



Mesophotic Coral Ecosystems A lifeboat for coral reefs?

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In memory of Dr. John J. Rooney and his dedication to exploring and understanding mesophotic coral ecosystems.



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Cover photo: Bright blue ascidians, known as sea squirts, are found thriving at 50 metres (164 feet) among corals, greenish brown algae (*Lobophora*) and red, orange, and brown sponges off La Parguera, Puerto Rico (photo Héctor Ruiz).

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Mesophotic Coral Ecosystems

A lifeboat for coral reefs?

4 Foreword

5 Summary and recommendations

9 1. Introduction

9 1.1. Coral reefs in peril

9 1.2. Mesophotic coral ecosystems — refuge for shallow-water coral ecosystems?

11 2. What are mesophotic coral ecosystems?

11 2.1. Introduction

13 2.2. Light reaching the mesophotic zone

17 2.3. Geomorphology of mesophotic coral ecosystems

18 2.4. Differences between shallow-water and mesophotic coral ecosystems

20 3. Mesophotic coral ecosystems examined

20 3.1. Introduction

21 3.2. The Great Barrier Reef, Australia

23 3.3. Pulley Ridge, Gulf of Mexico, USA

26 3.4. The United States Virgin Islands, USA

28 3.5. Eilat, Red Sea, Israel

31 3.6. Spotlight on Palau Island group

37 3.7. Gulf of Carpentaria, Australia

39 3.8. Hawaiian Archipelago, USA

43 3.9. Ryukyu Archipelago, Japan

45 3.10. La Parguera, Puerto Rico, USA

50 4. Biodiversity of mesophotic coral ecosystems

50 4.1. Introduction

51 4.2. Macroalgae

54 4.3. Sponges

55 4.4. Scleractinian corals

57 4.5. Symbionts

58 4.6. Fish

63 5. Ecosystem services provided by mesophotic coral ecosystems

63 5.1. Introduction

64 5.2. Essential habitat

65 5.3. Recovery source for shallow populations

65 5.4. Tourists exploring the mesophotic zone

65 5.5. A potential source of novel products

66 6. Threats to mesophotic coral ecosystems and management options

66 6.1. Introduction

67 6.2. Fisheries

69 6.3. Climate change

73 6.4. Sedimentation and pollution

74 6.5. Marine aquarium trade

76 6.6. Precious coral fishery

76 6.7. Invasive species

80 6.8. Management options

81 7. Understanding mesophotic coral ecosystems: knowledge gaps for management

81 7.1. Introduction

82 7.2. Where are mesophotic coral ecosystems located?

82 7.3. What controls where mesophotic coral ecosystems are found?

82 7.4. What ecological role do mesophotic coral ecosystems play and what organisms are found in them?

83 7.5. What are the impacts of natural and anthropogenic threats on mesophotic coral ecosystems ?

83 7.6. Are mesophotic coral ecosystems connected to shallower coral reef ecosystems and can they serve as refuges for impacted shallow reef species?

84 References

94 Acknowledgements

Foreword

(to come)

Summary and recommendations

Picture a coral reef — most people will probably imagine brightly coloured corals, fish and other animals swimming in well-lit shallow waters. In fact, the coral reefs that live close to the surface of the sea — the ones that we can swim, snorkel, or dive near and see from space — are only a small portion of the complete coral reef ecosystem. Light-dependent corals can live in much deeper water (up to a depth of 150 m in clear waters). The shallow coral reefs from the surface of the sea to 30–40 m below are more like the tip of an iceberg; they are the more visible part of an extensive coral ecosystem that reaches into depths far beyond where most people visit. These intermediate depth reefs, known as mesophotic coral ecosystems (MCEs), are the subject of this report.

Although MCEs are widespread and diverse, they remain largely unexplored in most parts of the world, and there is

MCEs are characterized by light-dependent corals and associated communities typically found at depths ranging from 30–40 m and extending to over 150 m in tropical and subtropical regions. They are populated with organisms typically associated with shallow coral reefs, such as corals, macroalgae, sponges, and fish, as well as species unique to mesophotic depths or deeper.

little awareness of their importance among policy makers and resource managers. As a result, MCEs are for the most part not considered in conservation planning, marine zoning and other marine policy and management frameworks. The goal of this report is to raise awareness in policy makers and resource managers by providing an accessible summary on MCEs, including a discussion of the ecosystem services they provide, the threats they face, and the gaps in our understanding.

Key questions addressed in this report include: can MCEs provide a refuge for the many species in shallow water reef ecosystems that are facing increasing threats from human activities? If shallow reefs (< 30–40 m) continue to decline, can MCEs provide the stock to re-populate them? The answer is of course that it depends on the species involved. In some situations, MCEs may provide this ecosystem service and act as “lifeboats” for nearby, connected shallower reefs that have been damaged. In other cases, however, MCEs may be just as vulnerable as shallower reefs to the range of human pressures exerted upon them.

Whether or not they are lifeboats for shallow reef species, MCEs are worthy of protection, both for their inherent biodiversity and for the wide range of ecosystem goods and

Table 1. Key differences between shallow and mesophotic coral ecosystems.

	Shallow-water coral reef ecosystems	Mesophotic coral ecosystems (MCEs)
Depth range	<ul style="list-style-type: none"> • 0 to approx. 30–40 m. • Lower depth corresponds to a moderate faunal transition. • Detectable in satellite images. 	<ul style="list-style-type: none"> • From approx. 30–40 m to deeper than 150 m. • Lower depth limit varies by location due to differences in light penetration and other abiotic factors. • Not detectable in satellite images.
Dominant habitat-building taxa	<ul style="list-style-type: none"> • Dominant species are zooxanthellate scleractinian corals, octocorals, calcareous and foliose macroalgae and sponges. 	<ul style="list-style-type: none"> • Dominant species are plate-like and encrusting zooxanthellate scleractinian corals, octocorals, antipatharians, calcareous and foliose macroalgae and sponges.
Light levels	<ul style="list-style-type: none"> • Generally well-lit environments. • Shallow reefs can become light-limited in turbid waters (e.g. near estuaries). 	<ul style="list-style-type: none"> • Generally middle- to low-light environments.
Thermal regime	<ul style="list-style-type: none"> • Generally stable thermal regime. • Shallow, stratified waters with high residence time may be subject to extreme thermal events causing coral bleaching. 	<ul style="list-style-type: none"> • Generally temperatures are cooler and naturally more variable on MCEs than on shallower reefs, especially those located on the continental slope, which are subject to internal waves. • Deeper water column may protect MCEs from extreme (warm) thermal events.
Hydrodynamic regime	<ul style="list-style-type: none"> • Subject to breaking waves and turbulence, except in sheltered lagoons. • Wave-induced shear stress and mobilization of sea floor sediments. • High residence times within lagoons. 	<ul style="list-style-type: none"> • Below the depth affected by breaking waves. • Sea floor generally unaffected by wave motion. Powerful storms can directly and indirectly impact MCEs (resuspend sediment or cause a debris avalanche), especially in the upper mesophotic zone (30–50 m).

Table 2. Summary of the major anthropogenic threats to MCEs and current and potential management actions that may help mitigate these threats.

	Shallow-water coral reef ecosystems	Mesophotic coral ecosystems (MCEs)
Major anthropogenic threats	<ul style="list-style-type: none"> • Fishing (overfishing, destructive fishing with dynamite and poison, and damage from lost fishing gear) • Thermal stress (bleaching) from ocean warming • Diseases • Pollution (land-based) • Invasive species • Tourism and recreation • Anchor damage • Coral mining (for aggregate and lime) • Coastal development • Marine aquarium trade 	<ul style="list-style-type: none"> • Fishing (overfishing and damage from lost fishing gear) • Thermal stress (bleaching) reduced exposure to warm water stress • Diseases • Pollution: reduced exposure to land-based sources; exposed to deep-water sewage outfalls and dredging spoils • Invasive species • Tourism and recreation (reduced exposure) • Anchor damage (reduced exposure) • Coral mining (reduced-negligible exposure) • Marine aquarium trade • Oil and gas exploration • Cable and pipelines
Management actions (current and potential)	<ul style="list-style-type: none"> • Fishing closures • Marine Protected Areas (MPAs) • Wastewater treatment and management to reduce pollution • Shipping industry guidelines to curb introduced species • Shipping industry guidelines to restrict discharge of oil • Ensure that international trade of reef species, their parts and products is sustainable. • Placement of fixed mooring buoys to reduce anchor damage • Tourism guidelines to reduce reef damage • Coral reef rehabilitation for damaged areas • Public education and involvement 	<ul style="list-style-type: none"> • Fishing closures • MPAs (MCEs are not considered in most countries) • Wastewater treatment and management to reduce pollution (potential) • Shipping industry guidelines to curb introduced species (potential) • Shipping industry guidelines to restrict discharge of oil (potential) • Ensure that international trade of mesophotic reef species, their parts and products is sustainable (potential). • Placement of fixed mooring buoys to reduce anchor damage (potential) • Diving guidelines to reduce reef damage (potential) • Guidelines for oil and gas exploration, alternative energy, cable and pipelines (potential)

services they provide. The biodiversity of MCEs is comparable to that of shallow reefs, yet there are also unique species that are found only in MCEs and/or deeper water. Table 1 shows key differences between MCEs and shallow reefs.

While buffered from some of the natural and anthropogenic threats faced by shallow reefs, MCEs are nevertheless vulnerable to many of the same threats, such as fishing, pollution, thermal stress, diseases and tropical cyclones, albeit to differing extents (Table 2). MCEs also face threats from oil and gas exploration and cable and pipeline laying, which are less common on shallow reefs. For light-dependent mesophotic reef organisms living at low light levels (1 per cent of that found at the sea surface), anything that inhibits light reaching the depths (e.g. sedimentation, turbidity or pollution) has an impact on their survival. In general, there remains much to be discovered about the extent of impacts from natural and anthropogenic threats on MCEs.

While some pressures on MCEs are global in origin, and require a global response, many others are regional or local. It is important that measures to protect an individual MCE take an adaptive, ecosystem-based approach to address the cumulative impacts, considering both global pressures and specific local pressures. Most of the management tools used to protect and conserve shallow coral reefs can also be used to protect and conserve MCEs (Table 2).

Guidance for resource managers

While this report primarily provides scientific background information for policy makers and resource managers on MCEs to improve their awareness of these ecosystems, we would be remiss if we did not also provide some guidance on actions that could be taken, based on our current knowledge. To this end, we have identified the following actions that resource managers may take to improve the conservation and management of MCEs.

1. Identify whether MCEs may exist within your jurisdiction.
2. Identify threats to the MCEs that exist in your area and viable options for managing them (see Table 2 for examples of management actions).
3. Determine whether existing marine managed areas for shallow reefs needs to be extended to include nearby MCEs.
4. Expand shallow reef monitoring programmes to include MCE habitats.
5. Introduce awareness-raising and education programmes for the public and policy and decision-makers about MCEs and the need for them to be included in marine spatial planning.

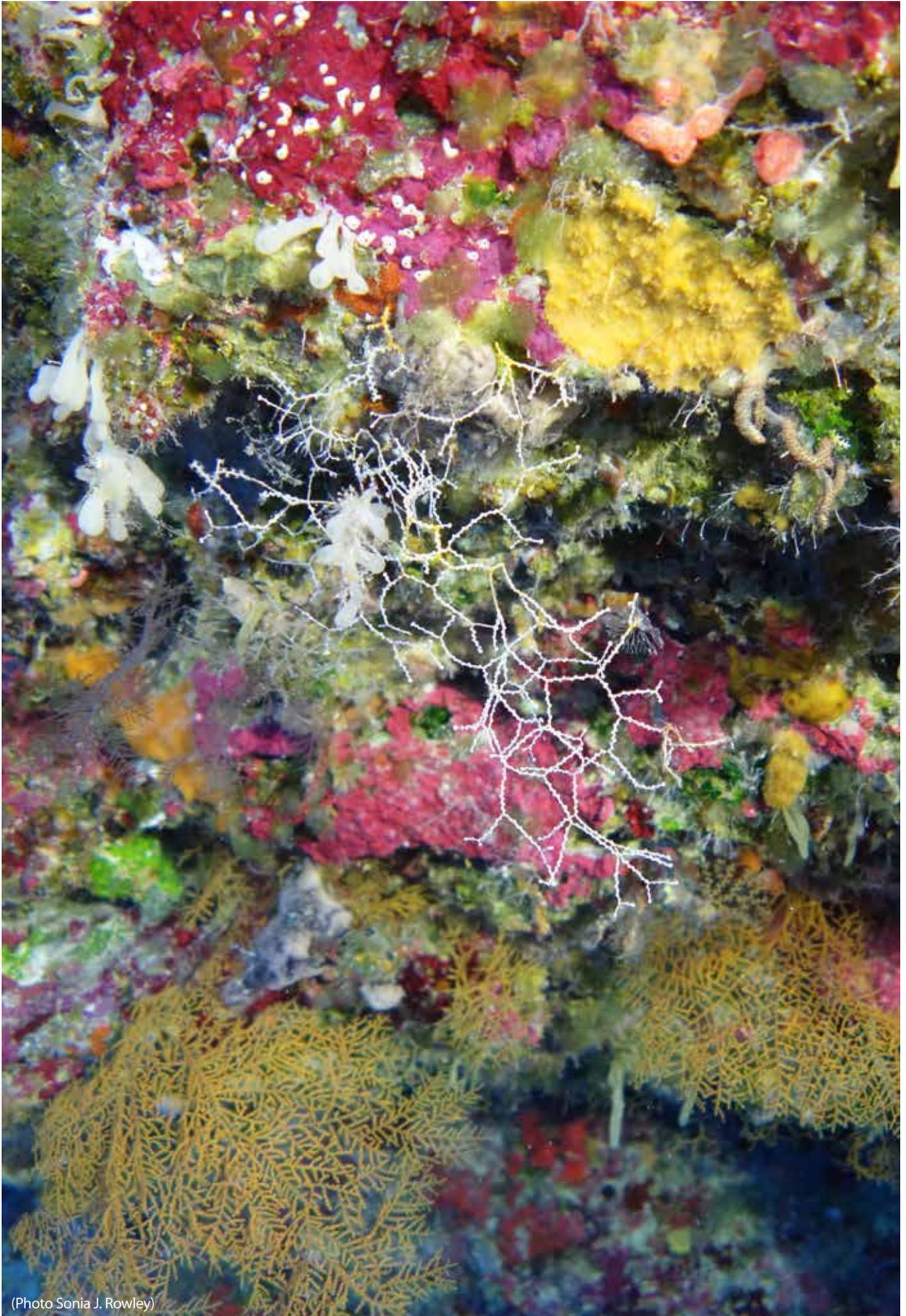
The main recommendations made in this report (see text box on guidance for resource managers) relate to this lack of awareness of MCEs, the anthropogenic threats facing them, and the immediate actions that can be taken, at the local and regional levels, to protect and conserve them.

Table 3. Key management questions and their related research priorities that would enable policy makers and resource managers to make informed decisions on MCE protection and conservation.

	Management questions	Research priority	Anticipated management focused products
<p>High priority</p>	Where are MCEs located	Locate where MCEs exist, with a priority in the equatorial regions of the Indo-West Pacific region, eastern Atlantic Ocean, and the Pacific coasts of Mexico, Central America and South America.	Detailed maps showing the distribution of MCEs.
	What controls where MCEs are found?	Understand the geological and physical processes that control MCE distribution to enable us to predict where MCEs occur.	Models and maps showing predicted MCE habitat.
	Are MCEs connected to shallower coral ecosystems and can they serve as refuges for impacted shallow reef species?	Understand the genetic, ecological and oceanographic connectivity of MCEs with shallow reefs and other MCEs. Determine whether MCEs can serve as refugia and reseed shallow reefs (or vice versa).	Maps of larval dispersal pathways for key mesophotic species under different oceanographic scenarios. Population connectivity information for key mesophotic species.
	What organisms are found in MCEs?	Characterize MCE biodiversity to better understand, protect and conserve MCEs. Characterize community structure, including patterns of distribution and abundance.	Inventory of species associated with MCEs. Information on mesophotic species taxonomy, life history, and responses to environmental conditions (including tolerance limits) that are useful for modelling impacts to climate change and other disturbances. Distribution and abundance estimates for key mesophotic mobile and sessile
	What ecological role do MCEs play?	Understand the role of MCEs in supporting various life stages of living marine resources and the processes that regulate these ecosystems.	Descriptions of trophic structures and food web models. Descriptions of the range of habitat types and their distribution, how they are utilized and how these relationships change over time.
	What are the impacts from natural and anthropogenic threats on MCEs?	Determine the anthropogenic and natural threats to MCEs and assess the ecological impacts and their subsequent recovery, if any, from them.	Maps depicting the distribution and intensity of human activities in areas known to contain MCEs. Areas recommended for protection as a marine protected area. Technologies or methods designed to reduce interactions between harmful activities (such as fishing gear) and MCEs.

Although the study of MCEs has increased exponentially in the past 30 years, there are still large gaps in our scientific knowledge of them, especially in comparison with shallow reefs. The best way to close these information gaps is to focus research efforts on answering questions that are critical to enabling resource managers to make informed decisions about MCE protection and conservation. For

MCEs, the most crucial information is what scientists would call “baseline information”, including information on their location, biological and physical characteristics, threats, condition and the causes and consequences of that condition. The key questions for resource managers and the corresponding research priorities to address them are detailed in Table 3.



(Photo Sonia J. Rowley)

Chapter 1.

Introduction

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1.1. Coral reefs in peril

Globally, coral reefs are deteriorating rapidly due to elevated sea surface temperatures, coastal development, pollution and unsustainable fishing practices (Hughes et al. 2003, Pandolfi et al. 2003). About 19 per cent of coral reefs have already been lost, with a further 35 per cent expected to disappear in the next 40 years (Wilkinson 2008). Unless something changes, almost all shallow-water coral reefs will experience thermal stress sufficient to induce severe bleaching every year by the 2050s.

Coral reefs most likely to survive the twenty-first century include those that sustain low impact from terrestrial runoff and that occur in locations safeguarded from extreme sea surface temperatures. These include large areas of intermediate depth reefs, also known as mesophotic coral ecosystems (MCEs; Glynn 1996, Riegl and Piller 2003). Occurring at depths greater than 30–40 m, MCEs may be buffered from some human and natural disturbances that negatively affect shallow-water reefs (Bongaerts et al. 2010a, Bridge et al. 2013), but not all stressors (Stokes et al. 2010, Lesser and Slattery 2011).

Science has shown that MCEs are far more widespread and diverse than previously thought (Locker et al. 2010, Harris et al. 2013). However, they remain largely understudied in most parts of the world and there is little awareness of their importance among policy makers and resource managers

Mesophotic coral ecosystems are characterized by the presence of light-dependent corals and associated communities typically found at depths ranging from 30–40 m and extending to over 150 m in tropical and subtropical regions. The dominant communities providing structural habitat in the mesophotic zone can be comprised of coral, sponge, and algal species (Puglise et al. 2009, Hinderstein et al. 2010).

(Bridge et al. 2013, Madin and Madin 2015). Consequently, they are for the most part not considered in conservation planning, marine zoning and other marine policy and management frameworks.

This report aims to raise awareness of the importance of MCEs in order to improve their protection and catalyze appropriate policy, management and research responses. The potential that MCEs may act as “refugia” and a source of replenishment for some shallow reef species (Glynn 1996, Riegl and Piller 2003, Bongaerts et al. 2010a) or, in other words, “lifeboats”, offers a glimmer of hope that MCEs may aid in the recovery of degraded shallow reefs. This report provides an accessible summary on MCEs, including a discussion of the ecosystem services they provide, the threats they face, and gaps in our understanding, as well as addressing the question of whether MCEs can serve as lifeboats for coral reefs.

1.2. Mesophotic coral ecosystems — a refuge for shallow-water coral reefs?

The notion that MCEs could provide a refuge for coral reef biodiversity from natural and human impacts has been formalized in the ‘deep reef refugia hypothesis’ (Glynn 1996, Bongaerts et al. 2010a). Some disturbances affecting coral reefs are most acute in shallow waters (Figure 1.1): for example, wave energy attenuates with increasing depth, making MCEs less likely to be affected by storm waves (De’ath et al. 2012). Similarly, warm-water coral bleaching, resulting from overheating of the upper few metres of surface waters (in calm, stratified water columns) and a synergistic effect between heat and light, has less of an impact on MCEs located in deeper water (> 30–40 m to over 150 m) and receiving lower irradiance. In addition, many MCEs occur in remote, offshore locations, such as along the edge of the continental shelf or on remote, submerged patch reefs. These isolated MCEs are less exposed to many stressors commonly affecting

shallower reefs, such as terrestrial runoff. MCEs may also offer a refuge from fishing pressure, particularly for commercially-important species (Bejarano et al. 2014, Lindfield et al. 2014).

