

## Chapter 4.

# Biodiversity of mesophotic coral ecosystems

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## 4.1. Introduction

MCEs are known to include complex and diverse assemblages of flora and fauna, but there is limited quantitative documentation of the degree of biodiversity and the number of unique or depth-restricted species that occur in these habitats. Studies conducted to date have consistently suggested that MCEs may be more diverse than previously believed, may be considered important biodiversity and chemical reservoirs (Kahng et al. 2010), and include species of considerable ecological and economic importance (Bejarano et al. 2014).

Study of MCEs has lagged behind that of their shallow reef counterparts due to the difficulty in accessing these communities

using conventional scuba diving. Although mesophotic species have been known to exist since the nineteenth century, it was not until the 1960s and 1970s that direct observation of MCEs by divers or submersibles became a reality (Gilmartin 1960, Starck and Starck 1972, Yamazato 1972, Wells 1973). Studies began reporting that MCEs have a high species diversity and richness (Lang 1974, Thresher and Colin 1986, Pyle 1996a, b, Armstrong et al. 2006) and may play important roles as corridors between biogeographic regions (Feitoza et al. 2005, Olavo et al. 2011, Ludt et al. 2012). Despite these important advancements, the majority of research on MCEs has been limited to just a few geographic regions; primarily the tropical Western Atlantic Ocean (including the Gulf of Mexico and



**Figure 4.1.** A diverse array of marine invertebrates dominate the fauna of most MCE habitats, as illustrated in this photo from Pohnpei, Micronesia, 75 m in depth. Most of these invertebrates are very poorly documented and many species are new to science (photo Sonia J. Rowley).

Caribbean), the Hawaiian Archipelago, the Great Barrier Reef and the Red Sea—which are not necessarily representative of the vast majority of MCE habitats found throughout the tropical Indian and Pacific Oceans. Consequently, most MCE biodiversity remains unknown.

This chapter provides a generalized snapshot of what is known about the biodiversity of the primary habitat-forming mesophotic organisms (except ocotocorals and antipatharians) and mesophotic fish. The sections are presented in the following order: macroalgae, sponges, scleractinian corals, symbionts and fish. Except for sessile invertebrates (sponges and corals) and invertebrates of the Gulf of Mexico, this chapter does not cover the vast array of marine invertebrates found in MCEs, as very little is known about them (Figure 4.1), or the diverse mesophotic microbial community (reviewed in Olson and Kellogg 2010). Throughout this section, the similarities and differences between shallow coral ecosystems and MCEs

**Early recognition of the uniqueness of Mesophotic Coral Ecosystems:**

“They lie in a twilight zone belonging neither to the shallower water species nor the abyssal species, but to the intermediate dwellers themselves.” Porter 1973 (Jamaica)

“A true ‘deep-reef’ fauna exists.” Colin 1974 (Jamaica and Belize)

“Represents a transitional zone in which only the deepest of hermatypic (zooxanthellate) corals exist...and the stylasterids (‘hydrocorals’) and ahermatypic (azooxanthellate) corals start to diversify.” Macintyre et al. 1991 (Barbados)

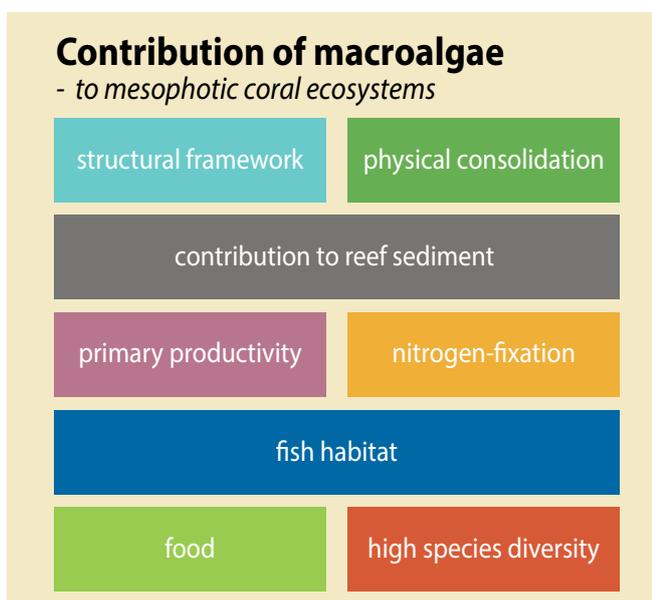
should become apparent, as well as how much there is still to be learned about MCEs.

## 4.2. Macroalgae

Macroalgae are important, if not essential, components of coral reef communities (Figure 4.2). While substantially less information is available on deep-water macroalgae than on their shallow-water counterparts, information does exist on their composition, productivity, abundance and potential importance (Gilmartin 1960, Jensen et al. 1985, Littler et al. 1986, Ballantine and Aponte 2003, 2005). Exploration of MCEs has yielded new records and descriptions of macroalgal species using a combination of morphological and molecular techniques. It is currently difficult to determine the degree of depth restriction, given that few mesophotic regions have been adequately sampled. While some mesophotic algal assemblages often contain a combination of shallow- and deep-water macroalgae (Kajimura 1987, Searles and Schneider 1987, Hanisak and Blair 1988), other algal assemblages contain a mesophotic flora composed largely of species unique to the mesophotic (Aegian and Abbott 1985, Spalding 2012).

Due to their ability to adapt to a wide range of light and nutrient conditions, macroalgae are commonly encountered over the entire depth range of MCEs, although regional differences are found in algal species’ composition and lower depth limits. For instance, in Hawai‘i, macroalgae are found in high abundance throughout the mesophotic zone, with expansive meadows of calcified green algae found as deep as 90 m (Figure 4.3) and beds of other foliose algae as deep as 160 m (Spalding 2012). In southwest Puerto Rico, calcified macroalgae tend to dominate the lower limit of MCEs from 70 m to approaching 100 m in terms of cover (Ballantine et al. 2010).

Several different functional forms of macroalgae are found in MCEs, with subtle patterns in the distribution and abundance of dominant assemblages. Increasing depth and the interplay of biotic and abiotic factors likely influence mesophotic algal abundance and distribution at site-specific depths and



**Figure 4.2.** Contribution of macroalgae to MCEs.



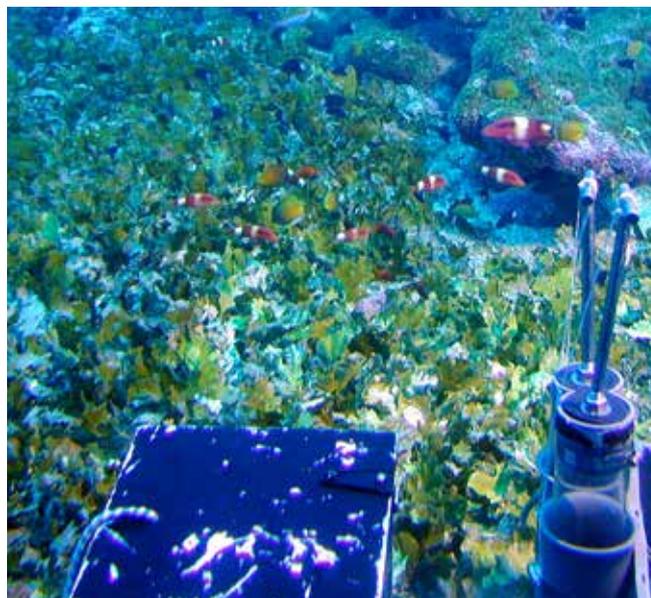
**Figure 4.3.** A typical macroalgal community in the ‘Au‘au Channel offshore of Maui, USA. Small plates of the coral *Leptoseris* sp. are shown amidst a dense bed of the calcified green alga *Halimeda distorta* at 80 m depth in the Maui Keyhole area (photo NOAA’s Hawai‘i Undersea Research Laboratory).

locations. These factors include availability of appropriate substrata, cold nutrient-rich water from upwelling or internal waves and changes in irradiance quantity and quality, as well as reduced herbivory and physical disturbances (such as sand scour), efficient nutrient uptake, and low respiration rates (Kirk 1994, Leichter et al. 2008). Distribution patterns can be uncomplicated and represent broadly overlapping zones (e.g. communities dominated by *Lobophora*, *Halimeda*, *Peyssonnelia* and crustose coralline algae in the Bahamas; Littler et al. 1986, Aponte and Ballantine 2001), but in some locations, dominant algal assemblages may be diverse, forming complex distributional patterns that are spatially heterogeneous (Spalding 2012). Other dominant assemblages found in MCEs include lush beds of foliose red algae (Gavio and Fredericq 2005), tangled mats of the green alga *Microdictyon* (Abbott and Huisman 2004, Huisman et al. 2007), leafy green algae such as *Ulva* and *Umbraulva* (Spalding 2012) and lush fields of *Anadyomene menziesii* (Reed et al. 2015), the sand-dwelling green alga *Udotea* sp. (Figure 4.4; Spalding 2012), delicate webs of the green alga *Anadyomene* (Culter et al. 2006, Littler and Littler 2012), and even deep-water kelp beds (Graham et al. 2007).

