., 2006). Understanding the sources and sinks of larvae for different populations on deep and shallow reefs and the processes that connect those populations is essential to understand the ecology of mesophotic coral reefs, to develop successful conservation strategies such as MPAs and to assess the resilience of both shallow and mesophotic coral reefs (van Oppen and Gates, 2006; Hellberg, 2007; Baums, 2008).

1.7. Conclusions and research directions

Mesophotic coral reefs provide unique challenges and opportunities both for the organisms that live in these habitats, and for the researchers who study them. The distribution and abundance of organisms across gradients of light and nutrients common to mesophotic reefs results in reduced coral diversity with increasing

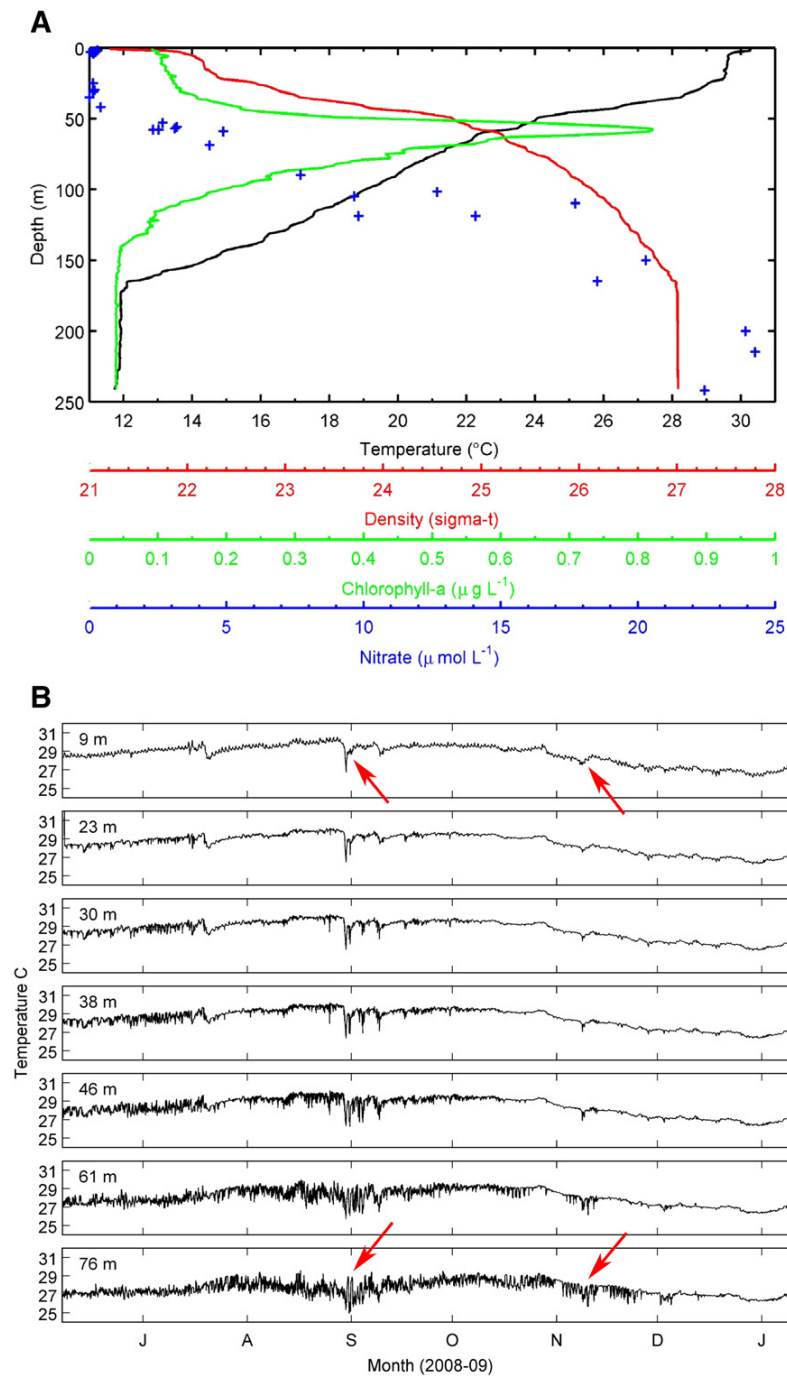


Fig. 3. A) Profiles of temperature, water density, chlorophyll concentration and nitrate concentration with increasing depth collected off of Florida Keys. Data redrawn from Leichter et al. (2007) with the addition of new data from same profile not previously published. B) Seven months of continuous recorded temperatures at depths of 10, 23, 30, 38, 46, 61, and 76 m on the north side of Little Cayman Island (Rock Bottom Wall). All data were collected using HOBO Pro V2 underwater temperature loggers. The red arrows indicate significant hurricane event passing close to or over Little Cayman Island on August 29, 2008 (Category 4, Gustav from the Northeast) and November 8, 2008 (Category 4, Paloma from the South). While the hurricanes were in the same category their approach to Little Cayman produced significantly difference effects as observed in the differences in the magnitude of the depth of mixing observed. Note also the increase in the magnitude of the temperature anomalies produced by internal waves which dissipates as depth decreases but can be observed at depths as shallow as 23–30 m.

depth but increasing sponge diversity with depth, the expression of phenotypically plastic characters (e.g. transition from mounding to plating morphology in corals) and potentially a “switch” to zooxanthellae genotype(s) whose photophysiology is better suited for low light photosynthesis (Frade et al., 2008b; Lesser et al., in review). The widespread occurrence of internal waves in mesophotic zones, and

the resulting influx of waters rich in plankton, suspended particles and dissolved nutrients is an environment that favors mixotrophic feeding strategies. The few reports available support the hypothesis that high biodiversity and endemism in mesophotic coral reef ecosystems exists but the multiple mechanisms involved for this pattern have not yet been described. Studies involving larval dispersal and genetic

connectivity, habitat stability, and quantifying changes in ecologically important processes such as herbivory and predation with depth would improve our understanding of the connectivity between shallow and mesophotic reefs significantly. These studies would also help answer other interesting questions such as the origin of mesophotic fauna and whether the fauna is derived from other mesophotic reef systems, or a subset of the flora and fauna of adjacent shallow reefs?

To understand the ecology and biology of coral reefs we must incorporate coordinated studies on both the shallow and deep components of coral reef ecosystems. Moreover, it is clear from descriptions of Caribbean and Indo-pacific mesophotic coral reefs that there may be biogeography-specific factors that constrain the development of a broader model of mesophotic reef structure and function. Managers of coral reef resources are increasingly interested in understanding the influence of mesophotic coral reefs on shallow reef dynamics, and what measures might be put in place to protect these communities as refugia for crucial fish populations and potentially other taxa (e.g. corals) that could resupply diminished shallow populations. Long-term monitoring and experimental studies of the abiotic and biotic attributes of mesophotic coral reef ecosystems will be essential to understand the processes structuring these currently understudied systems.

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