The concept of ecological refugia as a potential option for mitigating biodiversity loss under climate change has been increasingly debated in the scientific literature of recent years (Ashcroft 2010, Keppel et al. 2012), including defining the spatial and temporal scales of what is termed a refugium (Keppel et al. 2012). It is now accepted that the term ‘refuge’ refers to short timescales (e.g. a particular MCE may be a refuge from the effects of a tropical cyclone), whereas ‘refugia’ operate on longer temporal scales. Most studies addressing refugia in relation to MCEs are actually referring to their role as a refuge; that is, whether mesophotic habitats were less affected by a particular disturbance, such as a cyclone or a

bleaching event, than adjacent shallow reefs (Bongaerts et al. 2010a, Bridge et al. 2014). MCEs may have the potential to act as refugia over longer timescales in some circumstances, particularly to provide lineage continuation for key coral reef taxa (Muir et al. 2015).

Currently, few long-term datasets exist to enable quantitative evaluation of the deep reef refugia hypothesis, particularly over longer temporal scales (years to decades), primarily due to the logistical difficulties involved in monitoring mesophotic habitats. There is evidence that mesophotic reef populations can mitigate against local extinction following disturbance (e.g. Sinniger et al. 2013, Smith et al. 2014). However, it is also clear that MCEs are not immune from natural and human threats, such as coral bleaching and tropical storms (see Chapter 6), and should not be considered as a panacea to addressing the threats faced by coral reef ecosystems. For example, bleaching of MCEs is known to occur where internal waves or vertical mixing brings over-heated surface waters or cooler deep waters into contact with mesophotic corals (Bak et al. 2005, Smith et al. 2015).

In addition to serving as a refuge, a second premise of the deep reef refugia hypothesis is whether MCEs can provide a source of larvae to repopulate adjacent shallow reefs following a disturbance on ecologically significant timescales. The viability of MCEs to serve as a source to reseed or replenish shallow reef species is dependent on several factors, including

whether the same species are present at both depths, the extent of species adaptation at particular depths, and whether there is oceanographic connectivity between the reefs. Studies addressing this question for coral species have, to date, generally looked at genetic connectivity between mesophotic and shallow populations, and have revealed complex patterns. In general, deeper mesophotic coral populations (> 60–70 m in depth) appear to be isolated from shallower populations (Bongaerts et al. 2015b). In contrast, coral connectivity between populations shallower than 60–70 m appears to be both species and location-specific and dependent on oceanographic connectivity (van Oppen et al. 2011, Serrano et al. 2014). For fish species, connectivity has been evaluated using genetics and ecology (presence of the same species at both depths). In the case of the common coral reef damselfish, *Chromis verater*, no genetic differences were found among shallow and mesophotic populations (Tenggardjaja et al. 2014), meaning they constitute a single population and should be managed as such. Meanwhile, ecological connectivity has been shown for fish species between shallow reefs and MCEs off La Parguera in southwest Puerto Rico. These MCEs serve as a refuge, particularly for exploited large groupers and snappers, and 76 per cent of species present at mesophotic depths were common inhabitants of shallow reefs, indicating that connectivity exists between shallow reefs and MCEs (Bejarano et al. 2014). Irrespective of their potential to repopulate shallow-water reefs, MCEs support unique biodiversity and warrant appropriate attention from managers.

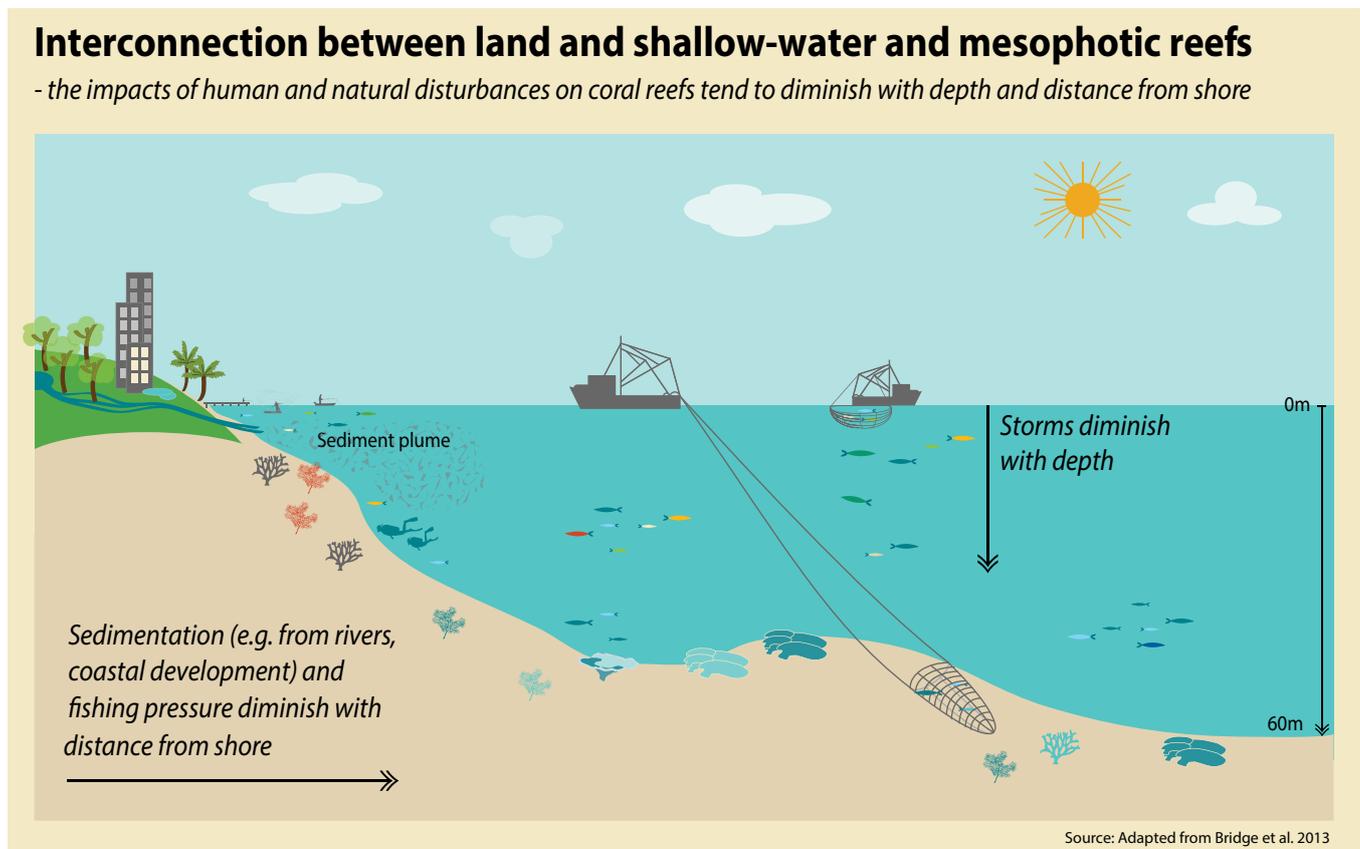


Figure 1.1. Impacts of human and natural disturbances tend to decrease with depth and distance from the coast, making shallow reefs generally more vulnerable than MCEs.

Chapter 2.

What are mesophotic coral ecosystems?

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2.1. Introduction

MCEs are dominated by light-dependent coral, sponge and/or algal communities that live in the middle light ('meso' = middle and 'photic' = light) zone. MCEs have often been

referred to as the coral reef 'twilight zone' because they represent the transition between the brightly lit surface waters and the perpetually dark deeper depths. They are

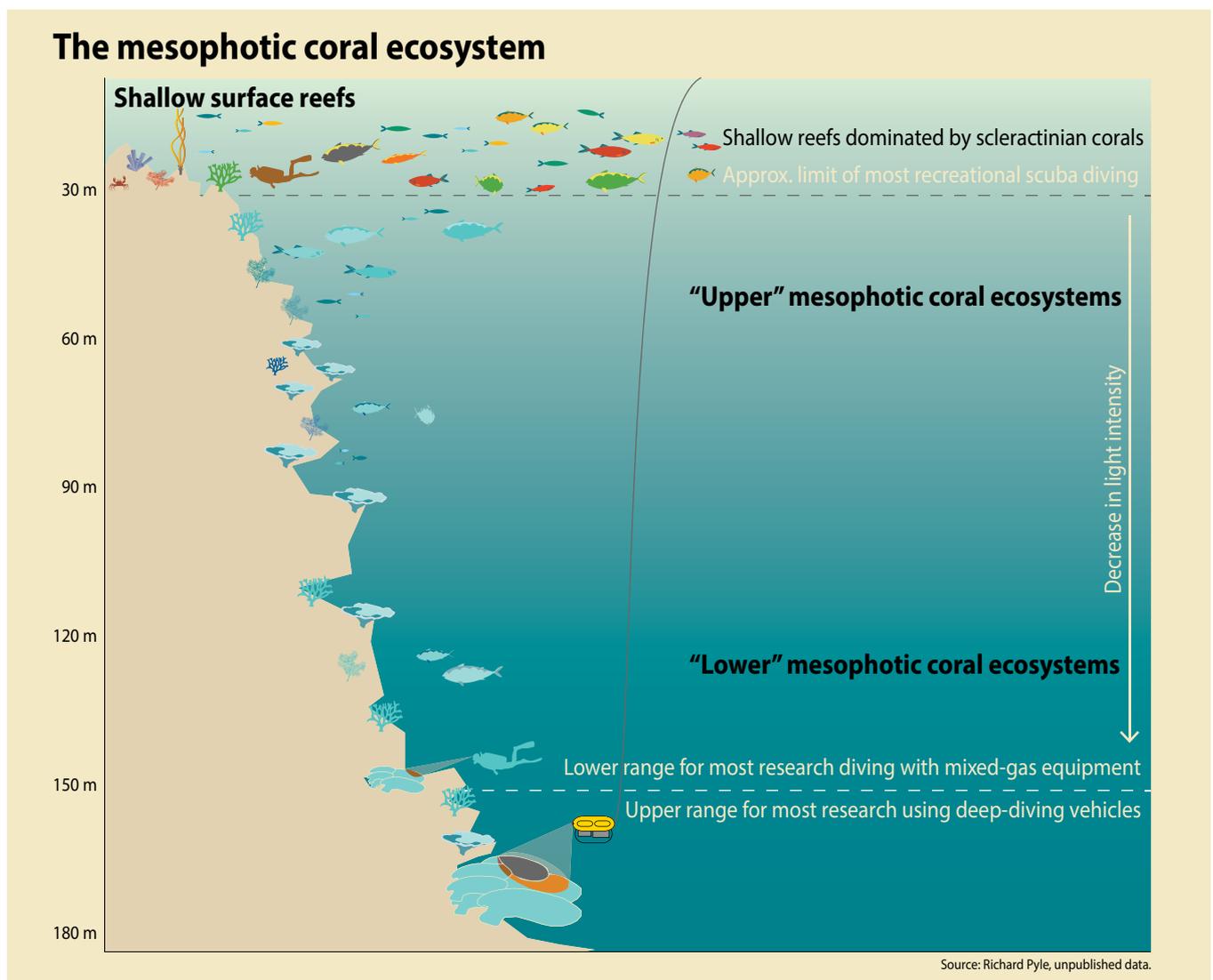


Figure 2.1. MCEs can form on high-angle continental and insular slopes as illustrated here, or on low-angle outer insular shelves and on the tops of submerged banks. Decreased light penetration rather than reduced temperature appears to be the primary limiting factor controlling the depth distribution of MCEs at most locations (Kahng et al. 2010).

typically found at depths from 30–40 m and extending to depths of over 150 m in tropical and subtropical waters (Hinderstein et al. 2010; Figure 2.1). The occurrence of MCEs is dependent not only on light availability, but also on water temperature and quality, substrate and

geomorphology. However, there is little understanding of the degree to which these factors (and potentially others, such as nutrient levels, currents and competition) control the distribution and community structure of MCEs (Puglise et al. 2009).

Key facts about MCEs

MCEs are defined by the presence of corals that have zooxanthellae and to some extent are light-dependent. Some corals that live in the mesophotic depth range, such as black corals and octocorals, are azooxanthellate and not dependent on light.

MCEs are populated with organisms typically associated with shallow coral reefs: macroalgae, scleractinian corals, octocorals, antipatharians, sponges, a wide assortment of other sessile invertebrates and families of fish common on shallow reefs (Figure 2.2), as well as species unique to mesophotic depths or deeper.

Dominant communities providing structural habitat include macroalgae, sponges and corals.

MCEs are defined by their ecology, not their absolute depth range.

Few of the world's known MCEs have been mapped or studied. The more we look, the more we find (Figure 2.3).

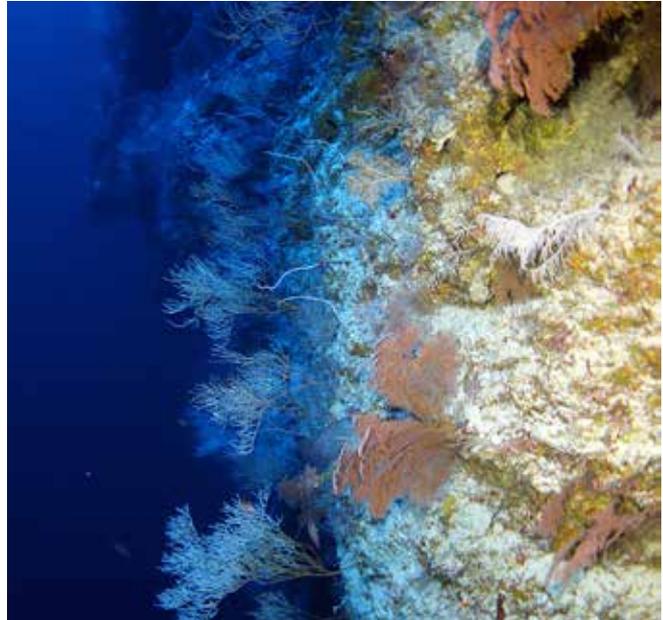
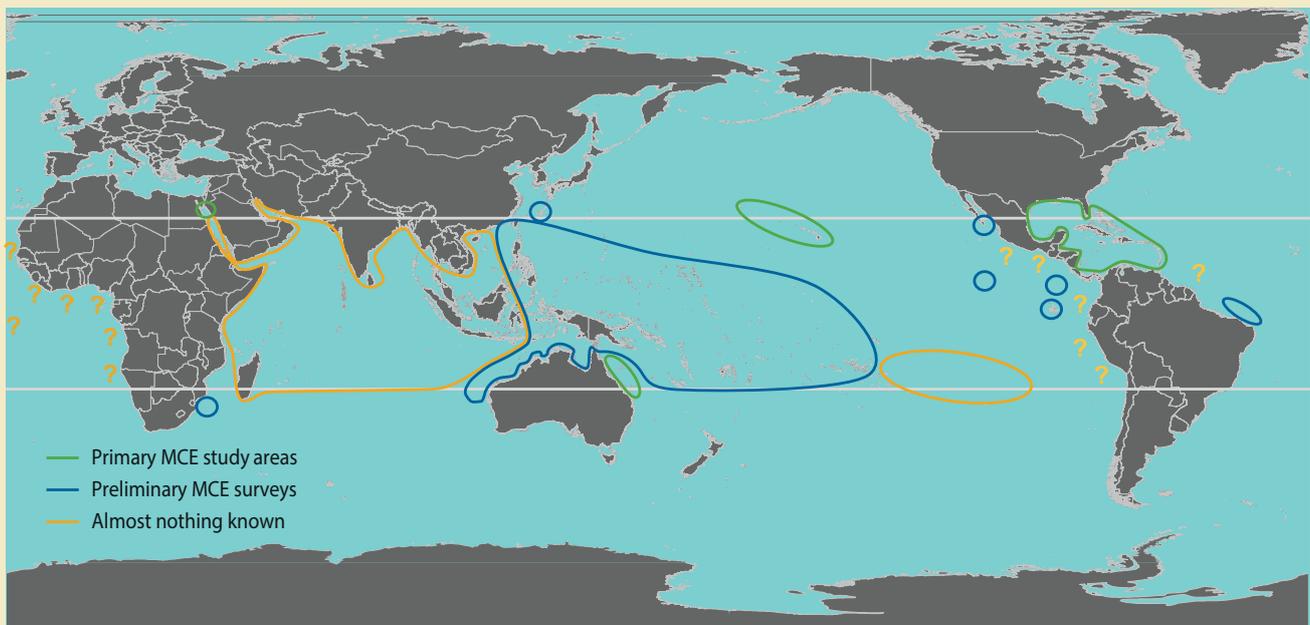


Figure 2.2. Many MCEs are dominated by macroalgae, gorgonian and antipatharian corals, sponges and other invertebrates as illustrated in this image from 130 m in Pohnpei, Federated States of Micronesia (photo Sonia J. Rowley).

Current extent of MCE studies



Source: Adapted from Richard Pyle, unpublished data

Figure 2.3. Extent of MCE investigations to date (adapted from Richard Pyle unpublished data). At least 80 countries (those with documented shallow reefs; Spalding et al. 2001) have potential MCEs. Countries that do not have surface reefs, but potentially have MCEs, include those on the west coasts of Africa and South America.

2.2. Light reaching the mesophotic zone

Light attenuation in the ocean rapidly reduces both the amount and quality of visible light with depth, so that only a portion of the light spectrum is available at mesophotic depths. Attenuation is due to absorption and scattering of light by seawater, dissolved constituents and suspended particles. Long wavelength colours such as red, orange and yellow are most quickly absorbed, so that by the time the light reaches the mesophotic zone, only the blue wavelengths of the spectrum remain (Figure 2.4). This zone of light penetration

in the water column is referred to as the euphotic zone, and it extends to the depth where light diminishes to approximately 1 per cent of its surface value. The depth of the euphotic zone depends on the concentration of dissolved and suspended light-absorbing and light-scattering materials in the water column. In the clearest ocean water, zooxanthellate (light-dependent) scleractinian corals have been documented at depths as great as 165 m at Johnston Atoll in the Pacific Ocean (Maragos and Jokiel 1986; Figure 2.5).

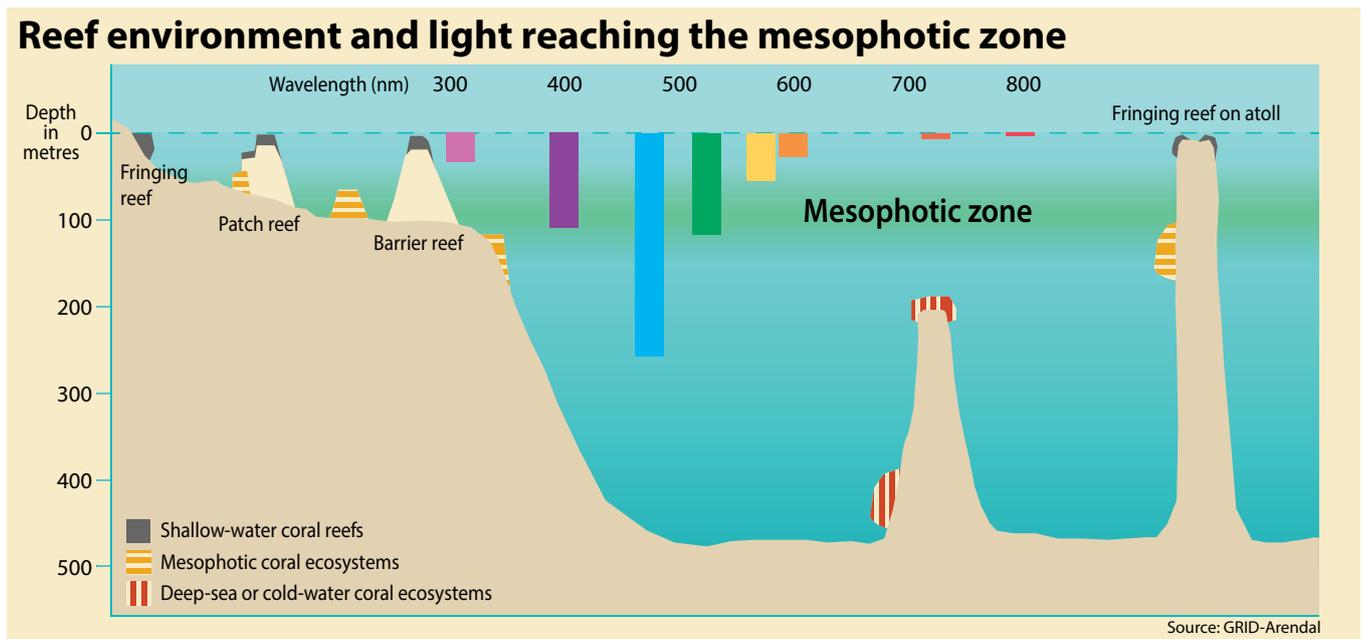


Figure 2.4. Conceptual model of light penetration in the ocean. Blue light dominates the photic zone below 30 m, but the actual depth of light penetration is site-specific and dependent on a variety of physical factors, such as suspended particulate matter.