Calcified red algal nodules or multi-dimensional aggregations, called rhodoliths, are also a common constituent of MCEs, forming dense, pink beds over both hard and soft substrata. Rhodolith beds are major calcium carbonate producers, with a total production rate comparable to the world's largest biogenic calcium carbonate deposits (Amado-Filho et al. 2012). Shallow-water rhodoliths appear to be highly susceptible to increasing ocean acidification (Jokiel et al. 2008), but the impact on mesophotic rhodoliths is unknown. Mesophotic rhodolith beds have been reported worldwide (Table 4.1).

**Table 4.1.** Depth of mesophotic rhodoliths.

Depth of mesophotic rhodoliths		
Location	Depth (m)	Reference
U.S. Virgin Islands	41	Weinstein et al. 2014
Bermuda	50	Reid and Macintyre 1988
Caribbean	60	Focke and Gebelein 1978
Puerto Rico	60	Ballantine et al. 2008, Rivero-Calle et al. 2009
Australia	80	Bridge et al. 2011a
Bahamas	91	Littler et al. 1991
Brazil	100	- Amado-Filho et al. 2012
Japan's Ryukyu archipelago	135	Iryu et al. 1995
Hawai'i	171	Agegian and Abbott 1985



**Figure 4.4.** Foliose (leafy) algal beds are a common component of mesophotic assemblages in Hawai'i, USA. Dense beds of the green, sand-dwelling alga *Udotea* sp. surrounding a carbonate outcropping with pink crustose coralline and turf algae at 50 m off south O'ahu (photo NOAA's Hawai'i Undersea Research Laboratory).

Siphonous green algae of the Order Bryopsidales (e.g. *Halimeda*, *Codium*, *Caulerpa*, *Udotea* and *Avrainvillea*) are often particularly abundant in MCEs (Littler et al. 1986, Blair and Norris 1988, Drew and Abel 1988, Norris and Olsen 1991, Aponte and Ballantine 2001, Leichter et al. 2008, Bongaerts et al. 2011b). The success of green algae in tropical waters may arise in part from the optimal irradiance field in deeper

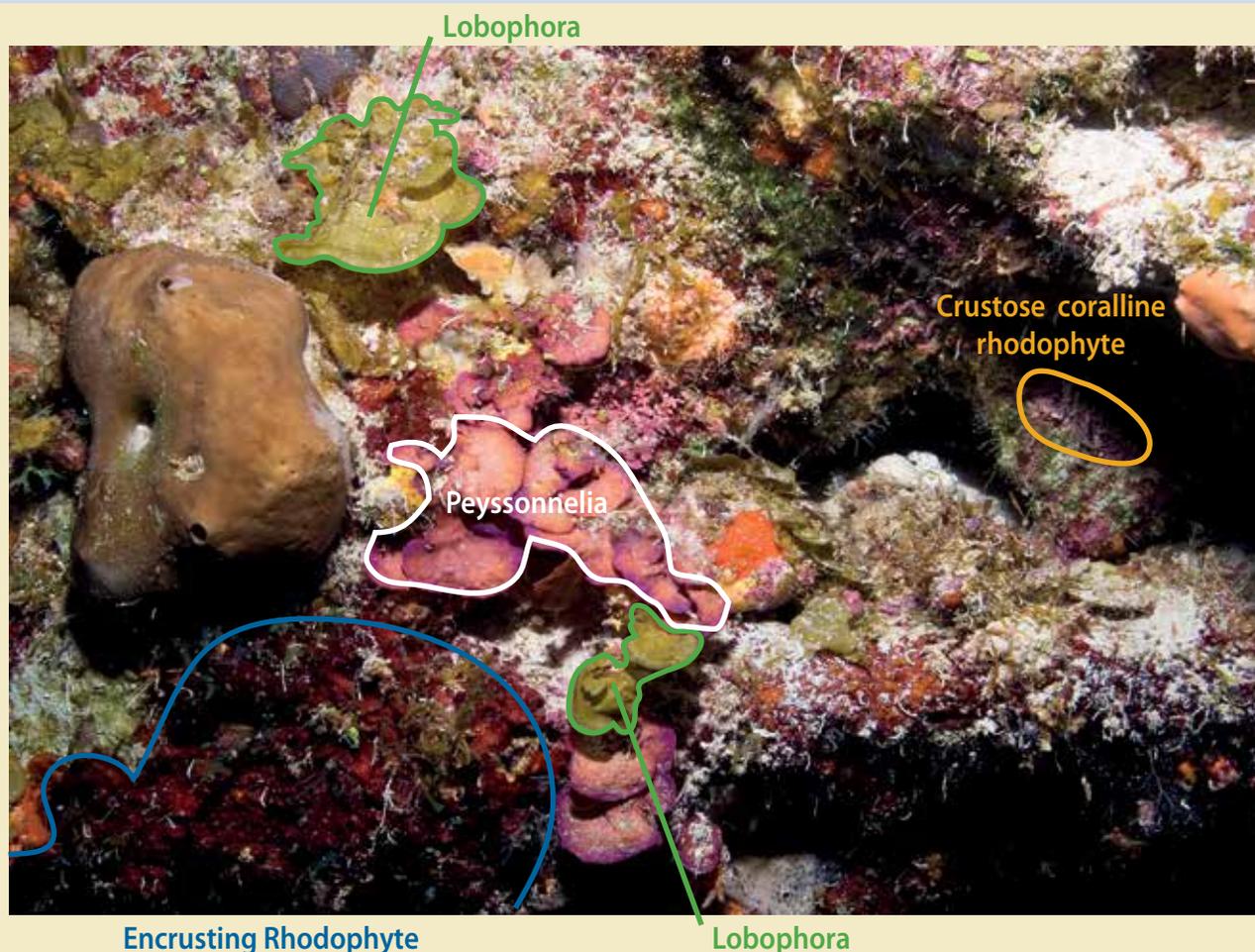
water for green algae; at these depths, the irradiance field is rich in blue and green wavelengths (Kirk 1994). Some green algae also possess unique pigments, such as the carotenoid siphonaxanthin, that enhance the absorbance of blue-green spectral regions (Yokohama et al. 1977, Yokohama 1981). Physical changes in plant construction and morphology also optimize light capture (Vroom and Smith 2001). For example, some species such as *Codium* are optically opaque, capturing

all ambient light that reaches the alga (Kirk 1994). Similarly, there are many red algae species that have flat and spreading morphologies to maximize light capture (Hanisak and Blair 1988, Ballantine and Aponte 2005). Deep-water *Halimeda copiosa* (to 152 m depth) have also been observed to increase surface area by increasing the diameter of the surface utricles by 15 per cent compared with shallower plants of the same species (Blair and Norris 1988).