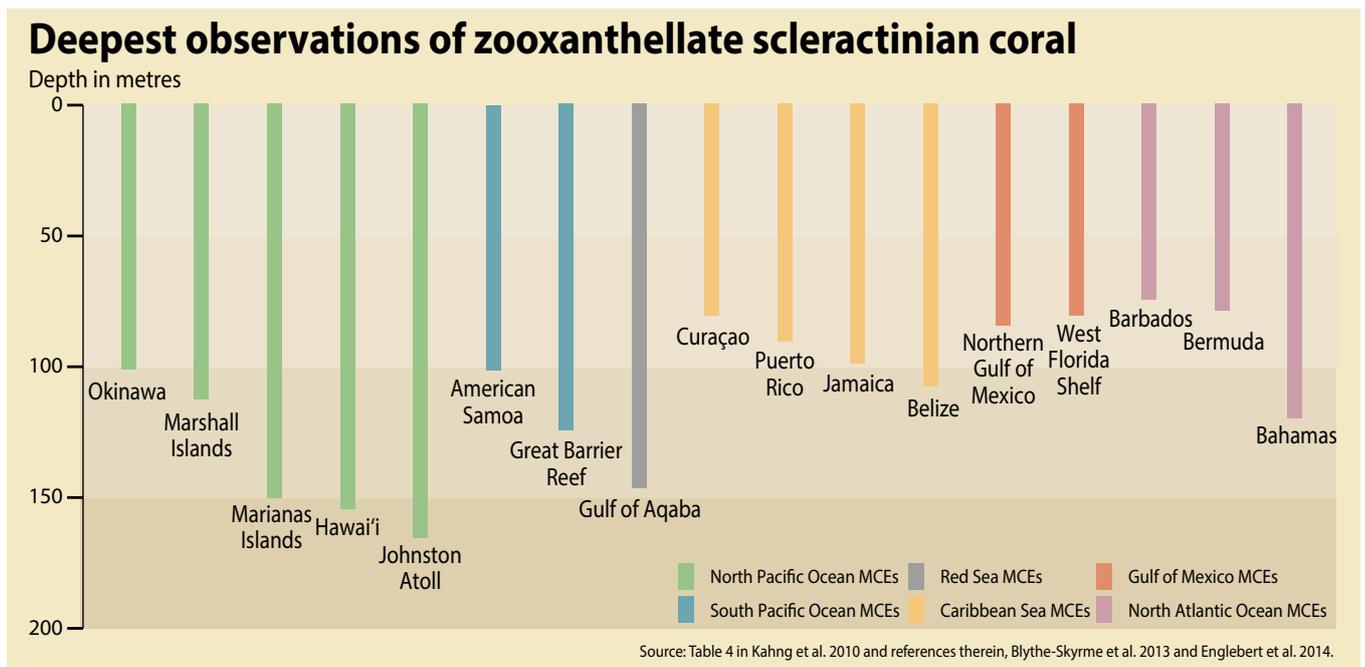


Figure 2.5. The depth range of zooxanthellate mesophotic scleractinian corals is location-dependent due to differences in light penetration and other abiotic factors.

Habitat-forming organisms

The dominant habitat-forming communities in the mesophotic zone can be comprised of coral, sponge and macroalgal species (Figures 2.6–2.8).

MCEs, similar to shallow-water reefs, include habitat-forming scleractinian corals that exploit a symbiotic relationship with zooxanthellae (genus *Symbiodinium*), a type of microscopic algae (see also section 4.5). This single-celled organism lives within the cells of the coral's gastrodermis. The coral provides a safe home and essential compounds for the algae, and in return the algae supply the coral with nutrients from photosynthesis (hence the need for light). The algae are generous guests, and on shallow reefs can provide as much as 100 per cent of the organic material needed by the host's coral tissue (Muscatine 1990). However, mesophotic coral zooxanthellae often cannot produce enough energy given the light limitations, thus mesophotic corals may also rely on planktonic food captured by their tentacles (Davies 1977, Lesser et al. 2010).

As coral and algal cover decline with decreasing light at depth, the benthic communities of MCEs may shift towards communities dominated by particle-capturing species, such as sponges and gorgonians (e.g. Bridge et al. 2012b, Slattery and Lesser 2012). Ecological work in the Caribbean has shown that mesophotic sponges rely less on photosymbionts, and more on plankton feeding. In some Caribbean MCEs, sponge biodiversity and biomass exceed that of shallow reefs by almost ten to one (Slattery and

Lesser 2012), and growth rates are higher (Lesser and Slattery 2013). Thus, faster growth and enhanced competitive strategies may allow mesophotic sponges to thrive while coral reefs worldwide are on the decline (Slattery et al. 2011). This may not be the case outside the Caribbean, such as in the Pacific Ocean (Pawlik et al. 2015a, b, see Slattery and Lesser 2015). In addition, the different selective pressures (e.g. predation) between shallow and mesophotic reefs have resulted in significant phenotypic differences in sponges with increasing depth (Slattery et al. 2015).

Macroalgae, or seaweed, can also form vast beds and meadows over rocky or sandy substrate in the mesophotic zone, or grow intermixed with mesophotic corals. Although some native macroalgae, such as the brown alga *Lobophora*, can be invasive — overgrowing corals in areas where native herbivores are removed (Lesser and Slattery 2011, Slattery and Lesser 2014) — luxuriant stands of native macroalgae also occur naturally and are important ecologically. For example, species such as the mesh-shaped alga *Microdictyon* create bottom complexity, which forms significant habitat for reef fish (Abbott and Huisman 2004, Huisman et al. 2007). Calcified green algae, such as the meadow-forming *Halimeda* spp., can live for several years and are important sand producers (Spalding 2012). Thirteen different dominant macroalgal mesophotic communities have been documented in the Hawaiian Archipelago alone, suggesting that rich and diverse assemblages of macroalgal species may exist at mesophotic depths, and many are distinct from shallow-water populations (Spalding 2012).



Figure 2.6. A *Leptoseris* coral-dominated MCE in the 'Au'au Channel, offshore of Maui, Hawai'i, depth of 70 m (photo NOAA's Hawai'i Undersea Research Laboratory).



Figure 2.7. A 0.25 m² mosaic of a Caribbean mesophotic reef (depth 60 m). Note the high coverage and diversity of sponges in the quadrat, which is typical of many Atlantic MCEs (photo Marc Slattery).



Figure 2.8. A green algal-dominated MCE in the 'Au'au Channel, offshore of Maui, Hawai'i, of *Halimeda distorta*, 75 m depth (photo NOAA's Hawai'i Undersea Research Laboratory).

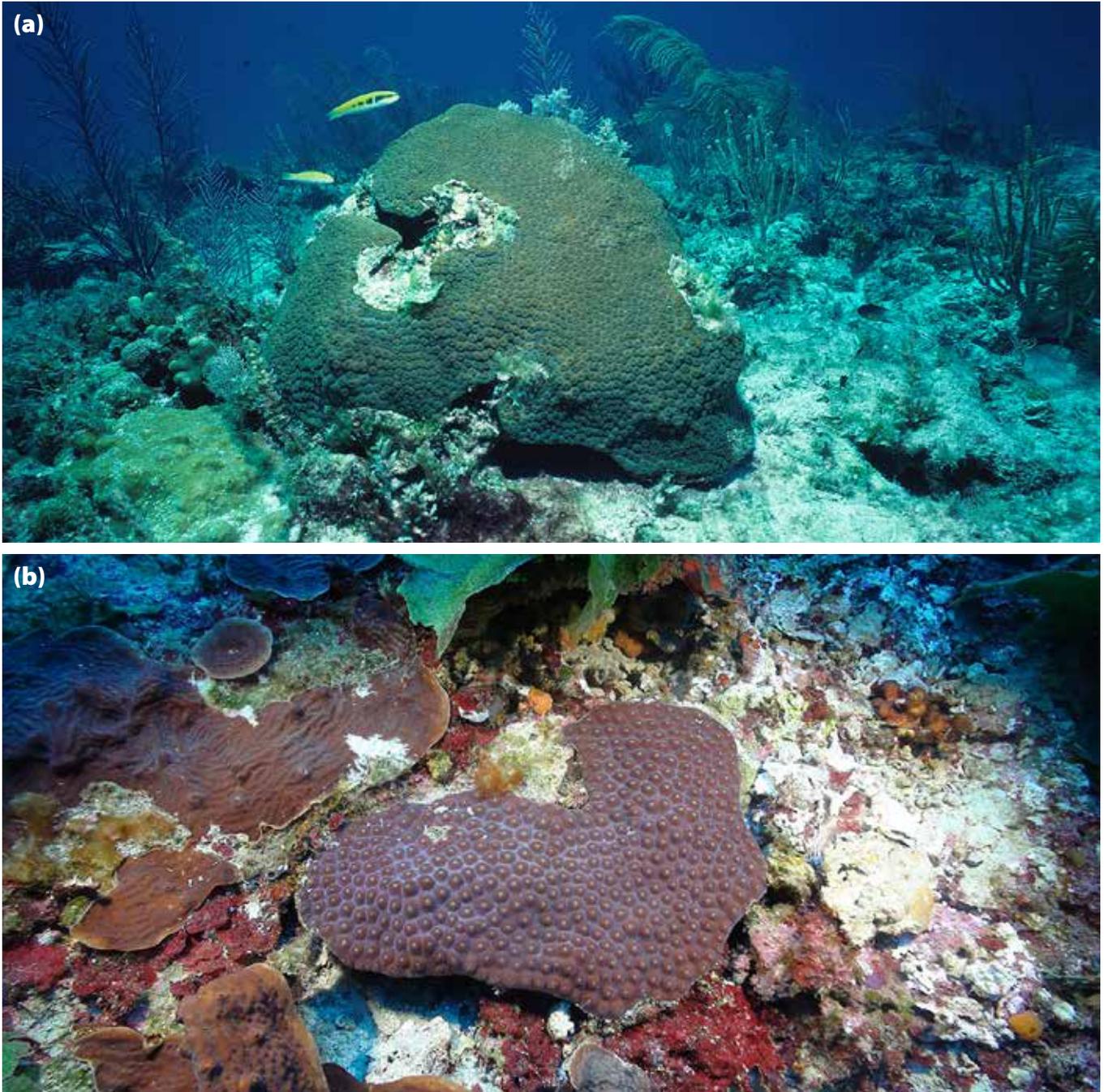


Figure 2.9. (a) In shallow waters, the Caribbean coral *Montastraea cavernosa* exhibits a boulder-like morphology, shown at 5 m (photo John Reed), and (b) in mesophotic waters, a flattened morphology, shown at 75 m (photo Mike Echevarria).

2.2.1. Living in the shade

Corals existing in the low-light environment of the mesophotic zone, like the plants in the understory of a rainforest, can have specialized morphology and physiological traits (Kuhlmann 1983, Kahng et al. 2014) that enable capture and efficient use of as much light as possible. For example, in shallow water, the Caribbean coral *Montastraea cavernosa* normally has a boulder-like shape (Figure 2.9a), while at mesophotic depths, it exhibits a flattened phenotype, which enhances light capture (Figure 2.9b; Lesser et al. 2010). Moreover, deep (> 50 m) mesophotic corals can have unique zooxanthellae clades that are adapted to low light and not found in shallower depths (Lesser et al. 2010, Bongaerts et al. 2011a, 2013b, Nir et al. 2011, Pochon et al. 2015).

In shallow water, adaptation to high light irradiance dominates coral photophysiology (e.g. photo-protective proteins, antioxidant enzyme capacity and self-shading morphologies; Falkowski and Raven 2007). However, because light attenuates exponentially with increasing depth, photosynthetic organisms eventually become light-limited (Kirk 1994). Corals (and algae) transplanted to lower light regimes often increase photosynthetic pigment concentrations per unit area to maximize utilization of ambient light. While potentially advantageous at intermediate depths, this form of shade adaptation becomes self-limiting with increasing depth, as the incremental gain in photosynthetic production per unit pigment diminishes (Falkowski et al. 1990, Stambler and Dubinsky 2007). Therefore at lower mesophotic depths, zooxanthellate corals employ multiple adaptation and

Effect of morphology on light harvesting

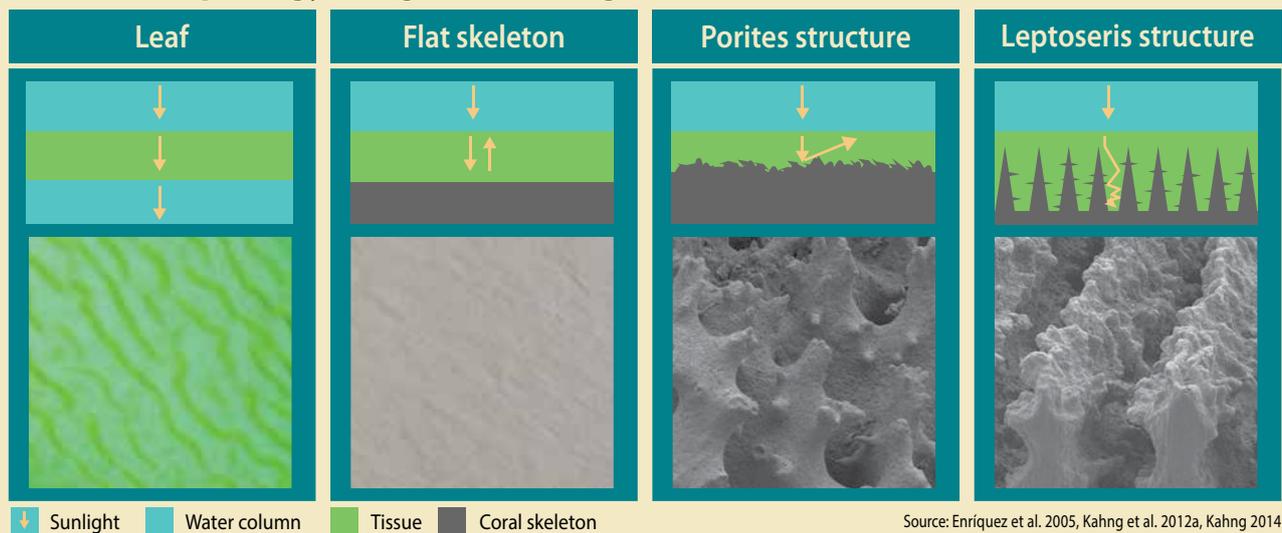


Figure 2.10. The absorption of light is influenced by the micromorphology of coral and algal skeletons.

acclimatization strategies (both ecological and biological). These include the following (reviewed in Kahng et al. 2010, 2014):

- Minimizing self-shading and maximizing surface area at a colony morphology level (e.g. horizontally flattened or encrusting colony morphologies), at a cellular level (e.g. monolayered zooxanthellate), and possibly at a subcellular level.
- Reducing the amount of tissue biomass, surface area and respiratory demand to increase growth efficiency.
- Reducing skeletal mass per unit colony area to reduce energy requirements.
- Optimizing skeletal light-scattering properties (Figure 2.10).

The reflective properties of calcium carbonate play an important role in increasing the light-harvesting efficiency of mesophotic corals (Enríquez et al. 2005, Kahng et al. 2012a, Kahng 2014) and may also occur in other organisms, such as calcareous green algae and coralline red algae. For a plant leaf (or non-calcareous macroalgae), light passes through the tissue only once and, unless absorbed by pigments, is lost. In contrast, the skeleton of a coral can reflect light back through the tissue, thereby increasing the probability of absorption. Light-harvesting efficiency is not only influenced by skeletal composition, but can also be affected by the light-scattering properties of skeletal micromorphology. Internal scattering can increase the probability of light absorption, independent of pigment concentration, by increasing the photon path length within the coral tissue (Figure 2.10).

Location can also affect the amount of ambient light available for mesophotic corals and algae. On flat or gently sloping areas, sessile organisms can be exposed to diffuse low light throughout the day, but on a steep slope, light is limited because the slope obstructs the light for a portion of the day (Brakel 1979). Thus, an MCE in clear water may have ample light at a given depth in areas with flat open seafloor, but may

become light-limited on a slope that is shaded for much of the day (Figure 2.11).

Mesophotic corals exhibit several adaptations relative to dependence on low light at depth, one of which is the switch from autotrophic (i.e., energy from light) to heterotrophic (i.e., energy from consumed foods) nutrition. This has been demonstrated using stable isotope techniques in scleractinian corals, *Montastraea cavernosa* (Lesser et al. 2010) and in a facultative zooxanthellate gorgonian from a temperate ecosystem (Gori et al. 2012). Specifically, planktonic resources, which are often higher on mesophotic reefs (e.g. Lesser and Slattery 2013) due to upwelled nutrients (Leichter and Genovese 2006, Leichter et al. 2007), are captured by the coral's tentacles, thereby offsetting the loss of energy from phototrophic sources.



Figure 2.11. A near-vertical mesophotic reef slope on the western side of Tobi (Hatohobei) Island, Palau at 55 m in depth. This area is heavily shaded during morning periods when the sun is in the east, casting a shadow across the area (photo Patrick L. Colin).

2.3. Geomorphology of mesophotic coral ecosystems

MCE habitats may be broadly characterized as either platforms or slopes (Locker et al. 2010). Low-gradient platform MCE habitats include outer continental and insular shelves, relic terraces and isolated banks with relatively flat tops. Slope habitats include the steep margins of continental and insular shelves and banks that extend from the platform break to the adjacent basin. MCEs are often extensions of shallow coral ecosystems, located directly below shallow reefs. However, not all MCEs have a shallow-water counterpart, for example Pulley Ridge and Gulf of Carpentaria MCEs, described in Chapter 3, are not adjacent to shallow reefs and are located offshore.

2.3.1. Platform habitats

Platform habitats that dip gently into the mesophotic zone can include relict ridges, terraces and banks that formed during periods of lower sea level (Harris and Davies 1989, Macintyre et al. 1991, Beaman et al. 2008, Harris et al. 2008; see text box). These features may be the result of erosional processes (e.g. wave cut platforms), constructional processes (i.e., relict reefs) or a combination of the two. Importantly,

they are hard substrates that are topographically high or prominent slope breaks that are conducive to colonization by MCEs. Examples include extensive areas (> 25,000 km²) of submerged banks in the Great Barrier Reef (Harris et al. 2013), submerged ridges off the south coast of Barbados, and relict terraces on many Pacific Islands (Bare et al. 2010). Often, a series of terraces can be found off a given stretch of coastline (e.g. Barbados), with the terraces at different mesophotic depths being colonized by different species and growth forms of corals (Rooney et al. 2010).

2.3.2. Slope habitats

MCEs in slope habitats are influenced by slope gradient and geomorphology (Sherman et al. 2010). Optimal slope habitats for MCEs are stable, rocky protrusions affording access to light and away from gullies and submarine canyons in which sediment and debris are transported downslope (Sherman et al. 2010). In the Caribbean, many islands and banks have steep outer slopes within the mesophotic zone, and in the tropical Indian and Pacific Oceans, both barrier and fringing reefs may have MCEs on their lower slopes.

MCEs established after the last ice age

All MCE habitats were established under rising global sea levels after the last ice age (Figure 2.12). Sea level was 120 m below its present position at around 18,000 years before present (BP) when Pleistocene reefs lived on the continental slope. Sea level rose to 50 m by around 12,000 years BP and corals colonized relict limestone platforms and other rocky surfaces on the outer shelf (or on atoll rims), leaving the Pleistocene reefs stranded below rising sea levels on the slope.

Sea level rose rapidly to 30 m by around 10,500 years BP. Some reefs were able to keep up with sea level rise but others, for reasons that are not fully understood, were not (Montaggioni 2005, Harris et al. 2008, Woodroffe and Webster 2014). By the time sea level reached its present position around 6,500 years BP, only some reefs had kept pace with rising sea levels; those that had not are sites of many of today's MCEs (sensu Macintyre 1972).

Mesophotic coral ecosystems (MCEs) established under rising sea levels

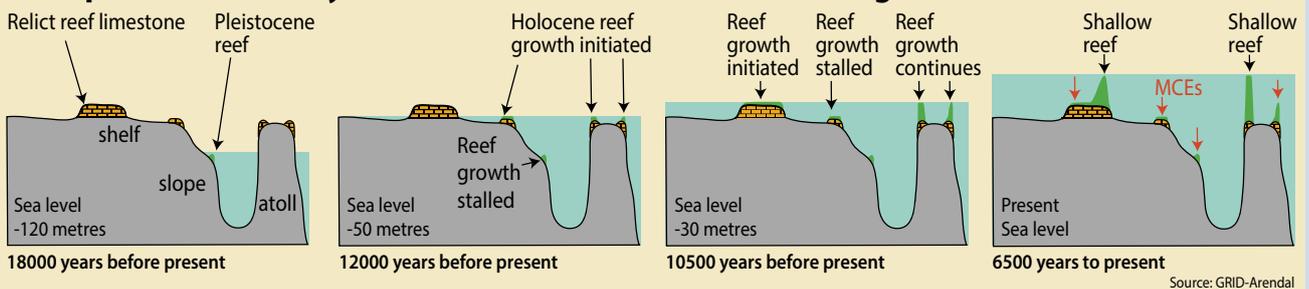


Figure 2.12. MCEs established under rising sea level.

History of mesophotic reef investigation

Patrick L. Colin, Coral Reef Research Foundation, Palau

Scientific knowledge of mesophotic reefs and their resident species largely began in the Age of Exploration in the eighteenth and nineteenth centuries, when dredging and trawling revealed new mesophotic reef species. Pioneering ichthyologists, such as Felipe Poey in Cuba and Pieter Bleeker in Indonesia, produced surprisingly thorough surveys, unsurpassed until recent times. In the early and mid-twentieth century, knowledge of the geology and origin of coral reefs — and by inference, MCEs — grew rapidly. Geologic investigations into submerged reefs focused on the back-stepping of reefs, some of which developed into MCEs, under rising global sea levels at the end of the last ice age (Macintyre 1967, Harris and Davies 1989; Fig 2.12).

After World War II, open-circuit scuba diving was adopted by scientists, and by the 1960s and 1970s collections were being made using compressed air at mesophotic depths down to approximately 70–75 m. In the Western Atlantic, early investigators were exploring Jamaican reefs (Goreau and Goreau 1973, Goreau and Land 1974, Lang et al. 1975) and documenting the carbonate framework producing sclerosponges (Hartmann 1969, Hartmann and Goreau 1970) and a diverse variety of deeper water Caribbean corals (Wells 1973). Work in the Indo-West Pacific also brought new deep-water species to the attention of scientists. Much of the work on the ecology of MCEs in Hawai'i was undertaken to understand antipatharians (Grigg 1965) and other precious corals (Grigg 1984). In the Indo-Pacific and Caribbean, scientists also discovered that species diversity at depths below 40 m were similar between the two regions (Kuhlmann 1983).

Some early coral reef field guides for the Western Atlantic region also included mesophotic fauna (Randall 1968, Bohlke and Chaplin 1968, Colin 1978) and today many mesophotic reef organisms, both fish and invertebrates, are in field guides with excellent in situ photographs (e.g. Veron 2000, Fabricius and Alderslade 2001, Allen and Erdmann 2014). Much of the interest in MCEs was inspired by the underwater photographers who first penetrated these depths, including Douglas Faulkner (Faulkner and Chesher 1979). Photographic documentation techniques have since become a mainstay of MCE research.

The potential for nitrogen narcosis (and the risks of decompression “sickness”) and the need for decompression were recognized quickly in the early days of open-circuit scuba diving, but it was not until the advent of mixed-gas diving that depth and time limits could be extended, making MCEs more readily accessible. The ability to monitor and control the oxygen content of a breathing gas mixture resulted in the development of mixed-gas rebreathers — first for the military and later for civilian applications. Walter A. Starck II and John Kanwisher developed the first practical closed-circuit mixed-gas rebreather, the Electrolung, in the later 1960s (Starck 1969, Starck and Starck 1972). At the upper depths of the mesophotic

zone (30–40 m), the introduction of Nitrox (enriched oxygen air) diving in 1977 allowed increased bottom times compared with compressed air diving. In the last decade, use of mixed-gas rebreathers with galvanic oxygen sensors and computer technology for gas control and decompression computation has become increasingly common for scientific research (Pyle 1996b), and has made diving to the lower depths of the mesophotic zone (90–100 m) practical.

Small research submersibles (Figure 2.13) have been used on many occasions to document mesophotic environments. The first notable reef projects were carried out in Hawai'i in the late 1960s (Strasburg et al. 1968), and later in Belize (James and Ginsburg 1979) and Jamaica using the Nekton submersible in the 1970s. In the Pacific, a fishery resource study in 1967 provided the first report of dense mesophotic scleractinian coral communities in Japan (Yamazato 1972). In the Red Sea, submersibles allowed for the first studies on the ecophysiology of mesophotic corals and their distribution (Fricke and Schumacher 1983, Fricke and Knauer 1986).

Other technological advances have improved our knowledge of MCEs. Multibeam sonar allowed the first detailed mapping of mesophotic areas, providing accurate depictions of slope and geomorphology. Small remotely operated vehicles or ROVs intended for relatively shallow water use (down to approximately 300 m depth) have also become widely available. Autonomous underwater vehicles (AUVs) provide new environmental information, often including otherwise hard-to-obtain time-series data.



Figure 2.13. Small submersibles make it possible for researchers to study mesophotic coral ecosystems in situ for longer time periods than technical diving (maximum of 20 minutes) permits. The author (Patrick Colin) pictured with Adrien “Dutch” Schrier off western Curacao (photo Barry Brown).

2.4. Differences between shallow-water and mesophotic coral ecosystems

While MCEs are viewed as extensions of shallow-water coral reef ecosystems, there are some notable differences between them (Table 2.1). It is important to note that the transition from shallow-water reefs to MCEs does not occur at a specific depth; rather the depth of transition varies between locations depending on water clarity (depth of light penetration), temperature, substrate type and other factors. In general, in tropical and subtropical areas, coral reefs shallower than approximately 30–40 m are considered to be shallow-water reefs. For example, in the Great Barrier Reef, shallow reefs cover an area of 20,680 km² and have a mean depth of 14.9 ± 15.4 m (Harris et al. 2013). MCEs generally occur below a depth of approximately 30–40 m and may extend to over 150 m in clear waters. There is no specific lower depth limit of MCEs because this also varies by location.

Shallow reefs may occur adjacent to land, as in the case of fringing reefs, or they may be located a distance offshore, such

as in the case of platform reefs, shelf-edge barrier reefs and atolls. MCEs may be located close to shore in areas with steep bathymetry, but are also found a distance from land, either independently or as deep-water extensions of shallow reefs. Overall, distance from land is not a reliable predictor of reef occurrence for either shallow coral reefs or MCEs.

The hydrodynamic environment of surface coral reefs is quite different from that of MCEs. Breaking waves over surface reefs induce flow and circulation within the reef (Gourlay and Colleter 2005). Surface reefs may locally amplify tidal currents such that they are accelerated through narrow, inter-reef channels, a process which controls their geomorphic evolution (Hopley 2006). Finally, shallow lagoon waters may become thermally stratified (e.g. Andrews et al. 1984). These processes are much reduced or non-existent on MCEs.

Table 2.1. General differences between shallow-water coral reef ecosystems and MCEs.

	Shallow-water coral reef ecosystems	Mesophotic coral ecosystems (MCEs)
Depth range	<ul style="list-style-type: none"> • 0 to approx. 30–40 m. • Lower depth corresponds to a moderate faunal transition. • Detectable in satellite images. 	<ul style="list-style-type: none"> • From approx. 30–40 m to deeper than 150 m. • Lower depth limit varies by location due to differences in light penetration and other abiotic factors. • Not detectable in satellite images.
Dominant habitat-building taxa	<ul style="list-style-type: none"> • Dominant species are zooxanthellate scleractinian corals, octocorals, calcareous and foliose macroalgae and sponges. 	<ul style="list-style-type: none"> • Dominant species are plate-like and encrusting zooxanthellate scleractinian corals, octocorals, antipatharians, calcareous and foliose macroalgae and sponges.
Light levels	<ul style="list-style-type: none"> • Generally well-lit environments. • Shallow reefs can become light-limited in turbid waters (e.g. near estuaries). 	<ul style="list-style-type: none"> • Generally middle- to low-light environments.
Thermal regime	<ul style="list-style-type: none"> • Generally stable thermal regime. • Shallow, stratified waters with high residence time may be subject to extreme thermal events causing coral bleaching. 	<ul style="list-style-type: none"> • Generally temperatures are cooler and naturally more variable on MCEs than on shallower reefs, especially those located on the continental slope, which are subject to internal waves. • Deeper water column may protect MCEs from extreme (warm) thermal events.
Hydrodynamic regime	<ul style="list-style-type: none"> • Subject to breaking waves and turbulence, except in sheltered lagoons. • Wave-induced shear stress and mobilization of seafloor sediments. • High residence times within lagoons. 	<ul style="list-style-type: none"> • Below the depth affected by breaking waves. • Seafloor generally unaffected by wave motion. Powerful storms can directly and indirectly impact MCEs (resuspend sediment or cause a debris avalanche), especially in the upper mesophotic zone (30–50 m).

Mesophotic coral ecosystems examined

3.1. Introduction

MCEs are found worldwide in tropical and subtropical waters. The existence of corals at mesophotic depths has been known since at least 1889, when Darwin reported the discovery of corals at depths of 128 m (Darwin 1889). However, it was not until the 1960s and 1970s that direct observation of MCEs began in earnest (Starck and Starck 1972, Wells 1973). As deep-diving technologies have advanced and been adopted by scientists, so has our ability to access and study MCEs. This chapter takes an in-depth look at some of the MCEs that have been studied to date (Figure 3.1) and demonstrates that while there are commonalities among MCEs, there are also differences; just as the shallow coral reefs of the Great Barrier Reef are similar but different from those found in the Florida Keys.

The MCEs discussed have a wide variety of geomorphologies. They include MCEs found on the edges of continental shelves and far from land, such as the Great Barrier Reef and Pulley Ridge in the Gulf of Mexico off the southwest Florida shelf; submerged fringing reefs and banks, such as in the United States Virgin Islands, the Main Palau Island group, Okinwa and the Gulf of Carpentaria in Northern Australia; canyon walls, such as Eilat in the Red Sea; and insular island shelves and submerged karst topography found in the Hawaiian Islands. Each MCE described below provides a snapshot of what is known about it, the dominant species present, any known limiting factors (e.g. sedimentation, temperature and terrigenous input) and any known impacts (e.g. hurricanes and El Niño Southern Oscillation), as well as whether there is a management regime in place. These case studies show the influences on MCEs and that there is still a lot to learn about them.

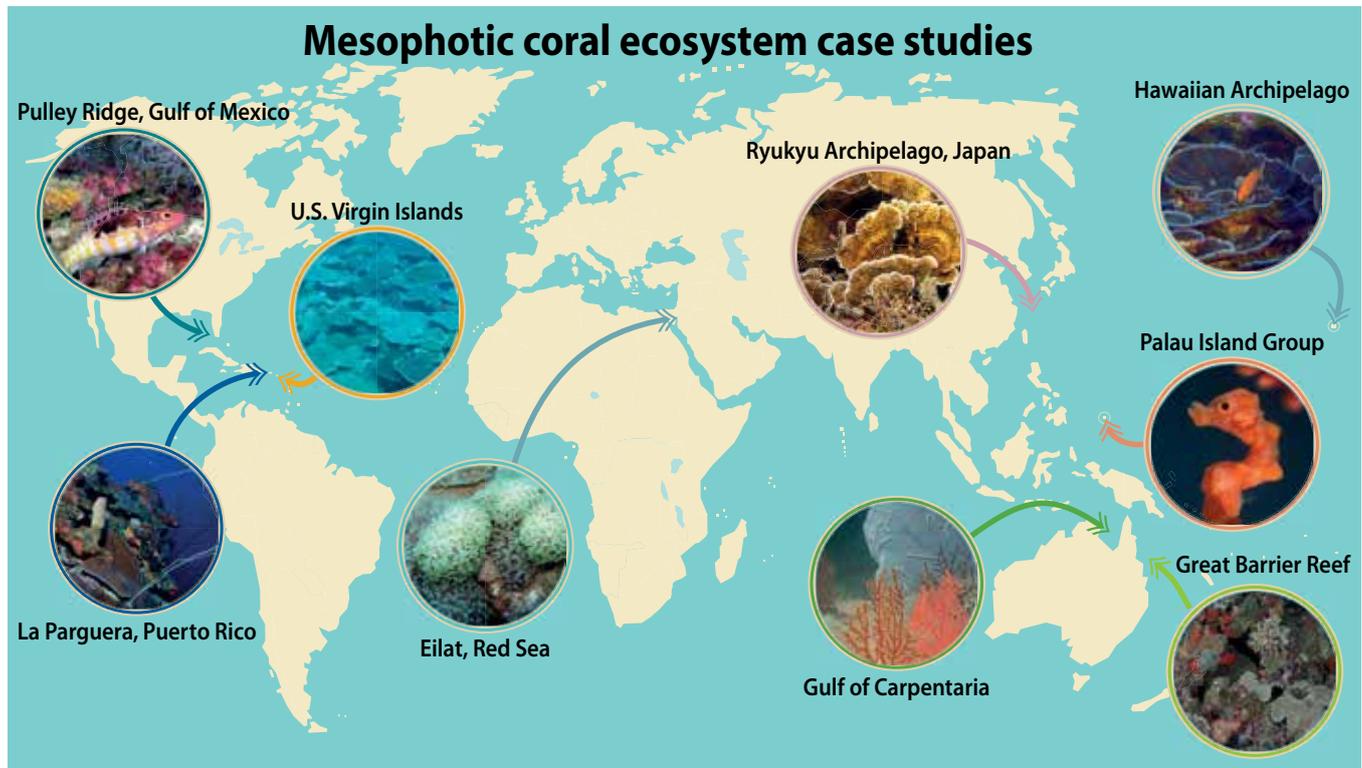


Figure 3.1. Location of MCE case studies.

3.2. The Great Barrier Reef, Australia

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The Great Barrier Reef (GBR) Marine Park contains over 2,900 individual shallow reefs and covers an area of 344,000 km², of which approximately 7 per cent (20,679 km²) is occupied by shallow-water coral reefs, mapped using aerial photography and satellite imagery (GBR Marine Park Authority, <http://www.gbrmpa.gov.au/resources-and-publications/spatial-data-information-services>).

MCEs are common within the GBR Marine Park and occur on the deeper flanks of shallow reefs and on submerged banks, both along the shelf edge and inside the GBR lagoon (Bridge et al. 2012a, Harris et al. 2013). The morphology of the GBR shelf changes significantly with latitude, being narrower and steeper in the north than in the south. These changes affect reef morphology, influencing both the amount and nature of habitats available for MCE development. The northernmost 800 km of the GBR is characterized by a relatively narrow continental shelf with a shallow lagoon (approximately 30 m), and long, narrow ribbon reefs separated by narrow passages occurring along the shelf edge (Figure 1). The seaward slope of the reefs drop steeply into very deep water, leaving limited room for the development of submerged reefs along the shelf edge. However, MCEs inhabited by diverse scleractinian and octocoral assemblages are known to occur along narrow submerged reefs seaward of the Ribbon Reefs at depths of approximately 50 to 70 m (Hopley et al. 2007, Beaman et al. 2008, Bridge et al. 2012b).

South of Cairns, the shelf widens and shallow reefs are set back from the shelf edge. The more gently sloping seafloor has resulted in a series of submerged reefs and terraces occurring along the shelf edge at depths of 50 to 130 m (Figure 2). Ecological communities inhabiting these MCEs have been examined at Noggin Pass, Viper Reef and Hydrographers Passage (Bridge et al. 2011a, b). In general, phototrophic taxa including hard and soft corals, phototrophic sponges and macroalgae are the dominant habitat-forming benthos at depths shallower than 65 m (Figure 3). In some regions, inter-reef terraces are occupied by dense fields of the macroalgae

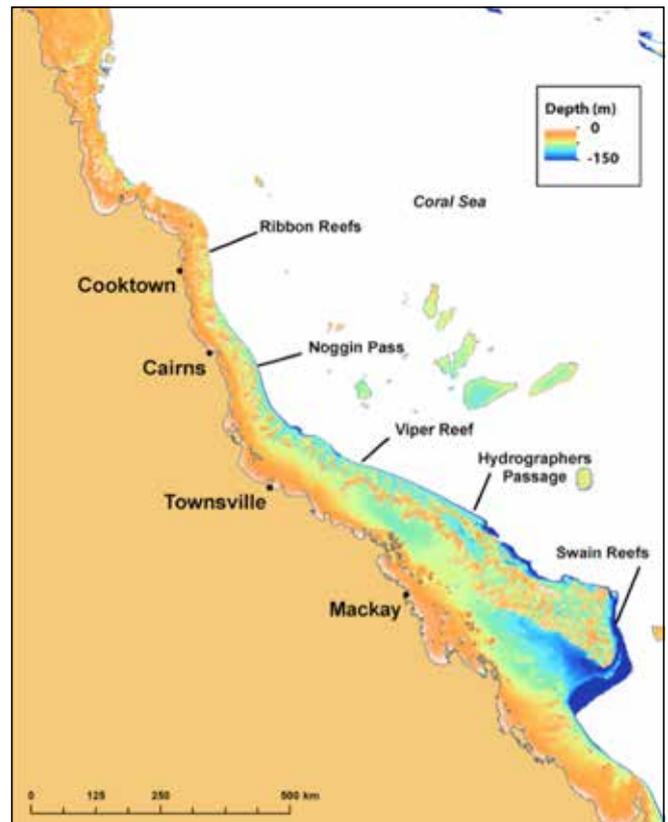


Figure 1. Great Barrier Reef.

Halimeda (Bridge et al. 2011b). Below 65 m, hard substratum is increasingly dominated by heterotrophic filter-feeders, particularly octocorals, with very large benthic foraminifera (particularly *Cycloclypeus carpenter*) occurring on soft sediments (Bridge et al. 2011a).

Given that submerged shelf-edge reefs appear to be consistent features of the GBR shelf edge over hundreds of kilometres, it is likely that MCEs also occur more or less continuously along the GBR shelf edge to at least the southernmost extent of the Swain Reefs at 23°S (Figure 1).

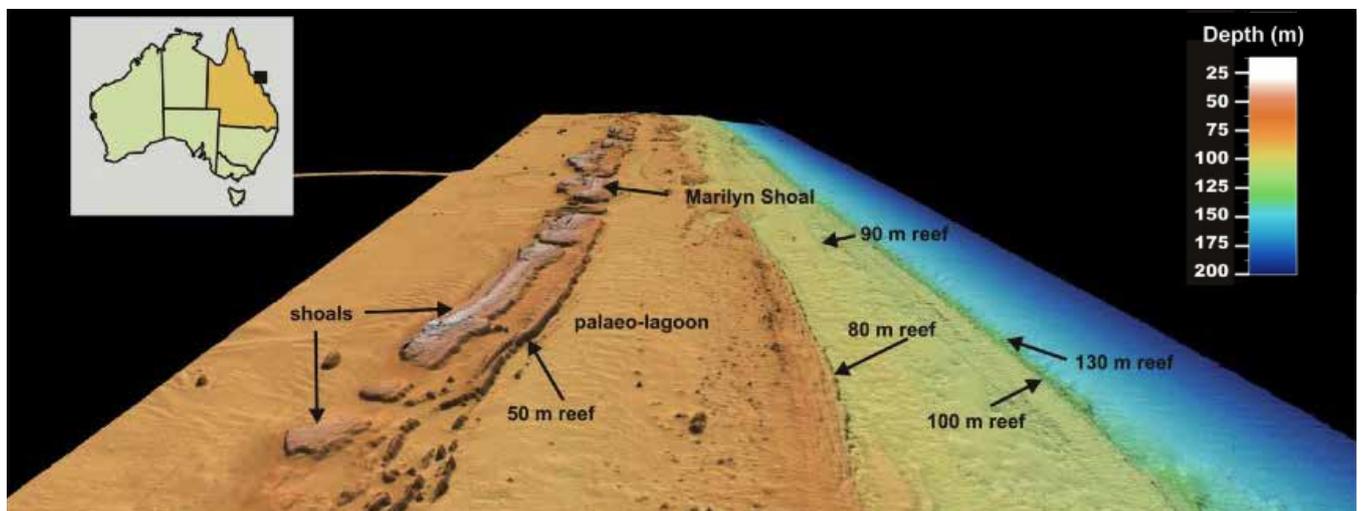


Figure 2. Bathymetry of the GBR outer-shelf at Hydrographers Passage, showing submerged shelf-edge reefs (from Bridge et al. 2011a).