### Algal-dominated mesophotic coral ecosystems in Puerto Rico

The MCEs on the Puerto Rico insular shelf host an abundance of algal species. Approximately 185 taxa have been identified at deeper than 35 m. These species comprise some 40 per cent of the total algal flora known from Puerto Rico (Ballantine and Aponte 2002, Ballantine et al. 2015; Figure 4.5) and this mesophotic flora is distributed between three depth groups. Nearly half of the species that are found in depths of 35 m or greater are found across the entire shelf, ranging from shallow nearshore habitats to the offshore mesophotic. A second distributional group (somewhat less than 25 per cent) consists of macroalgae that are found ranging from intermediate depths to the mesophotic. A third group comprised of exclusively deep-water taxa (38 identified to species) represents nearly a quarter of the mesophotic flora. Overall, 7 per cent of the total Puerto Rican algal flora appear to be restricted to water deeper than 35 m (Ballantine and Ruiz pers. obs.).

Between 50 and 70 m depth in southwest Puerto Rico, algal cover averages 52 per cent of mesophotic habitat followed by sponges, then corals. By composition, calcified Rhodophyta species (principally *Hydrolithon abyssophila* and *Peyssonnelia* species) in addition to leavy *Phaeophyceae* (*Dictyota* spp. and *Lobophora variegata*) and multispecies turfs are most abundant. A similar dominance of encrusting calcified red alga in MCEs has been observed in the Bahamas (Aponte and Ballantine 2001). The deep Corallinales/*Peyssonnelia* group may be universally characteristic of lower mesophotic reef benthic community structure. At some mesophotic sites off the southwest coast of Puerto Rico, coralline red algae and *Peyssonnelia* species constitute the principal cover by calcareous organisms. The relatively large number of geographical records, as well as the rate of discovery of new algal species encountered, indicates that there is undoubtedly a substantial diversity yet to be discovered even in a well studied area.



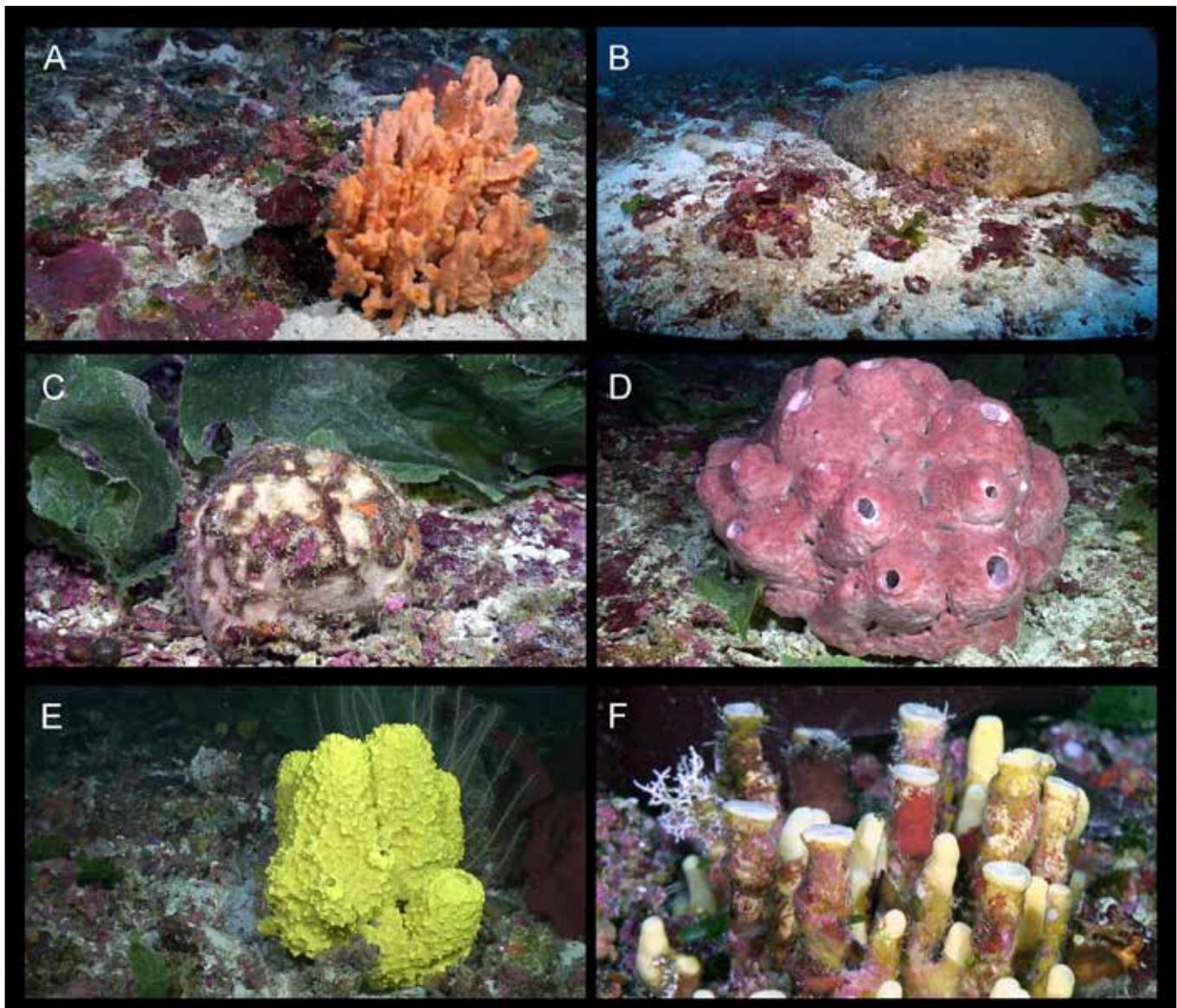
**Figure 4.5.** Algal dominated shelf-edge wall (65 m, La Parguera, Puerto Rico). Dominant macroalgae include: *Lobophora variegata*, *Peyssonnelia iridescens*, undescribed non-calcified encrusting rhodophyte and crustose coralline rhodophyte (photo Héctor Ruiz).

### 4.3. Sponges

Sponges are major components of most coral reef ecosystems, including MCEs. Recent surveys of Pulley Ridge in the Gulf of Mexico off the southwest Florida shelf have documented a high level of sponge biodiversity (relative to corals and other benthic invertebrates), with more than 100 distinct sponge “taxa” photographically identified. These included several common MCE sponges from Florida and the Caribbean (Figure 4.6), such as the giant barrel sponge (*Xestospongia muta*), the orange fan sponge (*Agelas clathrodes*), vase sponges (e.g. *Ircinia cf. campana*), branching sponges (e.g. *Callyspongia* sp. and *Niphates* sp.), tube sponges (e.g. *Aplysina* spp., *Callyspongia vaginalis* and some species of the Order Verongida), orange bushy sponges (various species in the Families Axinellidae and Clathriidae), ball sponges (*Geodia* spp., *Cinachyrella* sp. and *Tethya* sp.), bioeroding sponges (*Cliona varians*), various species of massive (e.g. *Spongisorites siliquaria*) and encrusting sponges and large and small finger sponges (*Oceanapia* sp., *Discodermia* sp. and *Theonella* sp.; Reed et al. 2014, 2015).

Massive, branching, tubular and vase/barrel sponges provide habitat for fish and invertebrates, including commercially-important species (e.g. Knudby et al. 2013). Because they have a large filter-feeding capacity, sponges contribute significantly to nutrient cycling (de Goeij et al. 2008, 2013). Clonid sponges bioerode limestone substrates (coral skeletons and bedrock; Weinstein et al. 2014), whereas encrusting sponges protect substrates from bioeroders. In some Caribbean locations, such as Jamaica, sclerosponges (sponges with both siliceous spicules and a calcium carbonate skeleton) replace corals as framework-builders (Lang et al. 1975). Although branching, leafy and massive lithistid demosponges (e.g. *Discodermia* spp., *Theonella* spp. and *Leiodermatium* sp.) occur in the Caribbean, unlike those found in the Pacific, they are not framework-builders.

Sponges and their associated microorganisms are the richest and most prolific source of marine natural products with human health applications (Nakao and Fusetani 2010). The actual biodiversity of sponges in MCEs is largely unknown, but



**Figure 4.6.** Sponges of Pulley Ridge off the southwest Florida shelf. Pulley Ridge is the deepest known light-dependent coral reef ecosystem off the continental United States at depths of 60–90 m. More than 100 distinct sponge “taxa” were photographed at Pulley Ridge. (a) Axinellidae, (b) *Spongisorites siliquaria*, (c) *Geodia* sp., (d) Verongida, (e) *Aiolochoiria crassa* and (f) *Oceanapia* sp. (photos from Reed et al. 2015, Plate 2).

recent exploration of the MCEs of the southwest Florida shelf suggests that there could in fact be several hundred species in that location alone. Thus, the potential for discovery of novel chemicals, processes or properties with biotechnological potential has yet to be unlocked.

As a result of change in the environment and ocean chemistry, some coral reefs may become sponge reefs in the future (Bell et al. 2013). Laboratory studies of shallow reef sponges (some of which also occur in MCEs) suggest that unlike shallow corals, the warmer, more acidic conditions expected by the end of the century will have little effect on sponge ecology

and physiology (Duckworth et al. 2012). However, lower pH may result in higher rates of bioerosion by clionid sponges (Duckworth and Peterson 2013).

The most critical knowledge gap concerns species diversity and ecosystem function of sponges in MCEs. In many MCEs, sponges are dominant taxa, yet their biodiversity, ecological importance, and biotechnological potential are relatively unknown. This knowledge is needed to improve the capacity to model, understand and predict threats, impacts and future anthropogenic and climate-driven changes to MCEs, and to develop tools for improved resource management.

## 4.4. Scleractinian corals

Reef-building scleractinian corals are limited in their depth distribution by the light requirements of their symbiotic association with zooxanthellae (Goreau and Goreau 1973). The quantity and quality of light reaching corals varies depending on water transparency, angle of incidence, substrate orientation, structural characteristics and geographic location. Thus, many mesophotic coral species grow in two-dimensional shapes (i.e., crusts, plates and small mounds), which maximizes their surface area for photosynthesis (Kuhlmann 1983).

The deepest distributions for zooxanthellate species are reported for localities with clear oligotrophic waters, such as the Bahamas (Hartman 1973, Reed 1985), Belize (James and Ginsburg 1979), Hawai'i (Kahng and Maragos 2006), Marshall Islands (Wells 1954, Colin et al. 1986), Johnston Atoll (Kahng and Maragos 2006) and the Red Sea (Fricke and Schuhmacher 1983). In general, zooxanthellate scleractinian corals are found at deeper depths in the Pacific Ocean in comparison with the Atlantic. Recent surveys suggest that the depth range of many



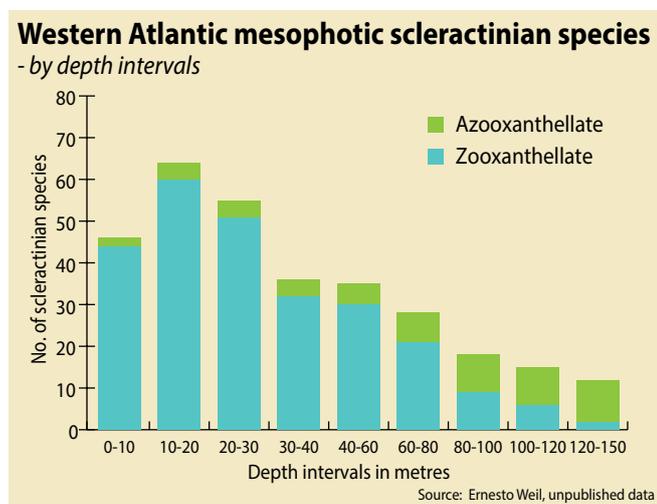
**Figure 4.7.** Upper mesophotic corals in Okinawa Island, Japan at 40 m in depth, including *Favites* sp., *Seriatopora hystrix*, *Pachyseris speciosa* and *Porites* sp. (photo Frederic Sinniger).

zooxanthellate corals may have been grossly underestimated. Reports from Saipan, the Great Barrier Reef and Hawai'i have extended the known depth range of more than 18 coral species by an average of 30 to 67 m (Bridge et al. 2012b, Dinesen et al. 2012, Blyth-Skyrme et al. 2013). As exploration of MCEs continues, especially in oceanic calcareous islands and atolls, the depth range of many species may be extended.

Mesophotic scleractinian corals, like their shallow-water counterparts, provide essential habitat for fish and other mobile species. However, the spatial heterogeneity (relief) is reduced to a flatter, more two-dimensional structure in comparison to shallow reefs. Nevertheless, through their skeletal structures, corals provide habitats for numerous other invertebrates and some fish species. For example, over 860 invertebrates have been found associated with shallow scleractinian corals (Stella et al. 2011).

MCEs are part of a coral reef ecosystem continuum that begins in shallow water and continues through the photic zone. Corals found at mesophotic depths can sometimes be divided into two zones: the upper mesophotic and the lower mesophotic (Slattery et al. 2011, Muir et al. 2015). Coral communities found in the upper mesophotic depths (30–50 m) tend to share many similarities with shallower corals (Figure 4.7). For example, in northeast Australia, 21 per cent of the 76 *Acropora* species (staghorn corals) recorded for shallow waters (< 30 m) extend to mesophotic depths, with some species found as deep as 73 m (Muir et al. 2015). Similarly, in the Hawaiian Islands, *Pocillopora damicornis*, *Porites lobata* and *Montipora capitata* observed in the upper mesophotic are found at shallower depths (Rooney et al. 2010). Shallow reef communities in the Caribbean extend as deep as 40 m in some well-lit localities, with upper mesophotic communities dominated by reef-building species, i.e., *Orbicella franksi*, *O. faveolata*, *Montastraea cavernosa*, *Siderastrea siderea*, *Stephanocoenia intersepta*, *Agaricia lamarcki* and *Pseudodiploria strigosa* (Goreau and Wells 1967, Wells 1973, Weil 2006, Armstrong et al. 2008, Reyes et al. 2010).

The lower part of the mesophotic depth range hosts a more distinct coral assemblage. In both the Atlantic and Pacific, agariciid corals usually dominate these communities, although



**Figure 4.8.** Relationship between the number of scleractinian coral species with and without zooxanthellae from shallow reefs to 150 m in the western Atlantic (Weil unpublished).

a few other species can be found from the shallows to lower mesophotic depths, such as some Indo-Pacific and Red Sea merulinids and pocilloporids (Yamazato 1972, Alamaru et al. 2009). In the Hawaiian Islands, the diversity of zooxanthellate coral species decreases in the lowest parts of the mesophotic zone (deeper than 90 m) to only a few species, including five species of *Leptoseris* (Pochon et al. 2015). In the Caribbean, mesophotic scleractinian coral communities below 40–50 m change dramatically, with plate-like and crustose species, such as *A. lamarcki*, *A. undata*, *A. grahamae*, *Undaria agaricites*, *O. franksi* and *Helioseris cucullata* populating the slopes and banks where low abundances of *Porites asteroides*, *S. siderea*, *Madracis formosa*, *M. pharensis* and *S. intersepta* are also found. In the lower mesophotic zone, a transition occurs from scleractinian-dominated communities to octocoral/antipatharian/sponge-dominated communities (Lehnert and van Soest 1999, Cairns 2000, Kahng and Kelley 2007, Bridge et al. 2011b).

A summary analysis (Weil unpublished) of the reported records and data on the depth distribution of zooxanthellate and azooxanthellate scleractinian coral species in the western Atlantic shows that, overall, as depth increases, the number of zooxanthellate species drops significantly from 64 to 12, with the proportion of azooxanthellate species increasing from 4 per cent to 83 per cent (Figure 4.8).