The deeper lagoon in the central GBR allows greater MCE development on the mid-shelf. The lower slopes of some reefs extend to depths of at least 50 m (Chalker and Dunlap 1983), and are occupied by scleractinian or hard corals. Submerged banks and shoals are also abundant throughout the GBR (Pitcher et al. 2007) covering an area of about 25,600 km² (Harris et al. 2013). Three types of banks having a vertical relief exceeding 15 m were recognized: Type 1 (n = 1,145), with a mean depth of 27 m, have some portion of their surface covered by shallow coral reefs (and are thus co-located with shallow reefs); Type 2 (n = 251), with a mean depth of 27 m, are located landward of the shelf-edge barrier reef on the middle- to outer-shelf, with no shallow reefs superimposed; and Type 3 (n = 150), with a mean depth of 59 m, are located on the outer shelf, commonly seaward of the outer-shelf barrier reef (Harris et al. 2013). The shelf position of the different bank types is an important determinant of their ecological composition (Harris et al. 2013). Shallower shoals are dominated by hard corals, while deeper shoals are often colonized by gorgonians or calcareous algal species such as *Halimeda* (Hopley et al. 2007, Pitcher et al. 2007, Roberts et al. 2015).

Interest in the biodiversity associated with MCEs in the GBR Marine Park has increased in recent years, although the majority of this research has focused on hard corals (Bridge and Guinotte 2012, Muir et al. 2015). Broad-scale patterns in community composition have been investigated primarily using an autonomous underwater vehicle (Williams et al. 2010). Several expeditions from 2011 to 2013 conducted extensive sampling of hard corals on lower reef slopes in the north and central GBR,

with most sampling occurring in the upper mesophotic (30–40 m), although some specimens were collected from deeper than 100 m (Englebert et al. 2014). MCEs clearly support a considerable diversity of hard corals, including common shallow-water species such as *Acropora* (Muir et al. 2015).

Considerable interest surrounds the question of whether MCEs are capable of providing refuges for shallow-water coral reef biodiversity. Quantitative, long-term data are currently unavailable for MCEs on the GBR, and understanding their potential vulnerability to disturbances is difficult. MCEs are well represented in no-take areas, aided by the robust and precautionary management approach taken in the 2003 rezoning process (Bridge et al. 2015), but severe tropical cyclones are currently the leading cause of coral decline on the GBR. Very severe storms, such as Tropical Cyclone Yasi in 2011, caused damage to depths of at least 70 m at Myrmidon Reef (Bongaerts et al. 2013a), although in general MCEs are less impacted by storms than shallower reefs (Roberts et al. 2015).

There have been no observations of warm-water bleaching of MCEs in the GBR to date, although observations are limited. Sediment accumulation, due to the lack of wave energy in deeper waters, appears to be a significant factor limiting the growth of corals in mesophotic depths. Controlling sediment loads is therefore likely to be important for MCEs, particularly on submerged banks closer to shore. Lack of knowledge of the spatial location and extent of submerged banks may increase their incidental exposure to threats such as dumping of dredge spoil and ship anchoring (Kininmonth et al. 2014).

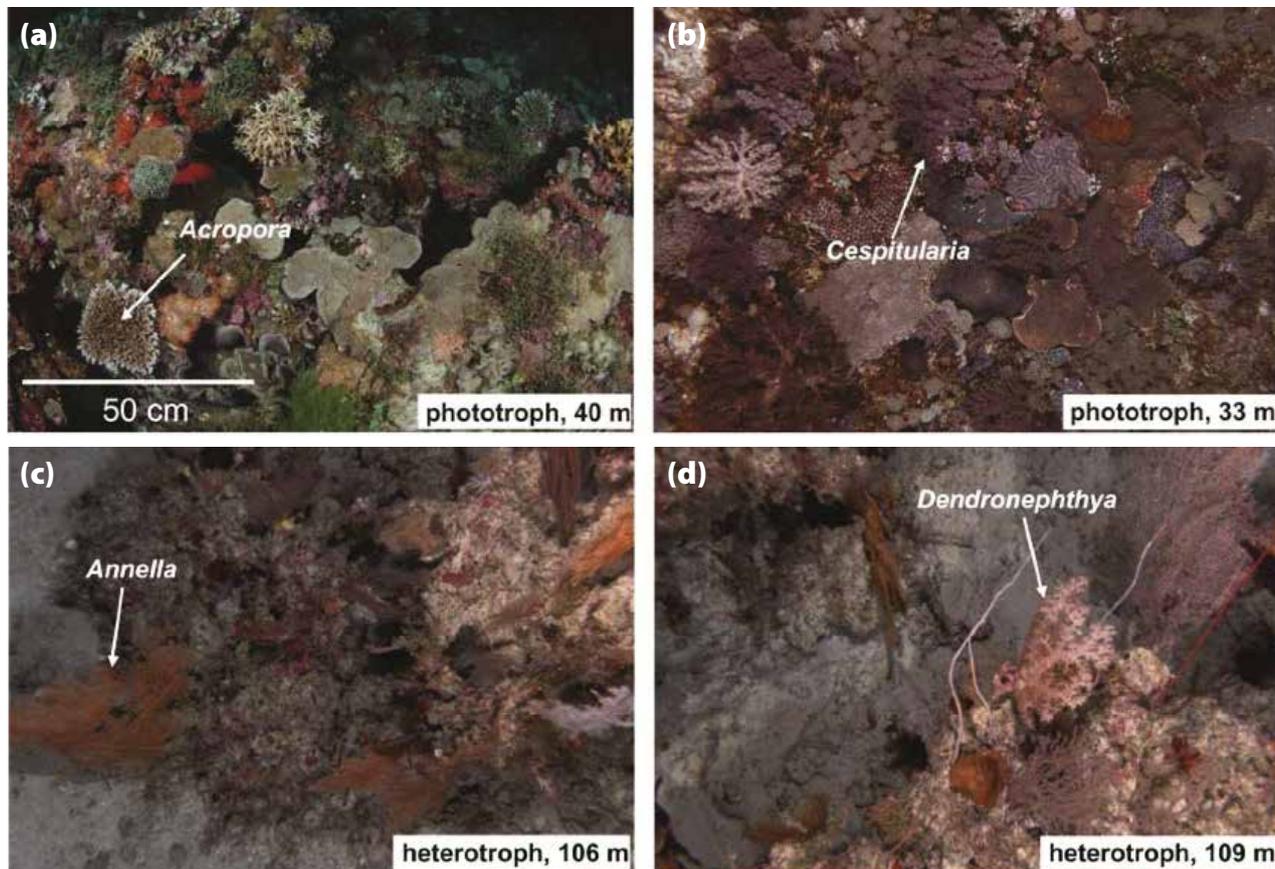


Figure 3. Examples of MCEs on the Great Barrier Reef: (a) hard-coral dominated community at Mantis reef (photo Ed Roberts), (b) soft-coral dominated assemblage at Hydrographers Passage, (c and d) heterotrophic octocoral-dominated assemblages at Hydrographers Passage (photos Australian Centre for Field Robotics at the University of Sydney, figure from Bridge et al. 2012a).

3.3. Pulley Ridge, Gulf of Mexico, USA

John Reed, Harbor Branch Oceanographic Institute — Florida Atlantic University, USA

Pulley Ridge, located in the Gulf of Mexico, lies about 250 km west of the Florida coast and extends from north to south along the southwestern Florida platform at depths of 60–90 m for nearly 300 km (Figure 1; Hine et al. 2008). Only the southernmost 34 km of Pulley Ridge, referred to as southern Pulley Ridge, supports MCEs (Figure 2; Cross et al. 2005, Reed et al. 2014, 2015). Southern Pulley Ridge is about 160 km² in size (Cross et al. 2005, Culter et al. 2006) with 10 m relief and represents a drowned barrier island from the last glacial period. Pulley Ridge is the deepest known light-dependent coral reef ecosystem off the continental United States (Halley et al. 2003).

Seismic maps indicate that drowned shoreline ridge complexes and pinnacles extend west of Pulley Ridge to depths of 100–150 m, suggesting the potential for other MCE habitat in the region (Ballard and Uchupi 1970, Holmes 1981, Phillips et al. 1990). In 2015, an additional 321 km² of MCE habitat adjacent to southern Pulley Ridge was documented (Reed et al. 2015). An analysis of the total area of mesophotic depth habitat at depths of 30–150 m indicates that the northern Gulf of Mexico region (Figure 1; 178,867 km²) has an order of magnitude area greater for potential MCEs than either the U.S. Caribbean or the Main Hawaiian Islands (Locker et al. 2010).

Coral growth is supported by the Loop Current, the prevailing western boundary current in the Gulf of Mexico, which provides warm, clear, nutrient-poor waters to Pulley

Ridge (Jarrett et al. 2005). This current separates the clear, oligotrophic, outer-shelf waters from cooler, higher nutrient, interior-shelf waters (Hine et al. 2008). Seafloor light measured at southern Pulley Ridge (65–70 m) is only 1–2 per cent (5–30 μE m⁻²s⁻¹) of available surface light, which is 5 per cent of the light typically available to shallow-water reefs (Jarrett et al. 2005).

Recent surveys of Pulley Ridge in 2012–2014 (Reed et al. 2014, 2015) show that the reef habitat supports a biologically diverse and dense community that is dominated by macroalgae (53.8 per cent cover), including plates of crustose coralline algae, *Peyssonnelia* spp., and the green alga *Anadyomene menziesii*; 1.6 per cent cover of sponges (102 taxa); and 1.3 per cent cover of hard coral. A total of 216 benthic macrobiota taxa have been identified from Pulley Ridge, including 14 Scleractinia, 15 Octocorallia (gorgonacea), and four Antipatharia (black corals; Figure 3). The scleractinian hard corals are dominated by the plate corals *Agaricia* sp., *A. fragilis*, *A. lamarcki/grahamae*, *Helioseris cucullata* and plate-forms of *Montastraea cavernosa*.

Previous surveys indicate that there has been a significant loss of coral cover on Pulley Ridge over the past 10 years. In 2003, the mean coral cover at southern Pulley Ridge was 11.9 per cent, with a maximum of 23.2 per cent in the central region of the ridge; and platy corals were up to 50 cm in diameter with coral cover as high as 60 per cent (Halley et al. 2003, Jarrett et al. 2005, Hine et al. 2008). By 2013, the



Figure 1. Map of U.S. Gulf of Mexico showing extent of mesophotic depth habitat (darker 30 m to 150 m depth contours) and major mesophotic reefs (boxes). Mesophotic depth marine reserves include marine protected areas (MPA), Habitat Areas of Particular Concern (HAPC), and National Marine Sanctuaries (NMS).

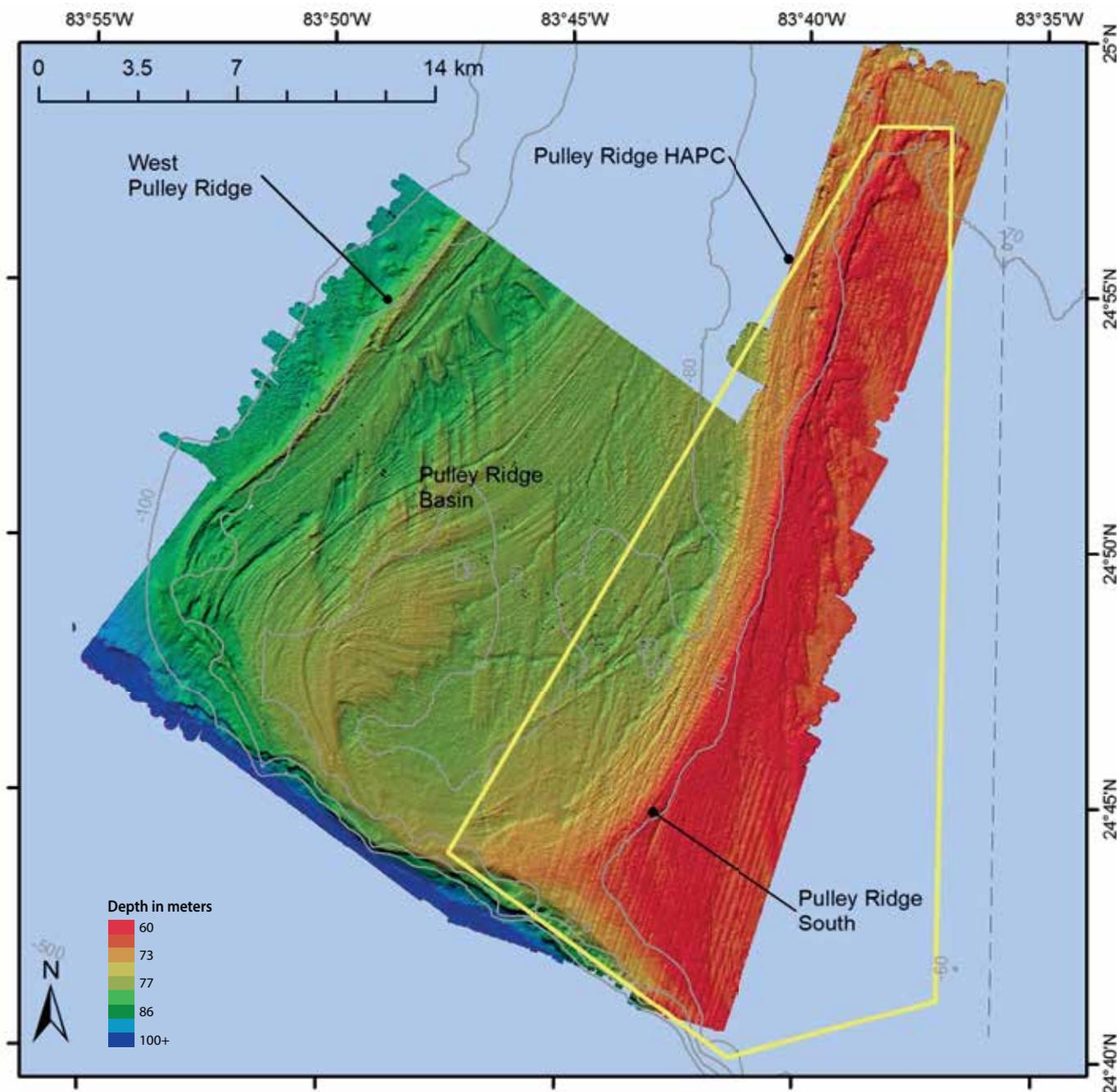


Figure 2. Multibeam map of the Pulley Ridge MCE in the U.S. Gulf of Mexico, the deepest known photosynthetic reef in U.S. continental waters. Pulley Ridge South (60–70 m depth) is a submerged intact barrier island. Pulley Ridge Basin and West Pulley Ridge are deeper geological features (80–90 m depth), which also provide MCE habitat. Yellow box= Pulley Ridge Habitat Area of Particular Concern, 346 km² (Multibeam Bathymetry Survey data, University of South Florida).

average hard coral cover was 0.85 per cent, with a maximum of 5.6 per cent, which is a 92.8 per cent loss of coral cover in a decade (Reed et al. 2014). In 2014, additional surveys to the west of southern Pulley Ridge, in an area known as the Pulley Ridge Central Basin, discovered a new coral area with the densest cover of mesophotic *Agaricia* corals known in the Gulf of Mexico (2.6–4.98 per cent cover with an average coral density of 5.6–16.8 colonies per m²; Figure 2). This new area is unprotected and outside of the Pulley Ridge marine protected area (Reed et al. 2015). On a positive note, a large number of these corals are relatively new recruits: 47.7 per cent are less than 5 cm in diameter, and 35.4 per cent are 5–9 cm. So it appears that the coral is growing back from the die-off that occurred after 2003.

A total of 78 fish taxa were identified in Pulley Ridge in 2012 and 2013 (Reed et al. 2014). The most common species included chalk bass, bicolor damselfish and cherubfish. Fifteen species of commercially- and recreationally-important grouper and snapper species were found (681 individuals in total), with the dominant species being vermilion snapper, black grouper, graysby, mutton snapper, red grouper and scamp. On southern Pulley Ridge, red groupers have excavated over 155,000 burrow pits from 5 m to over 15 m in diameter and 1–2 m in depth. Most active burrows have one adult red grouper with a total length of 50 cm or greater. The burrows provide habitat and act as oases for many small reef fish, but unfortunately most of the burrows seen in 2013 and 2014 had from several to 60 invasive lionfish per burrow (Reed et al. 2014; see Chapter 6).

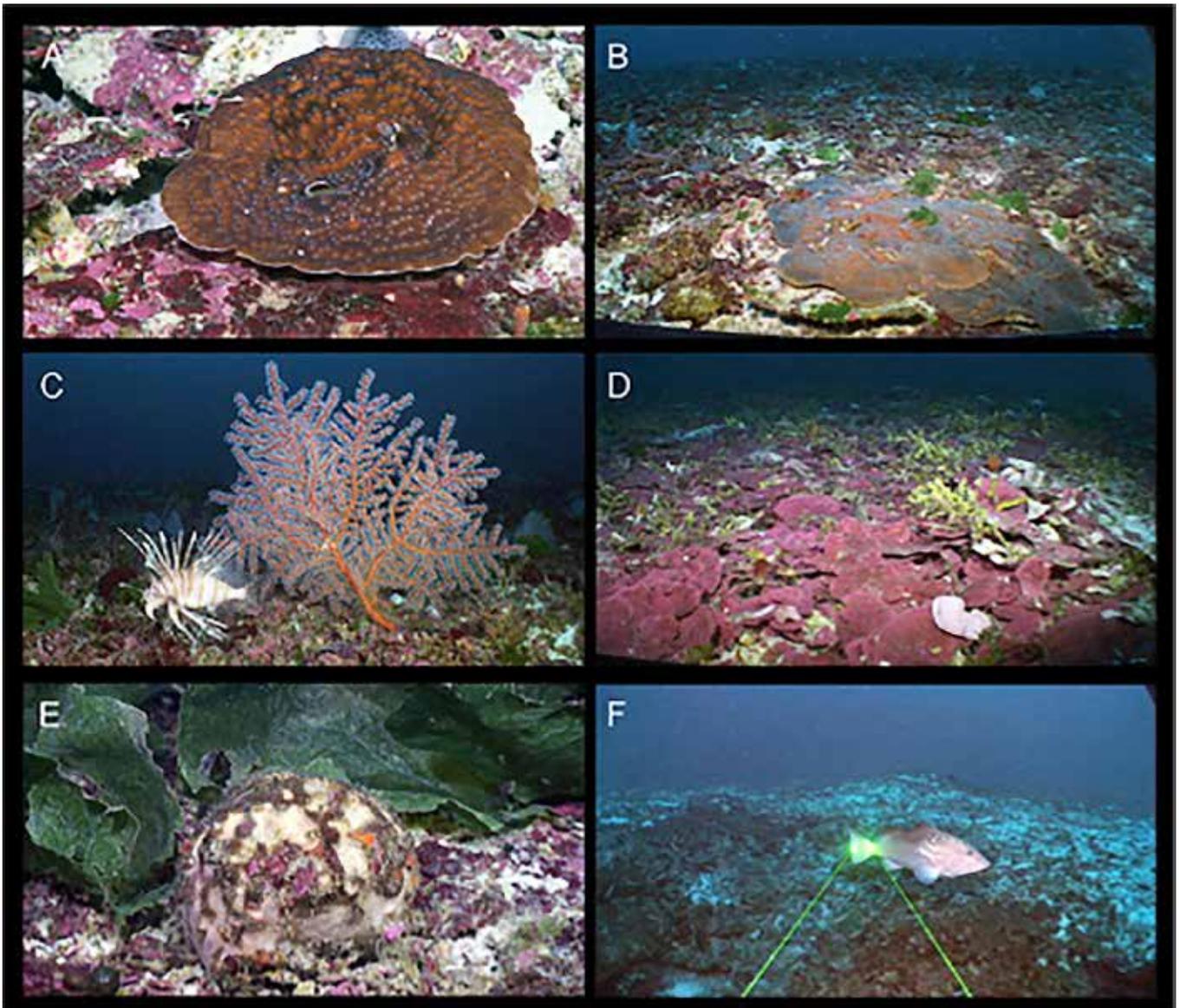


Figure 3. Habitat and biota of Pulley Ridge MCE in the U.S. Gulf of Mexico. (a) *Helioseris cucullata*, depth 74 m. (b) *Agaricia grahamae*, depth 82.5 m. (c) *Swiftia exserta* (octocoral with lionfish *Pterois volitans*), depth 79 m. (d) *Peyssonnelia* sp. (crustose coralline algae) and *Halimeda copiosa* (green algae), depth 80 m. (e) *Geodia neptuni* (sponge) and *Anadyomene menziesii* (green algae), depth 73 m. (f) *Epinephelus morio* (60 cm red grouper) guarding its burrow, depth 80 m, laser scale is 10 cm (photos Reed et al. 2015).

In the 2003 the corals generally appeared to be healthy, with little evidence of coral bleaching or disease (Jarrett et al. 2005, Hine et al. 2008). In 2014, a total of 7,329 individual plate corals (*Agaricia* spp. and *Helioseris cucullata*) were counted from the transect photos, of which 247 were noted to be bleached, partially bleached, totally bleached, partly dead, recently dead or diseased; resulting in 4 per cent morbidity of the total population measured (Reed et al. 2015). Bleaching (partial to total) ranged from 0 to 11.5 per cent per km² block.

The Gulf of Mexico Fishery Management Council (GMFMC) expressed concern over ongoing damage by fishing operations to Pulley Ridge habitat, and in 2005 designated Pulley Ridge a Habitat Area of Particular Concern (HAPC;

criteria for HAPCs include ecosystem services provided by the habitat, sensitivity to human impact, development stressors and rarity of habitat type). This 346 km² marine protected area is also considered essential habitat for coral and fish. Fishing restrictions within the Pulley Ridge HAPC include prohibition of bottom-tending gear, such as bottom trawls, bottom longline, buoy gear, pot or trap and bottom anchoring by fishing vessels (GMFMC 2005). In 2014, a proposal was submitted to the GMFMC to extend the Pulley Ridge HAPC boundaries to include the newly discovered MCE habitat (321 km²) in the Pulley Ridge Central Basin and West Pulley Ridge.

3.4. The United States Virgin Islands, USA

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Daniel Holstein, University of the Virgin Islands, USA

The insular shelf of the United States Virgin Islands (USVI) supports diverse MCEs that form on steep walls around the island of St. Croix and on the extensive banks and steep walls in the northern USVI around the islands of St. John and St. Thomas (Figure 1). Seventy-five per cent of the total shelf area above 65 m depth (1918 km²) is potentially MCE habitat (25–65 m), suggesting that MCEs could be more extensive than shallow reefs. This is certainly true around St. John and St. Thomas on the southeast Puerto Rican Shelf, where the identified hard bottom habitat below 30 m depth constitutes 60 per cent of the total hard bottom habitat (137 km²)*.

The northern USVI presents one of the most spectacular known examples of bank reef MCEs in the Caribbean (Figure 2). Within the well-characterized MCE depths (30–45m) of the southeastern Puerto Rican Shelf, there is strong habitat heterogeneity, with shelf-edge reefs forming on a drowned barrier reef complex and more inshore banks forming at similar depths (Smith et al. 2010). The most extensive area of reef development is on the southern entrance to the Virgin Passage, separating USVI from Puerto Rico. This area may represent one of the best developed MCEs within the U.S. Caribbean.

The shelf-edge reefs of the Virgin Passage tend to be low in coral cover (< 10 per cent), most likely as the result of natural disturbances from storms (Smith pers. obs.), whereas the

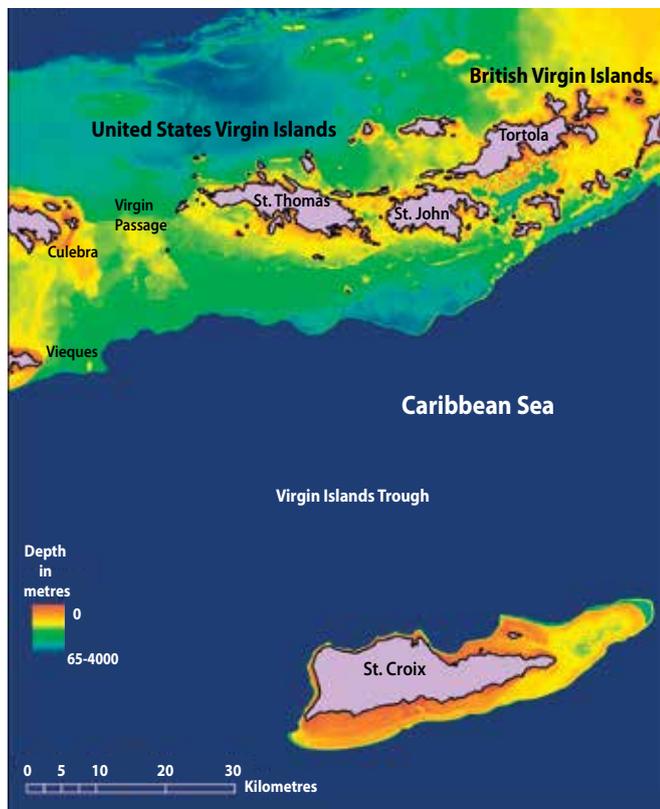


Figure 1. MCEs are found on shelves, slopes, and walls in USVI. The northern islands of St. Thomas and St. John are surrounded by a shelf largely in mesophotic depths with well-developed MCEs. The St. Croix shelf has less mesophotic shelf area, but extensive mesophotic wall systems. (Map Tyler B. Smith using NOAA bathymetric data.)

secondary and tertiary bank reefs have higher coral cover (25–50 per cent) — representing the highest in USVI and very high for the Caribbean (Smith et al. 2010). Importantly, the dominant coral genus that forms over 85 per cent of coral cover is *Orbicella*, which has recently been listed as threatened under the U.S. Endangered Species Act (NOAA 2014). This genus is very abundant in the upper mesophotic zone, with a conservative estimate of 50 million *Orbicella* colonies on the 23 km² of hard bottom habitats in the Hind Bank Marine Conservation District (Smith 2013). Other bank reef systems at similar depths in the Western Atlantic may be similarly dominated by *Orbicella* spp., while only 6 per cent of the MCEs of the south shelf are in the no-take or restricted-take fishery areas (Kadison pers. com.).

MCE development around St. Croix is limited by a mostly narrow shelf that drops steeply into deeper water, which may typify many small island MCEs of the Caribbean. Only 13 per cent (48 km²) of the St. Croix shelf is at mesophotic depths (25–65 m), which is a much smaller area than that of the northern USVI shelf (1385 km²). Most MCE development is on steep walls and slopes, the exception being some deeper linear reefs at the eastern extent of the Lang Bank (García-Sais et al. 2014, Smith et al. 2014). Since the 1970s, a few of the walls have been very well-studied, such as Salt River Canyon and Cane Bay walls on the northwest. These wall systems form dramatic precipices that extend from shallow depths to below 100 m.

Mesophotic coral cover was historically above 25 per cent for Salt River Canyon (Aronson et al. 1994) and Cane Bay (Sadd 1984), but there has been degradation in recent years due to the combination of several large hurricanes and a thermal stress and bleaching event in 2005. MCE coral cover at these sites is now below 10 per cent (Smith et al. 2014). The coral communities are a typical mix of plating forms; predominantly lettuce corals (*Agaricia* spp.) and star corals (*Orbicella* spp.), which form on vertical buttresses surrounded by channels where sediment is transported off-shelf. The Salt River Canyon and areas at the eastern end of the Lang Bank are in Fisheries Protected Areas, covering about 25 per cent of the potential MCE shelf depths. Despite the moderate coverage of Marine Protected Areas, fishing intensity on the narrow shelf is quite high and many commercially-important fish, such as large-bodied snappers and groupers, are absent or rare relative to historical levels (Kadison pers. com.).

The MCEs of USVI are not immune to anthropogenic disturbance. Local and global stressors have caused slow to precipitous declines in coral cover over the last 10 years or more. Potential climate change effects were noted between 2005–2014, with thermally induced coral bleaching occurring at least twice, and causing an approximately 28 per cent loss of coral cover in *Orbicella*. The nearshore MCEs of St. Croix are potentially vulnerable to sedimentation from natural reef processes (Hubbard 1989), whereas the offshore MCEs of the northern Virgin Islands are not influenced by terrestrial sediment (Smith et al. 2008).

* This calculation does not include any of the uncharacterized hard bottom MCE habitats on the deep and wide northern bank.



Figure 2. (a) Closed-circuit rebreather diver sampling corals at 65 m on a lettuce coral, *Agaricia undata*, fringe reef on the Grammanik Bank, St. Thomas. (b) Dense boulder star corals, *Orbicella franksi*, between USVI and Puerto Rico at 35 m. (c) A dog snapper, *Lutjanus jocu*, at a fish spawning site south of St. Thomas at 30 m (photos Tyler B. Smith).

3.5. Eilat, Red Sea, Israel

Gal Eyal, Tel Aviv University and the Interuniversity Institute (IUI) for Marine Studies in Eilat, Israel
Yossi Loya, Tel Aviv University, Israel

The Gulf of Eilat/Aqaba (the Gulf) is a 180 km long, narrow, blind-ended embayment connected to the Red Sea at its southern end. On average it is 18 km wide (varying between 6 and 26 km), with a maximum depth of 1,825 m. The circulation in the Gulf is driven by a combination of wind, heat fluxes and tides. Wind-generated surface currents, and what appear to be permanent anticlockwise gyres, move water up the Jordanian coast and down the Israeli coast (Anati 1974, Berman et al. 2000, Manasrah et al. 2006). Seasonal upwelling events also bring water laden with numerous organisms from the deeper reefs to the surface, and transport surface waters to depth (Genin et al. 1995). Although described as oligotrophic, these upwelling events can produce phytoplankton blooms in spring and autumn (Labiosa et al. 2003). The Gulf is highly saline — up to 41 parts per thousand in the north — and its sea surface temperature varies from a minimum of 20°C in the winter to a maximum of 28°C in the summer, with a deep-water temperature (down to 1,825 m) constant at ca. 21°C (NMP 2013).

The northern part of the Gulf is surrounded by arid mountainous terrain, which provides a constant input of wind-borne terrigenous sediment (Ben-Avraham et al. 1979). On rare occasions, flash floods transport terrestrial sediment into the deep waters of the Gulf via submarine canyons (Katz et al. 2015). Despite this, the Gulf has unusually clear

water, with high levels of light throughout the year, even at mesophotic depths (60–160 $\mu\text{mol m}^{-2}\text{s}^{-1}$ at 36 m and 7.1–26.7 $\mu\text{mol m}^{-2}\text{s}^{-1}$ at 72 m; Eyal et al. 2015). Surface levels of light at Eilat are 40 per cent higher than those found at other reefs in Heron Island, Australia; Puerto Morelos Quintana Roo, Mexico; and Coconut Island, Hawai'i (Winters et al. 2009).

The shallow coral reefs along the Gulf are among the world's most diverse in terms of average number of species per m^2 (Loya 1972). Due to the Gulf's unique geographic structure and its extreme oceanographic conditions, a high proportion of endemic species have evolved (Loya 2004). MCEs develop to a depth of at least 150 m and occur almost continuously along the coastline of Eilat, unlike the scattered nature of shallow reefs in this area. The fauna comprises many unique species found exclusively in mesophotic depths. So far, taxonomic assessment of the mesophotic communities in the Gulf has yielded 93 coral species (81 zooxanthellate and 12 azooxanthellate corals) from 13 families and two *incertae sedis* (meaning "of uncertain placement") genera, three suspected new coral species, eight new coral records to the Red Sea and 10 unidentified coral species (data from Tel Aviv University). The mesophotic corals at one site in Eilat exhibited an average coral cover of ca. 34 per cent compared with ca. 24 per cent in the shallow reef (Table 1). Altogether, these parameters indicate a healthy and flourishing MCE (Eyal 2012).

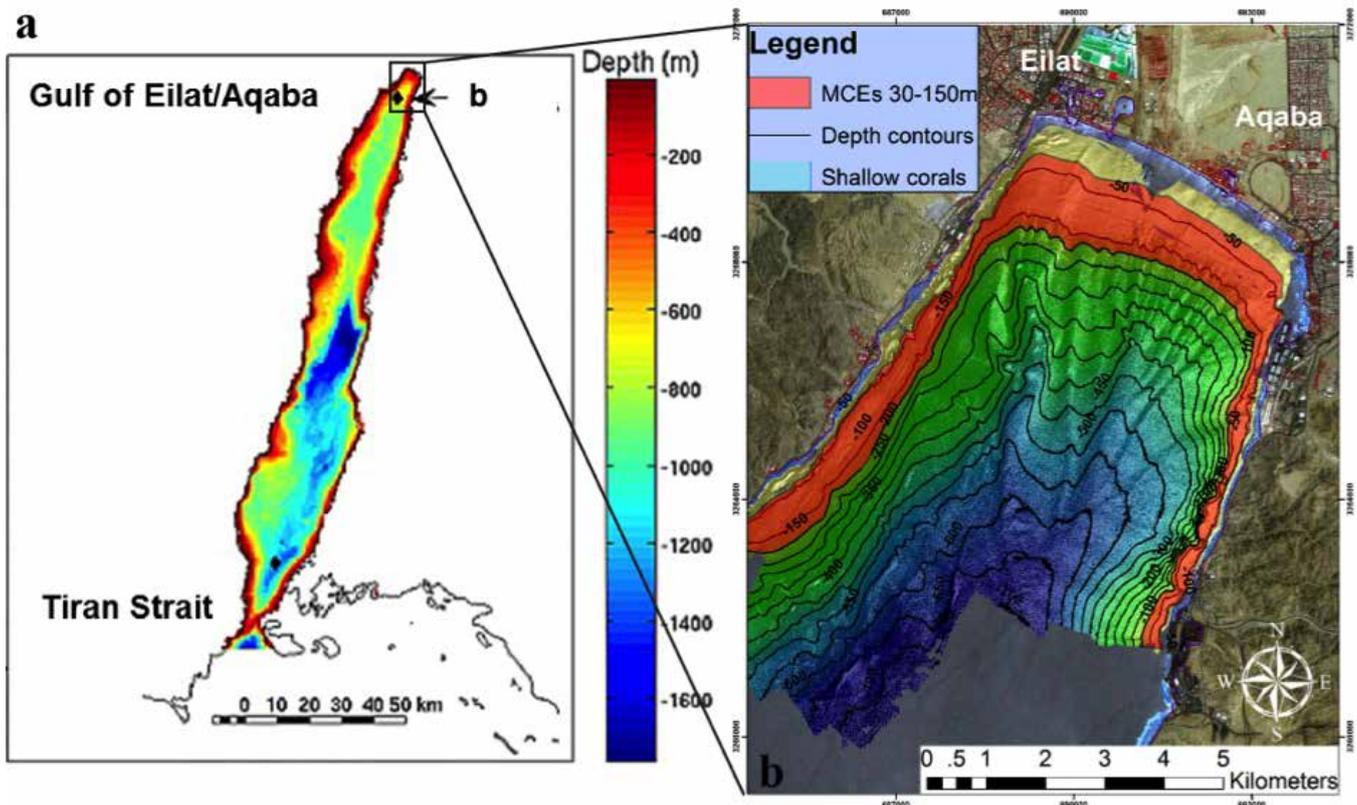


Figure 1. Bathymetric map of the northern Gulf of Eilat/Aqaba. (a) Illustration of the Gulf of Eilat/Aqaba (based on Biton and Gildor 2011). (b) Magnification of the Gulf head in high-resolution bathymetry. The pink represents the mesophotic zone at depths of 30–150 m (Background image based on Sade et al. 2008).

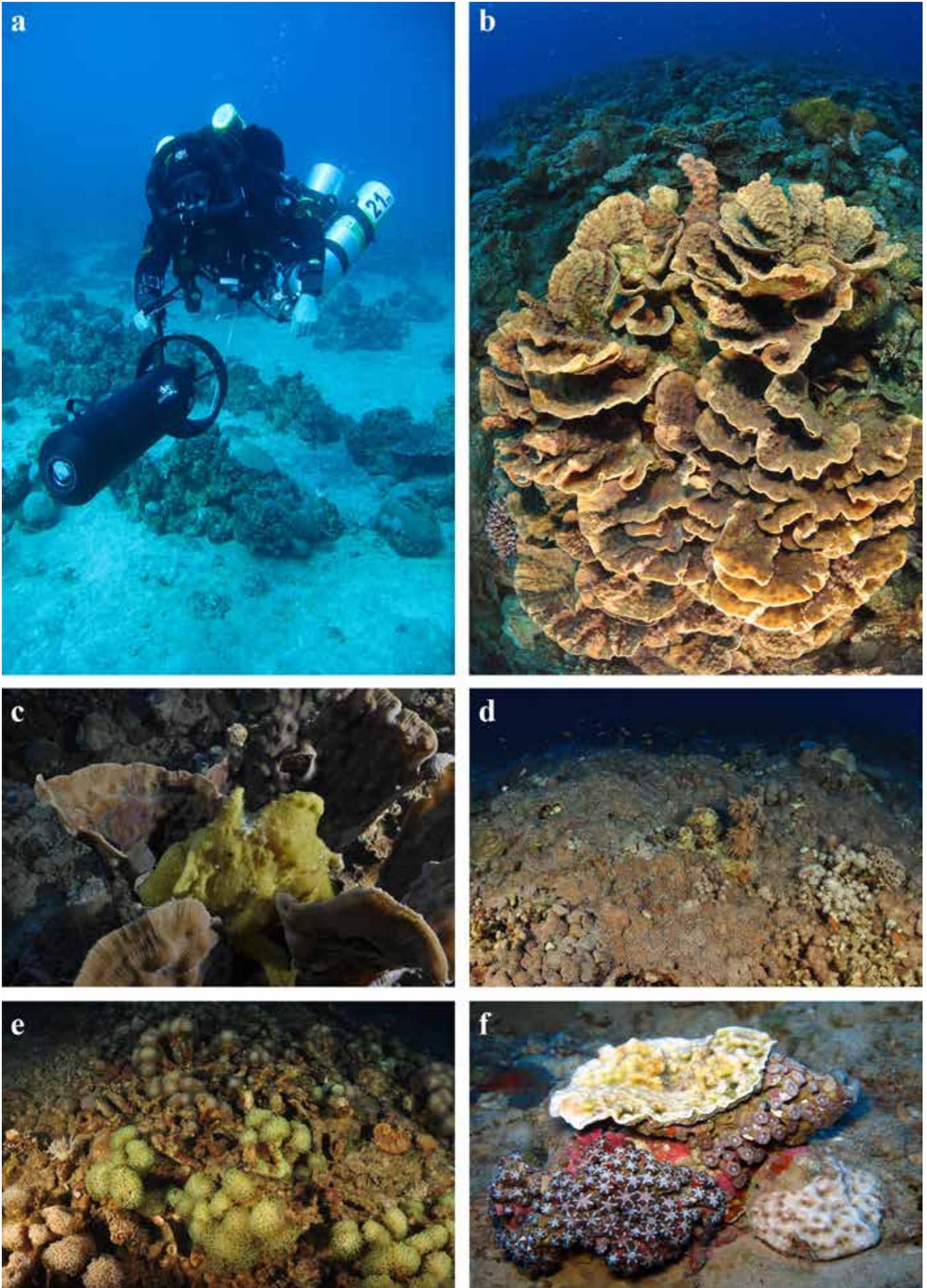


Figure 2. Eilat MCEs at 60 m depth. (a) A diver at work, aided by an underwater scooter and closed-circuit rebreather, exploring MCEs from the shoreline, (b) *Mycedium* sp., (c) Frogfish, *Antennatus nummifer*, "hiding" in *Oxypora egyptensis*, (d) *Alveopora* spp., (e) *Euphyllia paradivisa*, and (f) *Leptoseris* sp. and *Blastomussa merleti* (photos Gal Eyal).

Table 1. Data summary for scleractinian coral cover (per cent) at Eilat IUI reef, mean Shannon-Wiener index of diversity (H'), mean number of species per quadrat (#), and total number of species of all corals observed along the survey transects at 2 m, 40 m and 60 m. The survey includes three transects of 10 quadrats at each depth, with a total of 30 m² per depth (Eyal 2012).