Species level identification is often challenging on mesophotic scleractinian corals. Most coral species are described from shallow water, based on their morphological features (mainly skeletal characteristics). Because coral morphology can drastically change in response to environmental conditions, even within a colony (Wells 1973, Veron 1995, Todd 2008), it can be difficult to determine whether coral specimens from MCEs represent ecological variations of a known species, or a different species altogether. In such cases, the use of molecular tools may help to clarify coral identifications. For example, the presence of the genus *Pavona* in Hawaiian MCEs and the identification of a possible new species of *Leptoseris* were made possible only by the use of molecular tools (Luck et al. 2013). While molecular tools can validate morphological differences, the situation is not always that straightforward, especially in more diverse coral regions, where species hybridization and incomplete lineage sorting (i.e., shared ancestral polymorphism) add significant challenges to molecular taxonomy. Such issues are highlighted in a study of the genus *Acropora* from the Indo-Pacific, which revealed that, as a result of hybridization, the molecular data were not consistent with each other or with the morphology (Richards et al. 2008). Although the use of molecular tools to identify coral species has yet to be fully realized, recent studies on both morphology and molecular characteristics have greatly increased the knowledge of mesophotic coral biodiversity and distribution (e.g. Luck et al. 2013, Denis et al. 2014, Muir et al. 2015).

The reproductive biology of mesophotic coral species represents a further challenge for researchers, and is an important characteristic that can be used to assess connectivity, geographic distribution and taxonomic status of ecomorphs or species thought to be morphological variations of shallower taxa. Coral reef recovery, from losses due to coral bleaching, diseases and other environmental stressors (Hoegh-Guldberg 1999, Wilkinson 2008, Weil and Rogers 2011) will depend on successful reproduction, recruitment and juvenile survivorship. Knowledge

of coral reproductive biology is largely unknown for mesophotic species. While similarities with shallow coral colonies may be expected, reduced light irradiance would suggest lower growth and productivity rates in MCEs in comparison to shallow reefs, which may affect fecundity and maturation. Coral fragmentation (asexual reproduction) may also not be a common method by which coral populations increase in number at mesophotic depths as it is in shallow waters because of steep slopes, plate and crustose coral morphologies and protection from surface waves in mesophotic waters. This calls into question whether mesophotic coral colonies have the potential to seed shallower areas or are themselves maintained by larval import from shallow reefs. Recruitment rates are generally low in shallow reefs (Gardner et al. 2003, Pandolfi et al. 2003, Irizarry and Weil 2009). Recruitment rates in mesophotic waters are unknown, although some factors negatively impacting recruitment and survivorship in shallow water, such as wave energy, attenuate with depth.

Reproductive cycles are difficult to determine due to the need for frequent tissue samples from the same colonies of the same species. In the U.S. Virgin Islands, the reproductive performance

of *O. faveolata* was assessed over a five-week period at three depth ranges (5–10 m, 15–22 m and 35–40 m). The results showed that corals at the upper edge of the mesophotic zone (35–40 m) were more fecund and produced more eggs than those at shallower depths (Holstein et al. 2016). Meanwhile, preliminary results of a 13-month reproductive study of two species of agaricids, *Undaria agaricites* and *A. lamarcki*, at 20, 50 and 70 m off La Parguera, Puerto Rico indicated no difference in their reproductive cycles (Weil unpublished). These are limited, but potentially important results on fecundity of abundant mesophotic coral species in the Caribbean. In the Indo-Pacific, mesophotic coral reproductive cycles have only been investigated for two brooding species, *Pocillopora damicornis* and *Stylophora pistillata* (Richmond 1987, Rinkevich and Loya 1987), and the mesophotic specialist *Acropora tenella* (Prasetia et al. 2015). The spawning (brooding) periods, overall fecundity and recruitment rates and the survival of most mesophotic coral species remain unknown. This is an important research need to improve the understanding of the dynamics of these communities and their importance as refuges or as a source of seed populations for shallower species.

## 4.5. Symbionts

Dinoflagellates in the genus *Symbiodinium* (also called zooxanthellae) are a key component of coral reef ecosystems (Freudenthal 1962). These photosynthetic microorganisms reside in the tissues of a large diversity of marine invertebrates and some protists (Trench 1993). They provide nutrients to organisms that are otherwise unavailable in the nutrient-poor waters of tropical oceans. Research conducted during the last 25 years on shallow coral reefs has allowed extensive understanding of the genetic diversity and host-symbiont specificity across benthic host taxa at a variety of spatial and temporal scales (reviewed in Coffroth and Santos 2005, Stat et al. 2006, 2012). In contrast, far less is known about the diversity and biology of *Symbiodinium* in MCEs. Due to the logistical constraints in obtaining coral samples in the mesophotic zone, previous genetic studies have been largely limited to upper mesophotic

depths (i.e., 30–60 m; Frade et al. 2008, Bongaerts et al. 2010b, 2011a, 2013b, 2015b, Lesser et al. 2010, Serrano et al. 2014), and only two studies have explored *Symbiodinium* in the lower mesophotic (i.e., 60–125 m; Chan et al. 2009, Pochon et al. 2015). Collectively, these studies have shown that MCEs host a wide diversity of *Symbiodinium* genotypes, with most displaying marked zonation by depth in scleractinian corals. Recently, nuclear and mitochondrial markers were used to investigate host-symbiont associations across the lower mesophotic in the Hawaiian coral *Leptoseris* (Figure 4.9; Pochon et al. 2015). Strong host-symbiont depth specialization patterns and unique *Symbiodinium* genotypes were revealed, indicating limited connectivity between upper and lower mesophotic zones and suggesting that niche specialization plays a critical role in *Leptoseris-Symbiodinium* evolution at mesophotic extremes.



**Figure 4.9.** Representative *Leptoseris* sp. reef offshore of Maui, Hawai'i at 67 m depth (photo NOAA's Hawai'i Undersea Research Laboratory).

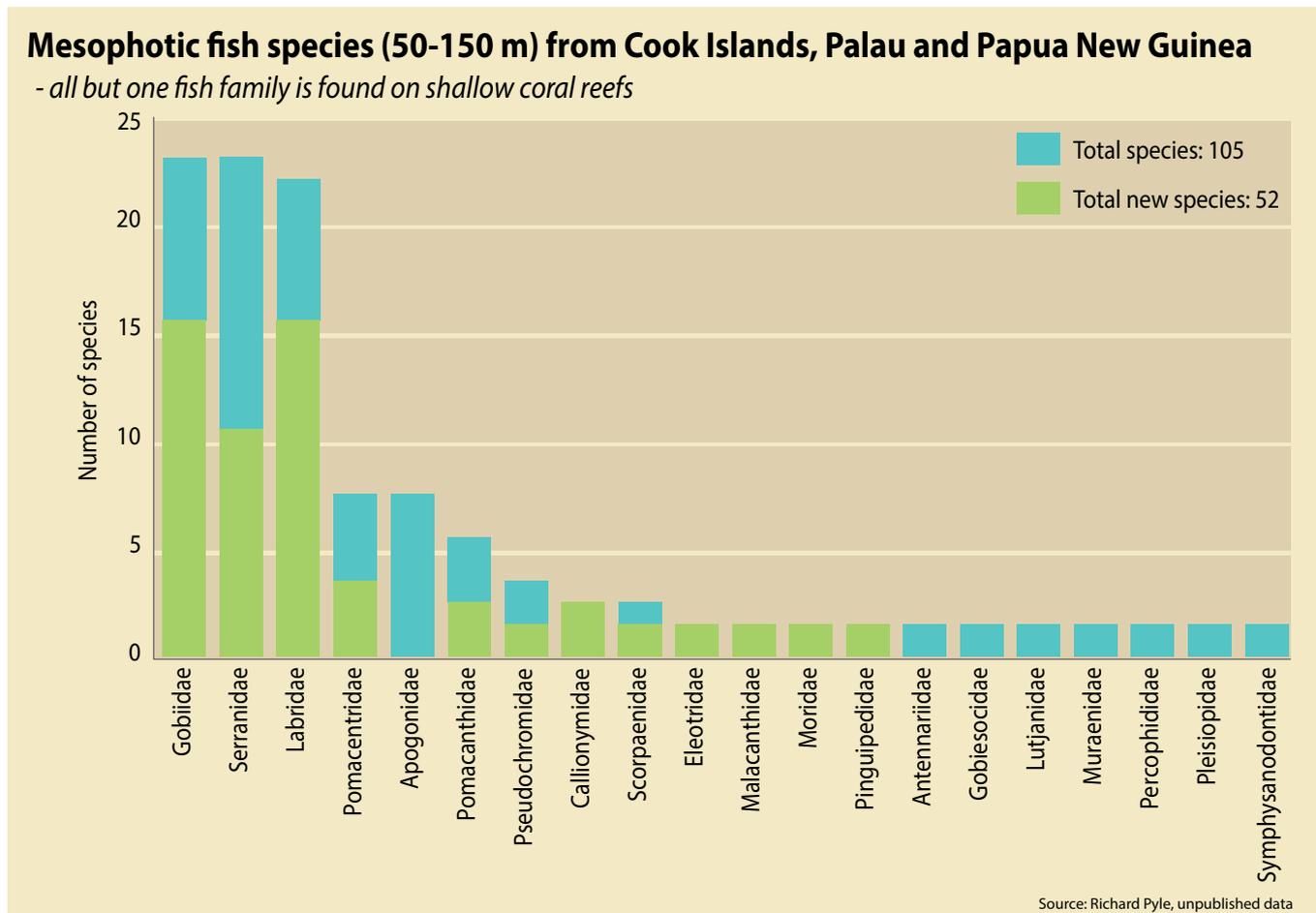
## 4.6. Fish

Fish are major mobile components of MCEs. They play key ecological roles and show high levels of biological diversity within these ecosystems (Brokovich et al. 2010, García-Sais 2010, Lesser and Slattery 2011, Bejarano et al. 2014).

The exploration of MCEs has resulted in the description of hundreds of new fish species (Colin 1974, Thresher and Colin 1986, Pyle et al. 2008, Baldwin and Robertson 2013, 2014) and new species records for some regions (Colin 1976, Feitoza et al. 2005, Reed et al. 2015). Initial results from exploratory work in the Cook Islands, Palau and Papua New Guinea revealed an unexpected wealth of new species, where 50 per cent of the fish collected from depths greater than 50 m were found to be new to science (Figure 4.10; Pyle and Randall 1993, Allen and Randall 1996, Randall and Pyle 2001a, b, Pyle et al. 2008). Similarly, of the 144 species collected at a single site in Fiji at depths of 50–120 m in 2002, more than 40 species were new (Figure 4.10). In 2004, additional exploratory dives on other MCEs in Fiji revealed many more species and relatively low faunal overlap among sites (Pyle 2005). Research on mesophotic fish so far has mostly been focused in the Caribbean, Hawai'i and Red Sea, thus the vast majority of MCEs have yet to be studied and many more fish species are still to be discovered.

Fish inhabiting MCEs are similar taxonomically to those found on shallow coral reefs—with a few exceptions, the same families of fish are found at both depths. For example, in the Pacific, of 105 species of fish collected in the MCEs of the Cook Islands, Palau and Papua New Guinea, only one belonged to a family not typically found on shallow reefs (Figure 4.11; Pyle 2005). Similarly, in the Atlantic, all families of fish encountered in mesophotic habitats are common on shallower reefs (Feitoza et al. 2005, Bryan et al. 2013, Bejarano et al. 2014).

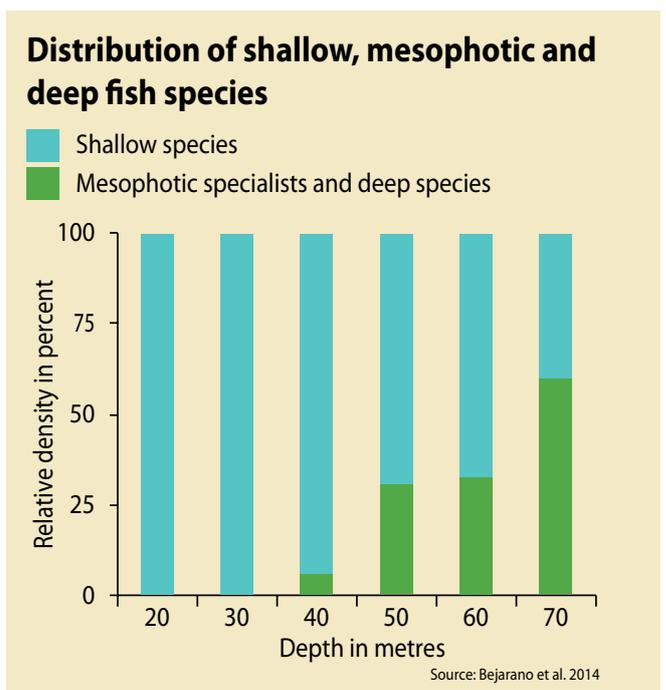
Several fish assemblages (collection of fish species co-occurring) have been described for MCEs (Colin 1974, 1976, Thresher and Colin 1986, Dennis and Bright 1988, García-Sais et al. 2004, Feitoza et al. 2005, Brokovich et al. 2008, García-Sais 2010, Bryan et al. 2013, Bejarano et al. 2014). Mesophotic fish assemblages differ from those on shallow reefs in terms of species composition and abundance (Colin 1974, 1976, Feitoza et al. 2005, Brokovich et al. 2008, García-Sais 2010, Bryan et al. 2013, Bejarano et al. 2014). Mesophotic depths represent the lower distribution of many shallow species (Colin 1974, 1976, Thresher and Colin 1986, Feitoza et al. 2005, Brokovich et al. 2008, García-Sais 2010, Bryan et al. 2013, Bejarano et al. 2014). Therefore, mesophotic assemblages show a combination of shallow species with a wide depth distribution, species restricted to mesophotic depths, and deeper species (Colin



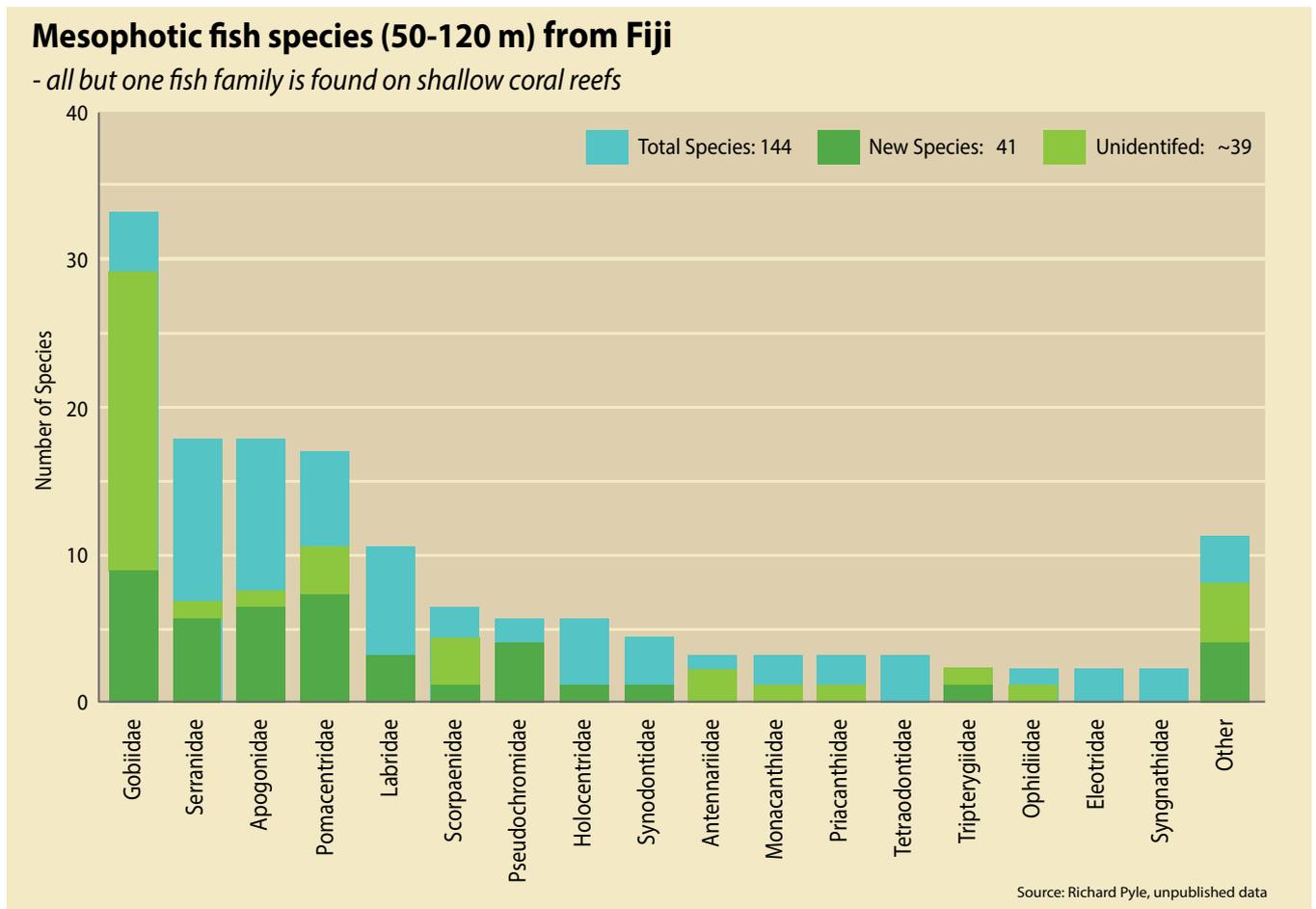
**Figure 4.10.** Total numbers of fish species within each family collected at depths of 50–150 m in the Cook Islands, Palau and Papua New Guinea, showing proportional numbers of new species. All but Symphysanodontidae (one specimen) are families characteristic of shallow coral reefs.