Data summary for scleractinian corals at Eilat reef					
Depth (m)	Cover (%)	Diversity (H')	Mean per quadrat (#)	Mean per quadrat (SD)	Total no. of species
2	23.95	1.00	3.714	1.329	10
40	34.23	2.33	8.375	2.918	25
60	33.04	1.83	6.121	1.728	20

The towns of Aqaba and Eilat, located on the northernmost coast of the Gulf, are both large population centers with significant infrastructure development. The 14 km long shallow reef in Eilat was once a flourishing natural ecosystem, but in the last 40 years has been increasingly impacted by human activities (Loya 1975, 1976a, 2004, 2007, Walker and Ormond 2003). Extensive parts of the reef have been destroyed as a result of multiple factors, including inexperienced divers (Walker and Ormond 2003), sewage spillages, oil spills (Loya and Rinkevich 1980) and natural disturbances, such as extreme low tides (Loya 1972, 1976a) and severe southern storms (Eyal et al. 2011, NMP 2013). The shallow-water corals do not generally experience bleaching — although it has been hypothesized that they have been genetically selected to tolerate periods of elevated water temperature (Fine et al. 2013), new coral diseases have been reported (Rosenberg and

Ben-Haim 2002). In contrast, some of the mesophotic corals have been observed to suffer from partial bleaching during the summer, followed by recovery in the autumn (Nir et al. 2014). Bleaching is most pronounced on the lower edge of the reef slope between 40 and 63 m. It has been suggested that temperature alone is not responsible for the bleaching. Instead it may be due to a complex seasonal acclimatization regime that results in an oscillation in the mesophotic coral-algae relationship from mutualistic in the summer to parasitic in the winter (Nir et al. 2014).

Currently, Eilat's reefs are continuously monitored by the Israel National Monitoring Program at the Gulf of Eilat. Gradual improvement in reef health has been recorded in some shallow-water locations, but there is still little information on MCEs (NMP 2013).

3.6. Spotlight on the Palau Island group

Patrick L. Colin, Coral Reef Research Foundation, Palau

Having been the focus of research for over 20 years, the MCEs of Palau are among the best-documented MCEs. Little research has been conducted in other areas of the tropical Indo-West Pacific, although a vast number of MCEs occur there. The great majority of research has been done around the main Palau Island group. The northern atolls, southwestern oceanic islands and low latitude Helen Reef atoll are not included in this case study. The MCEs of Palau have been investigated using standard and mixed-gas diving and small submersibles (Colin 1999, 2009). Mesophotic invertebrates were identified through collections for the U.S National Cancer Institute natural product screening programme (1994–2014), and fish are also well known (e.g. Myers 1999). Temperature monitoring arrays to 90 m depth were established after the 1998 bleaching event. Aspects of Palau’s MCEs are included in Colin (2009) and additional information is included here.

The outer margins of Palau, including the outer islands and atolls, generally have MCEs continuing below shallow reefs. The main island group reef system has approximately 300 km of barrier and fringing reef, with 80 per cent or more of this having a mesophotic component. This roughly 260 km long MCE covers approximately 24 km² (increasing to approximately 30 km² if Angaur, Kayangel and Velasco Reef are included). MCEs also occur in the deep channels in the barrier reef (to 80–90 m), as deep patch reefs within the lagoon (up to 55 m) and shallower lagoon area (30–36 m) with low light and high sediment.

Reefs built on the basaltic Palau-Kyushu Ridge have grown in shallow water since the Miocene, laying down extensive layers of carbonate rock. Some have been uplifted to form the Rock Islands, while other areas (i.e., Kayangel Atoll, Velasco Reef and the northern reef tract of the main Palau group) have subsided, with up to 1,000 m of carbonates deposited on top of the basaltic basement. The present MCEs developed only in the last 20,000 years as sea level rose from the last glacial lowstand of –120 m.

In general, the mesophotic zone of the outer slope of Palau’s reef ranges from steep (20–30° slope) to vertical, and is usually a narrow strip, often less than 100 m wide. On shallow reefs (10–40 m range) there is a distinct relationship between outer reef slope angle and exposure to winds and waves (Figure 1). Vertical to near-vertical slopes are found largely where the reef faces to the southwest or south, whereas those reefs exposed to the west, through to the north or the east, are gentler, with slopes usually in the 20–45° range. Deeper slope MCE geomorphology does not necessarily mirror the shallower reefs. Many areas with near-vertical shallow slopes have the MCEs sloping in the 30–45° range, with a distinct slope at some point. In other areas vertical MCE faces occur, with or without vertical shallow reefs (Figure 2).

The downward movement of sediment and reef rock controls the structural aspects of most MCEs. Build-ups of talus and

sediment produce occasional downslope movements of materials and serve to limit areas suitable for stony corals (cf. Figures 3a and 3b). Vertical faces have areas protected from downwelling materials by overhanging ledges. Erosional channels located at intervals along these faces act as sediment chutes to convey reef debris to the depths.

A number of Palau’s MCE faunal elements are now relatively well known, with Colin (2009) covering overall levels of species diversity, including many mesophotic groups.

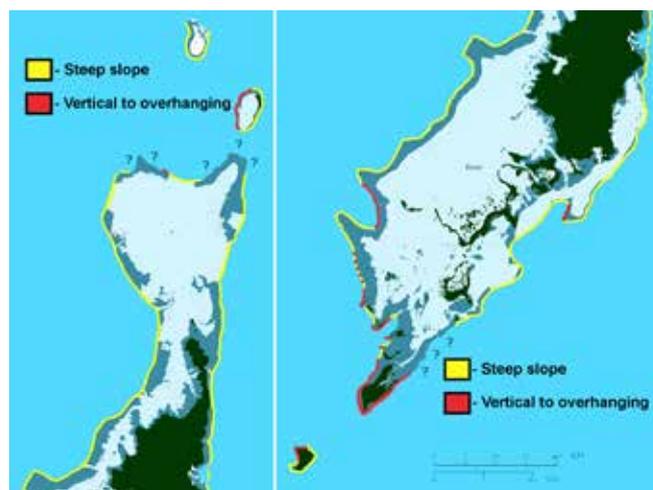


Figure 1. The slope of the outer reef face of Palau to depths of 50 m is related to wind and wave direction. Deeper MCE slopes do not show a similar correlation (from Colin 2009).

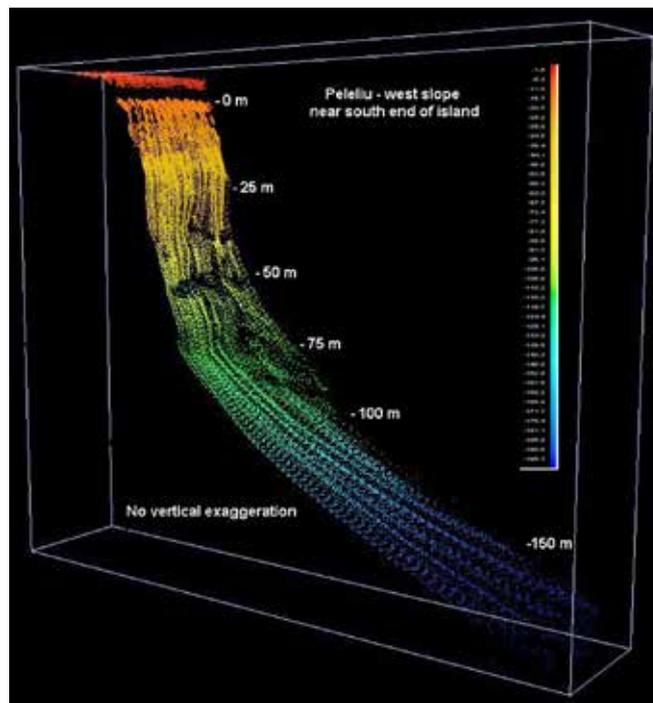


Figure 2. An example of an outer reef slope from southwestern Peleliu, Palau, imaged with multibeam sonar. This area has a very steep escarpment with near-vertical faces to depths of 70–90 m, and then slopes more gently to oceanic depths.

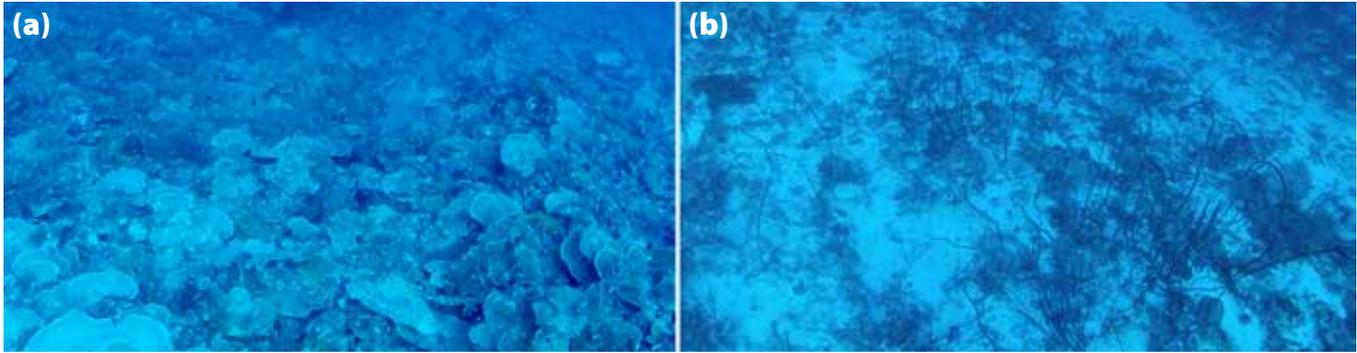


Figure 3. Deep slope MCEs at two locations in Palau. (a) Sloping bottom with very high coral cover (estimated 75 per cent) at 50 m depth on the western side of Ngeruangel reef, Palau. (b) Sloping bottom on a western-facing MCE, with low stony coral cover, many whip gorgonians and downslope sediment transport (photos Patrick L. Colin).

Scleractinian corals

While Palau's stony coral diversity is relatively high (roughly 320 species), it is limited in Palau's mesophotic zone (Veron 2000). The lower depth limit for the genus *Acropora* is about 45 m. The only branching coral commonly found at depths below 60 m is *Madracis asanoi*, growing as relatively short twisted branches in colonies up to one metre across. It is also found encrusting dead black corals or gorgonians. The coral is zooxanthellate, apparently the deepest such coral in Palau, down to about 90 m (Figure 4a), then continues deeper, becoming azooxanthellate (Figure 4b).

Most other mesophotic stony corals are plate-like with thin skeletons, typified by the genus *Leptoseris*, and are horizontally oriented to capture light (and are vulnerable to accumulating sediment). At least 22 species of ahermatypic and azooxanthellate, largely solitary, stony corals are also found in the mesophotic, some of which are illustrated in Veron (2000).

Other Cnidaria

The gorgonians and soft corals of Palau are relatively well known, with about 52 species (Alderslade 2002, Williams 2003, Fabricius et al. 2007, Colin unpublished); a number of which remain undescribed. Large seafans of *Anella* and *Muricella* and a number of whip gorgonians (Figures 3b and 5a) are common along the slope. The delicate yellow gorgonian

Stephanogorgia faulkneri, described from Palau, is spotty in its distribution, but indicative of mesophotic conditions where it occurs (Figure 5d). Other MCE cnidarians include stylasteridae, about a dozen black corals (Opresko 2004), and an assortment of anemones (Arellano and Fautin 2001, Fautin and den Hartog 2003) and hydroids.

Other invertebrates

The known MCE sponges (Porifera; Figures 5b and 5c) currently number at least 30–40 species. A number are “lithistid” or stony sponges, some of which build reef structure at mesophotic depths — an ability comparable to Western Atlantic sclerosponges. Other noteworthy MCE invertebrates include the large benthic ctenophore *Lyrocteis imperatoris*, which perches atop gorgonians and black corals and extends its tentacles to feed (Figure 5e). It is motile to an extent and has been documented to change its depth range with changing water column structure related to El Niño Southern Oscillation events.

Among molluscs, the large oyster *Empressostrea kostini* occurs beneath ledges at 60–90 m, where it is protected from downwelling sediment (Figure 5f). The Palau chambered nautilus, *Nautilus belauensis* (Figure 5g), is a mesophotic species, which has seen a number of studies on its occurrence and environment (Carlson et al. 1984, Saunders 1984, Ward et al. 1984, Hayasaka et al. 1995, Kakinuma 1995, Okytani

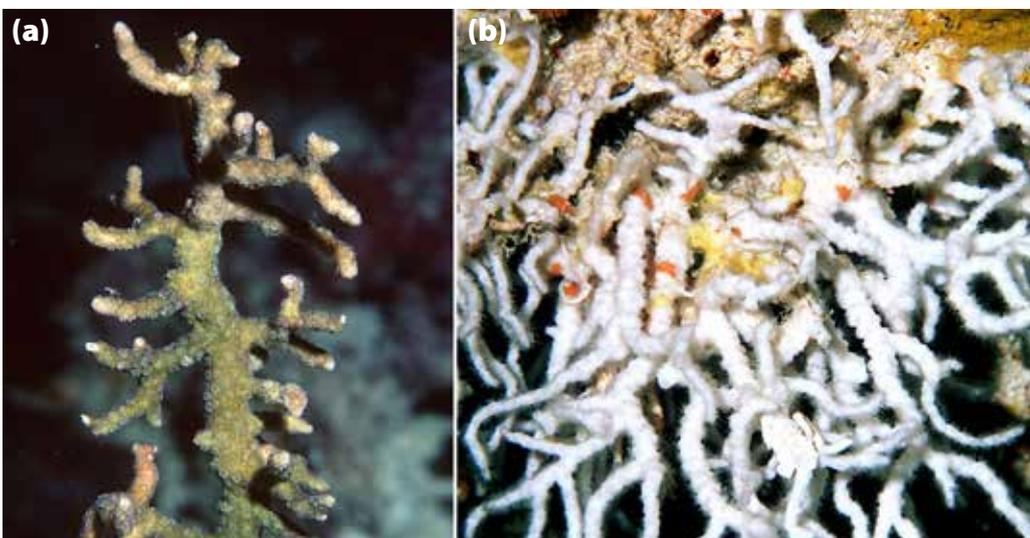


Figure 4. (a) The deep-dwelling branching stony coral *Madracis asanoi* is zooxanthellate at depths of 60–90 m. (b) It becomes azooxanthellate on vertical faces at 120 m depth (photos Patrick L. Colin).

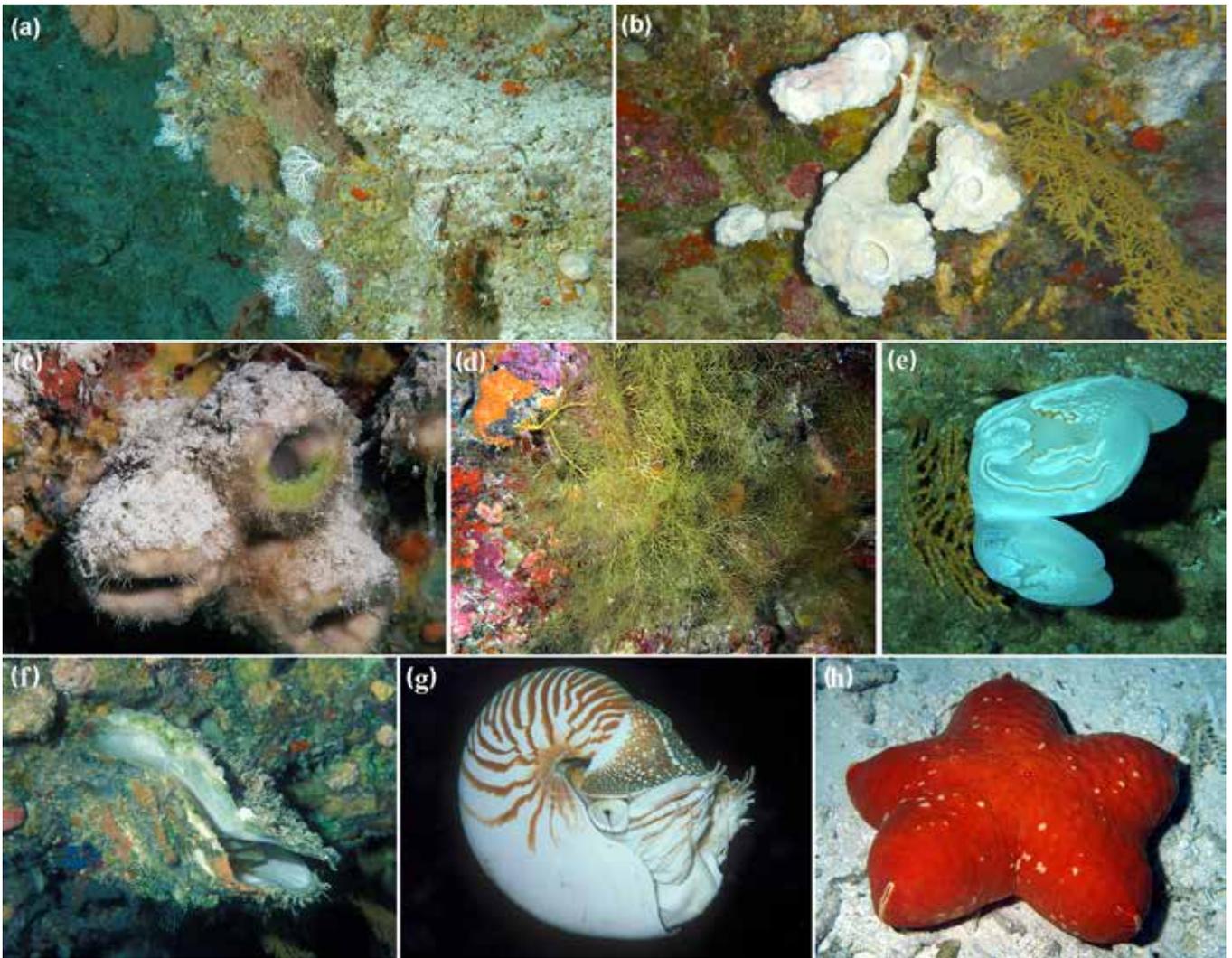


Figure 3. (a) Overhanging reef face, 80 m depth dominated by gorgonians and stylasterine corals. (b) The mesophotic sponge *Aplysinella strongylata* is found scattered on near-vertical reef faces. (c) The lithistid sponge, *Scleritoderma hermanni*, is common below 80–90 m depth. (d) The delicate gorgonian *Stephanogorgia faulkneri* is common along some MCE slopes. (e) The benthic ctenophore *Lyrocteis imperatoris* is a motile species occurring as shallow as 90 m during El Niño conditions. (f) The large oyster, *Empressostrea kostini*, occurs in small caverns at 60–90 m depth sheltered from sediment downflow. (g) The Palau chambered nautilus, *Nautilus belauensis*, is found at the lower limit of the mesophotic zone. (h) The sea star *Astrosarkus idipii* is found on steep slopes at 70–120 m depth (photos Patrick L. Colin).

and Kurata 1995). Similar species occur throughout the Indo-West Pacific, with temperature largely controlling their depth distribution.

Mesophotic echinoderms include the large sea star *Astrosarkus idipii* (Figure 5h; Mah 2003) and a considerable variety of other species (Mah 2005). The few ascidians (Chordata) known from

the mesophotic zone in Palau include species not known from other environments.

Fish

Known reef fishes of Palau were described by Myers (1999), but there are still new species and geographic records being

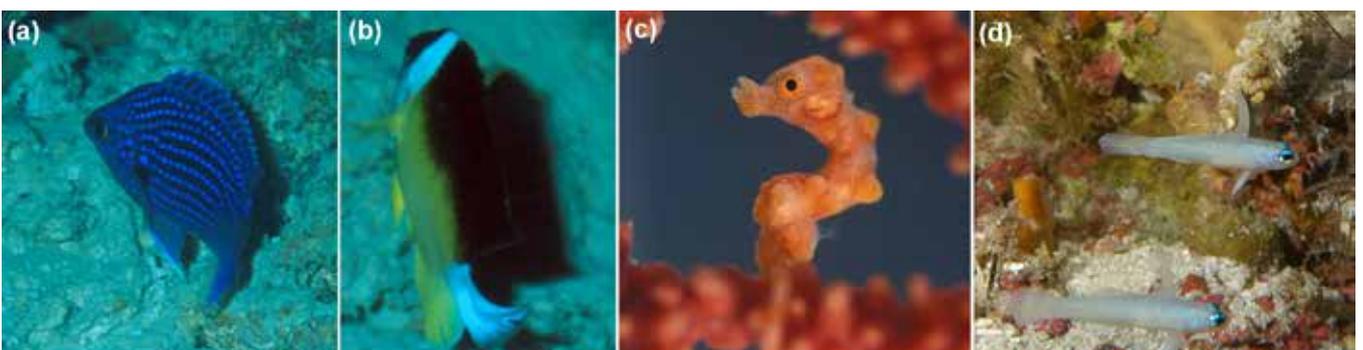


Figure 6. Recently described mesophotic reef fish from Palau. (a) *Chromis abyssus*, (b) *Centropyge abei*, (c) *Hippocampus denise* on the gorgonian *Muricella* spp., and (d) *Glossogobius colini* (photos Patrick L. Colin).

discovered, including in the mesophotic zone (Figure 6). One example is the pygmy angelfish, *Centropyge abei* (Allen et al. 2006)—unknown until direct investigation of the mesophotic was undertaken (Figure 6b). The small seahorse, *Hippocampus denise* (Figure 6c) is known elsewhere from shallow reef habitats, but in Palau is only found in the 35–80 m depth range, where its host gorgonians, *Muricella* spp., occur.