1974, 1976, Bejarano et al. 2014). As depth increases, the differences in species composition increase, and the abundance of fish common in shallow waters decreases, while species restricted to mesophotic depths and deeper increase (Figure 4.12). As a consequence of this continued shift in species composition with depth, major breaks in mesophotic fish species composition occur, at approximately 60 m on average (Thresher and Colin 1986, Bejarano et al. 2014, Pinheiro et al. 2015). However, these changes are likely driven by reduced light levels affecting photosynthesis, and in turn algae and subsequently herbivorous fish, as well as by additional local environmental factors. Thus, the depth at which major breaks occur can be variable and location-dependent, for example in clear waters, major breaks were found at 80 m in Curaçao (Pinheiro et al. 2015) and 120 m in the Hawaiian Islands (Pyle pers. obs.).

Mesophotic depth-restricted fish species are common globally, although the highest rates of depth-specificity of species tend to be in the Pacific. In the Hawaiian Islands, there is more overlap between shallow and mesophotic fish in comparison with other areas in the Pacific such as Fiji (Pyle unpublished). Of the species found deeper than 30 m, 84 per cent are also found on shallower reefs (Boland et al. 2011, Pyle unpublished). As depth increases, the degree of overlap with



**Figure 4.12.** Proportion of shallow species vs. mesophotic specialist and deep species per depth, along a gradient from 20–70 m in Puerto Rico (Bejarano et al. 2014).



**Figure 4.11.** Total numbers of fish species within each family collected at depths of 50–120 m in Fiji, showing proportional numbers of new species and unidentified species (more than half of which are likely new species). All but Trachichthyidae (one specimen) are families characteristic of shallow coral reefs.

shallow reefs diminishes and only 46 per cent of fish species occur both at depths shallower than 30 m and deeper than 60 m. Degrees of shallow and mesophotic species overlap similar to those found in Hawai'i are reported for MCEs in the Marshall Islands (65 per cent of the fish species seen at 75 m are common in shallow waters; Thresher and Colin 1986) and Puerto Rico (76 per cent of the fish species found in MCEs are common inhabitants of shallow reefs and 24 per cent are restricted to 40 m or deeper; Bejarano et al. 2014; Figures 4.13 and 4.14).

MCEs are disproportionately represented by geographically endemic fish species (Pyle 2000, Brokovich et al. 2008, Kane et al. 2014). For example, a comparison of horizontal overlap among fish assemblages in Fiji, Papua New Guinea and

Palau (Pyle 2000, 2005) shows that 50–60 per cent of shallow species overlapped between any two of these locations, while only 6–10 per cent of mesophotic fish species overlapped. This reflects higher rates of geographic endemism among mesophotic fish species. A similarly high representation of endemic species has been documented on MCEs in the Northwestern Hawaiian Islands, where 46 per cent of the reef fish species between 30 and 90 m are endemic to Hawai'i; more than those found in shallower reefs (< 30 m) in the same region (29.9 per cent; Figure 4.14; Kane et al. 2014). Endemic species are not as common in Atlantic MCEs as in the Pacific. However, a recent study in Bermuda reports endemic species in the upper mesophotic zone (Pinheiro et al. 2015). As endemism hotspots, MCEs should be afforded attention for both scientific and conservation purposes.



**Figure 4.13.** The bicolor basslet, *Lipogramma klayi*, is found only at mesophotic depths in Puerto Rico (photo Héctor Ruiz).



**Figure 4.14.** Almost all the individual fish in this image taken at 110 m off Maui are species endemic to the Hawaiian Islands (photo NOAA's Hawai'i Undersea Research Laboratory).

# A quantitative study of the biodiversity of coral and other groups of organisms in the mesophotic zone compared to shallower depths in the Gulf of Mexico, USA

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Comparisons of the levels of biodiversity in MCEs generally focus on specific depths, reefs or reef systems (e.g. Armstrong et al. 2006, García-sais 2010, Rooney et al. 2010, Bridge et al. 2011b, 2012b). Although ecological studies provide very valuable information about biodiversity in local regions, few provide data on sufficiently large numbers of species to quantitatively assess major patterns of biodiversity across environmental gradients such as the mesophotic zone for an entire region. The purpose of our investigation was to assess the magnitude of biodiversity in mesophotic versus shallower depths in the Gulf of Mexico.

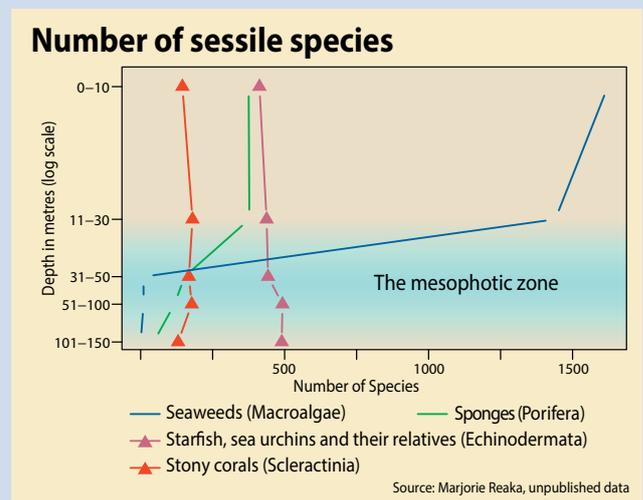
Large-scale quantitative assessments are valuable for spatial planners and resource managers because they provide information on the total number of species that can be affected by conservation or management policies. Prior to this report, we participated in an international effort that performed a 50-year re-analysis of the distribution and biodiversity of the biota of the Gulf of Mexico (Felder and Camp 2009). This project engaged leading taxonomists for every major group of marine flora and fauna, and thus provided especially rigorous taxonomy, as well as a uniquely large dataset of species from the Gulf of Mexico, allowing quantitative analysis of the distribution and biodiversity of 7,753 species (in the groups we examined herein) that have depth and habitat data. The data are available in a public database, BioGoMx, at [gulfbase.org](http://gulfbase.org).

In the present study, information was gathered for eight groups of organisms—four sessile or relatively sessile groups (i.e., scleractinian corals, macroalgae, sponges and echinoderms) and four relatively motile or highly motile groups (i.e., polychaete annelids, gastropod molluscs, crustaceans and fish). Depth distributions for each species were determined from data provided by each taxonomic expert in Felder and Camp (2009) and [gulfbase.org](http://gulfbase.org) so that the total number of species present and the number of species that occur *only* in each depth zone could be assessed.

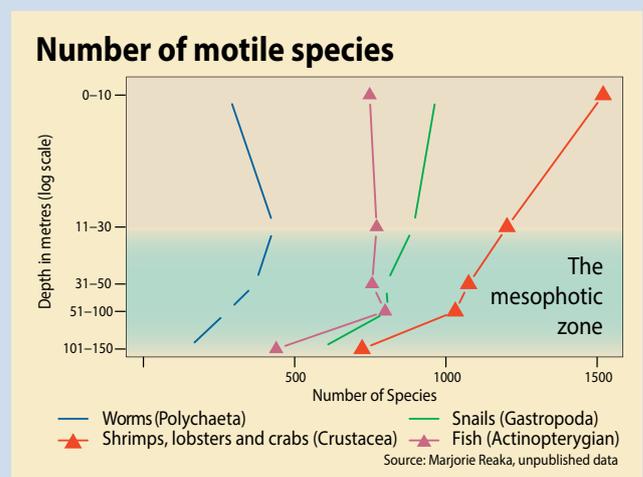
We found that about half of all species in these eight groups from the Gulf of Mexico occur at mesophotic depths (approximately 4,000 species, depending on how one measures the mesophotic zone). This represents a very significant amount of biodiversity, the ecology and management needs of which should be addressed. In addition, our data show that 5.1–8.6 per cent of these species have restricted depth ranges and inhabit only mesophotic depths. Concentrations of species with restricted depth or geographic ranges are important for management because they represent species that are vulnerable to extinction if not protected, thereby warranting the close attention of scientists, managers and policy makers. In contrast, scleractinian corals have relatively wide depth distributions and few species occur only in the mesophotic zone and nowhere else. Our data show that the ranges of 80.8 per cent of all coral species occurring in shallow water (< 30 m) extend to mesophotic depths (30–100 m), and that 63.4–69.4 per cent of all coral species occurring in the mesophotic zone (30–100 m or 30–150 m respectively) extend into shallow water (< 30 m). The ranges of 72.5 per cent of reef-building (zooxanthellate) corals extend into mesophotic

depths, and 100 per cent of the zooxanthellate coral species living in mesophotic depths extend into shallow water. Because of the continuity of species from shallow to mesophotic depths for scleractinian corals, these results provide evidence that MCEs have the potential to be a refuge or “lifeboat” for shallow corals in the Gulf of Mexico.

Figures 4.15 and 4.16 show the generally accepted depth categories for mesophotic habitats (30–150 m, Hinderstein et al. 2010) as a graded blue bar, but turbidity often limits the depth of light penetration in the Gulf of Mexico, with more than 90 per cent light attenuation at 30 m in some areas (Rabalais 1990). The extent and impact of this turbidity layer, derived from resuspension of terrigenous bottom sediments, varies temporally and geographically around the Gulf of Mexico due to river discharge, currents, proximity to shore and vertical relief of structures above the bottom (Darnell and Defenbaugh 1990).



**Figure 4.15.** Number of sessile or relatively sessile species observed at different depths in the Gulf of Mexico. The vertical axis is a log scale for depth, and the biologically important zones that we wished to investigate are noted at the appropriate sites in log scale.



**Figure 4.16.** Number of motile species observed at different depths in the Gulf of Mexico. The vertical axis is as described for Figure 4.15.

Turbidity strongly impacts nearshore areas of the northern Gulf and the Gulf of Campeche, but exerts less effect on offshore pinnacles in the northwestern Gulf and on carbonate platforms, such as the west Florida and Yucatan shelves (Darnell 1990), so that light penetration increases with distance from shore. In the northwestern Gulf, approximately 1 per cent of the light reaches the bottom at 50, 70, and 100 m, progressing from mid-shelf reefs to those closer to the shelf edge (Rezak et al. 1990). Thus, the lower limit of the mesophotic community can vary depending on local environmental conditions; we therefore analysed data for biodiversity and depth restriction from both 30–100 m and 30–150 m to include the different photic conditions that mesophotic organisms can encounter in different parts of the Gulf of Mexico.

The biodiversity of scleractinian corals increases from 73 species in shallow water (0–30 m) to 85 species (30–100 m) and 93 species (30–150 m) at mesophotic depths; 51 (69.8 per cent) of the species in shallow water and 37 species in the mesophotic zone (43.5 per cent from 30–100 m and 39.8 per cent from 30–150 m) are reef-building (zooxanthellate) corals. Similarly to corals, the number of species of echinoderms (starfish, sea urchins and their relatives) increases from shallow water to the mesophotic zone. Fish also have higher biodiversity in the mesophotic zone than in shallower water. Biodiversity of polychaete worms peaks just above the mesophotic zone and declines steadily through the mesophotic zone. All other groups (macroalgae,\* sponges, gastropod molluscs and crustaceans) have higher biodiversity in shallow water than in mesophotic or deeper environments.

Of the 7,753 known species in the Gulf of Mexico in the eight groups of organisms (i.e., scleractinian corals, macroalgae, sponges, echinoderms, polychaete annelids, gastropod molluscs, crustaceans and fish), 3,852 species occur from 30–100 m and 4,106 species occur from 30–150 m (Figures 4.15 and 4.16). Thus, approximately half (49.8–52.9 per cent) of all the

species in these eight groups are found in the mesophotic zone of the Gulf of Mexico. Many of these species also extend into other habitats, especially shallower environments. However, 5.1 per cent (196 species for 30–100 m) to 8.6 per cent (352 species for 30–150 m) of mesophotic species live only in mesophotic zones and nowhere else.

Table 4.2 illustrates the percentages of all mesophotic species that occur only in the mesophotic zone for individual groups of organisms. The data show that very few species of coral are restricted to mesophotic habitats; in contrast, most species of corals have relatively wide depth distributions that extend into other depth zones. Of the 73 species of scleractinian corals that occur in shallow water, 59 and 18 extend from shallow into mesophotic depths (30–100 m and 30–150 m, respectively). In shallow water, 51 (of the 73 species) are zooxanthellate or reef-building corals and of these 37 extend into both 30–100 m and 30–150 m depths. For non-reef-building (azooxanthellate) corals, 22 species live in shallow water and all extend into mesophotic depths (30–100 m and 30–150 m). These findings are significant because they provide evidence that the mesophotic zone in the Gulf of Mexico can offer a refuge to shallow-water coral species from environmental changes and impacts. On the other hand, the data in Table 4.2 show that sponges and polychaete worms have relatively high proportions of species that occur only in mesophotic habitats and nowhere else, and are thus vulnerable to environmental changes and impacts. Sponges represent significant structural and ecological components of reef assemblages, and polychaetes perform many ecological roles, but are particularly important in reef food chains; the potential vulnerability of these groups merits scientific and management attention.

\*The paucity of macroalgae species found below 30 m in our data may be due to lack of archived specimens in major collections up until 2009 when the data for gulfbase.org were established. Studies in other regions report substantial macroalgae at depths below 30 m (see Section 4.2), but the relative magnitude of the number of species compared to those in shallower (or deeper) areas is not known.

**Table 4.2.** Percentage of observed mesophotic species that occur only in mesophotic zones at either 30–100 m or 30–150 m.

### Species restricted to the mesophotic zone in the Gulf of Mexico

Species	Percentage of mesophotic species restricted to 30 - 100 m	Percentage of mesophotic species restricted to 30 - 150 m
Scleractinian corals	0 %	1.9 %
Echinoderms	1.3 %	4.7 %
Fish	2.5 %	8.6 %
Gastropods	3.8 %	7.3 %
Crustaceans	5.2 %	7.9 %
Sponges	9.9 %	20.3 %
Polychaetes	16.2 %	23.5 %