Macroalgae

Little is known about the mesophotic macroalgae from Palau. Green algae that do occur within the mesophotic, are members of the genus *Halimeda* and at least one other flattened species, presently unidentified (Colin 2009). Coralline algae occur at mesophotic depths, but are poorly known. There are no seagrasses below approximately 35 m in depth.

Pharmaceutical discoveries

Palau has been an important site for the collection of samples for drug development research, with well over 100 publications (as of 2004) on its natural marine products (Faulkner et al. 2004). Some chemically interesting samples have come from mesophotic depths (Qureshi et al. 2000, Sandler et al. 2006).

Physical Characteristics

Sloping areas in the mesophotic zone often have alternating cascades of rubble and sediment. Low percentages of stony corals often grow on the stable rubble, but deep slope environments are dominated by gorgonian fans, with some genera limited to deeper depths (Fabricius et al. 2007). The water close to the outer reef faces of Palau is not particularly clear compared with oceanic “warm pool” water, and may limit depths to which low-light scleractinian corals can grow. However, water temperatures may prove to be more significant in limiting the lowest depth of zooxanthellate coral growth.

The horizontal distance between the mesophotic and the shallow reefs is small, usually less than 100 m, but density stratification can restrict water exchange between shallow and deep regions. Stratified oceanic water moving inshore through channels on rising tides can be thoroughly mixed by turbulence, while the water exiting on falling tides remains mixed (Colin 2009).

Palau is in an area of very active internal waves (Wolanski et al. 2004); probably not unusual for tropical Western Pacific reef environments, but underappreciated as a mechanism influencing the ecology of MCEs. Over 15 years, weekly mean shallow reef water temperatures (10–15 m depth) ranged from 27.5° to 30° C, with only a 1–1.5° C annual range (Figure 7). In contrast, MCEs had a greater range, with two types of temporal dynamics. First, medium-term week to month variations in mean temperatures (weekly means at 57 m ranged from 21°–29.5° C) are related to the El Niño Southern Oscillation or other undetermined conditions and are essentially uncoupled from temperatures on shallow reefs. Second, internal waves produce rapid short-term changes (several degrees Celsius in an hour or less; Figure 8), upwelling cool, nutrient-rich waters at times to the benefit of shallow reefs. Combined with medium-term variation, this produces a thermally challenging environment, which is probably a major factor limiting the lower depth of MCEs in Palau.

During La Niña periods, such as in August 2010, the temperature stratification on MCEs ceases to exist, with mesophotic temperatures equalling those of shallow reefs and coral bleaching occurring at all depths (Bruno et al. 2001, Colin 2009). The oceanic water column around Palau can change very rapidly between El Niño and La Niña periods. For instance, the temperature, salinity and chlorophyll fluorescence determined by Spray gliders near the barrier reef in 2010 during El Niño (February) and La Niña (August) periods, only 200 days apart, exhibited tremendous differences (Figure 9). A similar shift almost certainly occurred during the 1997–1998 coral bleaching event. MCEs will have to accommodate these rapid shifts if they are to survive.

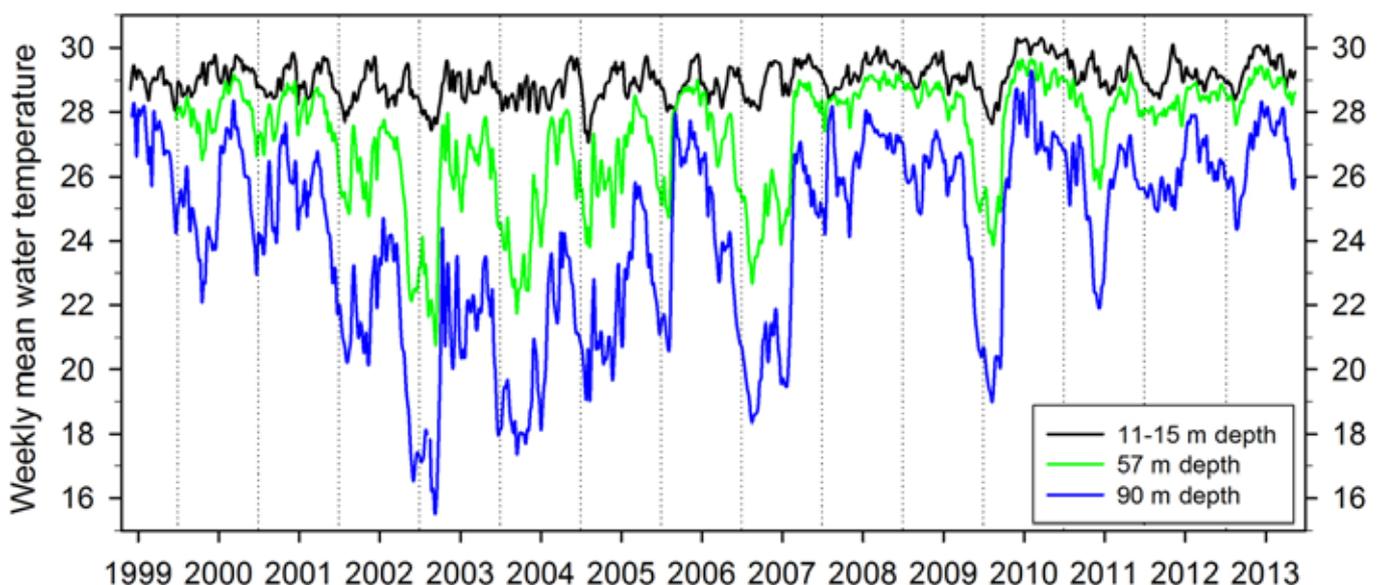


Figure 7. Weekly mean water temperature on the outer slope over 15 years has shown much greater variation in the mesophotic zone (57 and 90 m) than in shallow water (11–15 m).

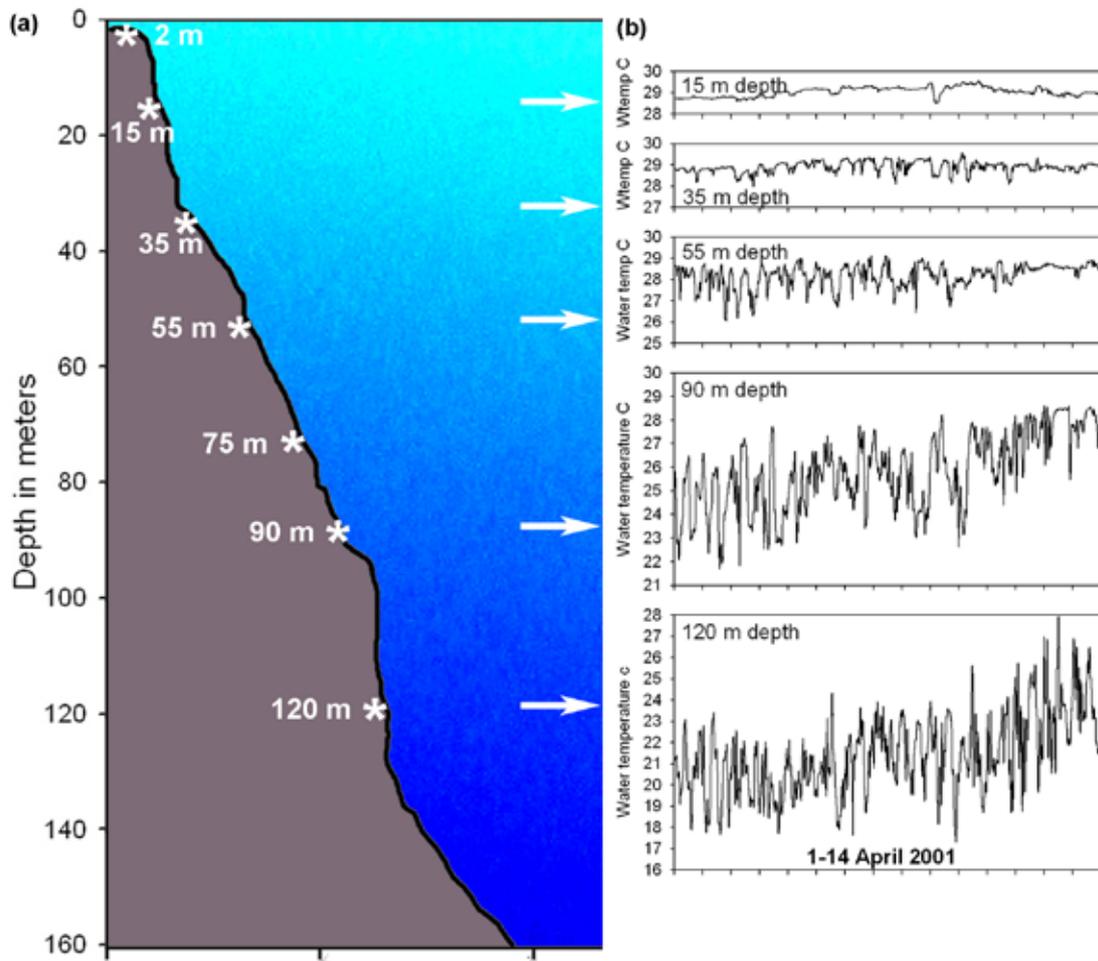


Figure 8. The mesophotic zone in Palau has a large variation in water temperature over short time periods (hours to days) due to internal waves impacting the outer slope. At depths of 50–90 m, the water temperature essentially becomes uncoupled with that of shallow reefs. Internal waves also upwell cool nutrient-rich waters at times (from Colin 2009).

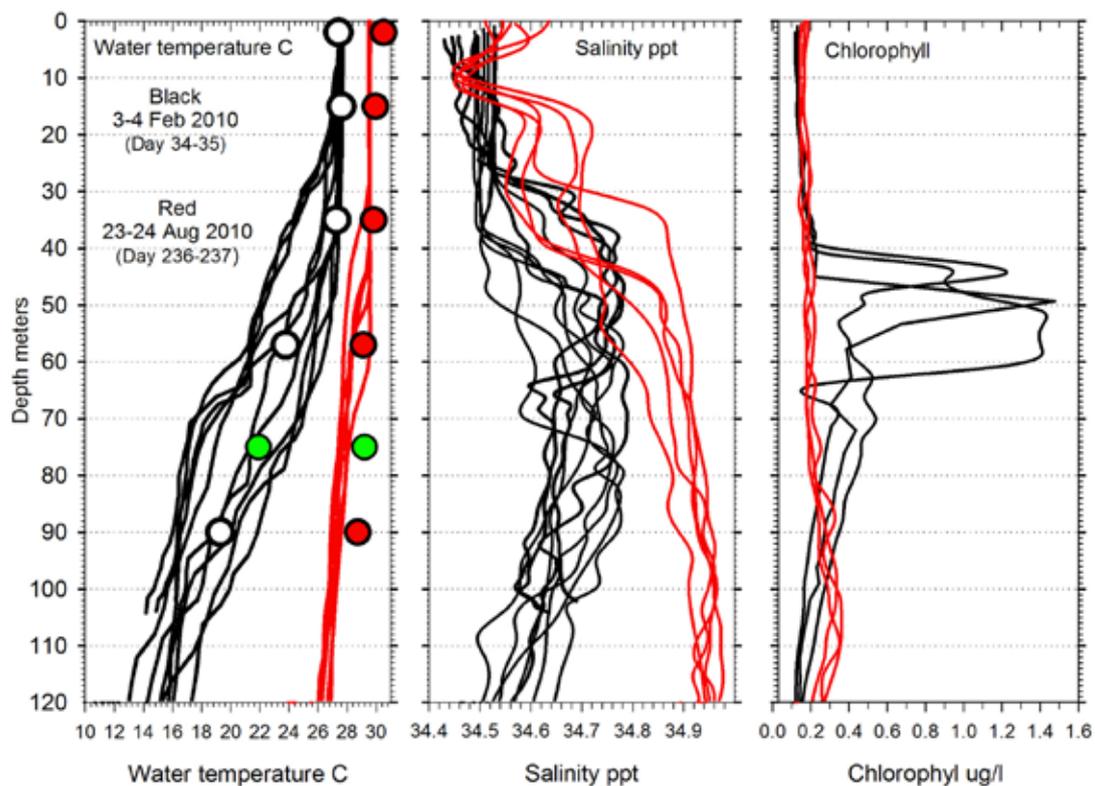


Figure 9. Water column conditions adjacent to the western barrier reef in 2010 determined by Spray gliders during El Niño (February) and La Niña (August) periods (only 200 days apart) were quite different, with a chlorophyll maximum as shallow as 40–50 m during August. (Data courtesy of Dan Rudnick, Scripps Institution of Oceanography).

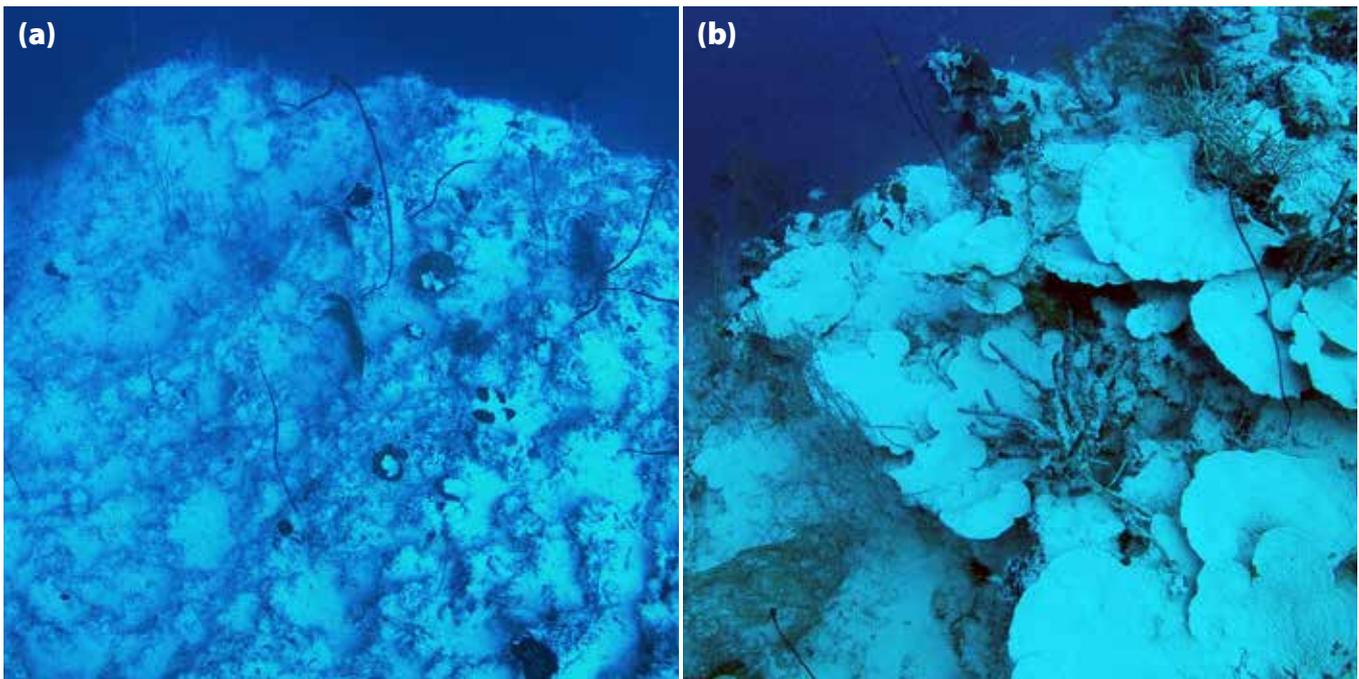


Figure 10. Typhoons can cause coral mortality at mesophotic depths through deposition of sediment suspended by wave action and reef destruction. (a) View downwards from 50 m to 80 m, Short Drop Off, Palau, two months (January 2013) after Typhoon Bopha. (b) Flattened stony corals adapted for light capture at 45 m in depth were smothered by several millimetres of fine sediment suspended by Typhoon Bopha (photos Patrick L. Colin).

It is assumed that there is upwelling of cooler, nutrient-enriched water into the shallow reef environment during El Niño periods, but such dynamics are not documented. Shifts in the “nutricline” over nearly a century (based on cross-sections of large gorgonians from 80 m) have been examined by Williams and Grottoli (2010).

Typhoons and tropical storms

Typhoon and tropical storms have affected Palau’s MCEs in several ways. With steep or vertical slopes, extreme storm

events can generate reef rubble and sediment in shallow water, which moves downslope, causing damage to all benthic communities. Typhoon Bopha in December 2012 caused massive destruction of shallow and mesophotic reefs on the eastern side of Palau. Wave action broke loose reef materials, causing massive debris slides down the slope and producing rubble berms on shallow reefs. In the weeks following the typhoon, suspended sediment was transported to distant areas that had not been impacted directly by waves, where it settled, blanketing reefs and smothering mesophotic corals (Figure 10).

3.7. Gulf of Carpentaria, Australia

Peter T. Harris, GRID-Arendal, Norway

The Gulf of Carpentaria (Figure 1) is known to contain fringing reefs and isolated coral colonies, but no shallow-water patch or barrier reefs (Veron 1993, 2000). This has, however, not always been the case: expeditions carried out in 2003 and 2005 revealed the presence of a new MCE province covering at least 300 km² in the southern Gulf (Harris et al. 2004, 2008). The upper surfaces of the patch reefs are at a mean water depth of 28.6 ± 0.5 m, were undetected by satellites or aerial photographs, and were only recognized using multibeam swath sonar surveys supplemented with seabed sampling and video. Their existence points to an earlier, late Quaternary phase of reef growth under cooler-climate and lower sea level conditions than those of today (Harris et al. 2008).

Submerged bank features identified on nautical charts were selected for detailed multibeam sonar surveys in the Gulf (Reefs R1–R7; Figure 1). They exhibited evidence of coral reef geomorphology. drilling and underwater video surveys have confirmed all seven reefs (R1–R7) to be composed of Holocene and Pleistocene coral limestone, which currently supports varying degrees of live coral (Harris et al. 2004, 2008; Figure 2). The reef complex includes several patch reefs (R1–R3 and R6–R7), as well as a submerged barrier reef (R4–R5) extending westwards from Mornington Island (Figure 1). In tropical northern Australia, west of Torres Strait, geomorphic banks on the continental shelf are estimated to cover 44,290 km² (Heap and Harris 2008), much of which is potentially submerged coral reef habitat.

Underwater video footage showed that generally the Gulf of Carpentaria MCEs could be classified as either: i) predominantly bare limestone substrate with a consistent, scattered coverage of sessile macrofauna, including single soft corals (alcyonaceans), gorgonians, hard plate corals (e.g. *Turbimaria* sp.) and sponges; or ii) dominated by a diverse, complex, coral reef-like coverage of macrofauna, consisting of these same species groups, and often interspersed with small patches of bare substrate. Luxuriant framework coral reef growth of *Acropora* sp., *Turbimaria* sp., and plate, brain and staghorn corals was observed in a few locations (e.g. Reefs R1, R2 and R6; Harris et al. 2008).

Age determinations from coral drill-core samples indicate that reef growth commenced shortly after the Pleistocene pedestals were submerged by rising sea level during the early Holocene (Harris et al. 2008). Coral growth commenced by around 9.9 to 9.5 kyr before present (BP) on all seven of the reefs and persisted for approximately 2,000 years, but had ceased at most locations by circa 8 kyr BP. Based on three measured intervals, reef growth (accretion) rates ranged from 0.95 to 4.0 m kyr⁻¹.

The coral ages and the thickness of Holocene-aged coral limestone deposits encountered in drill cores show that reef growth was widespread in the region during the early Holocene. Underwater video footage indicates that present-day luxuriant framework reef growth is observed only on Reef

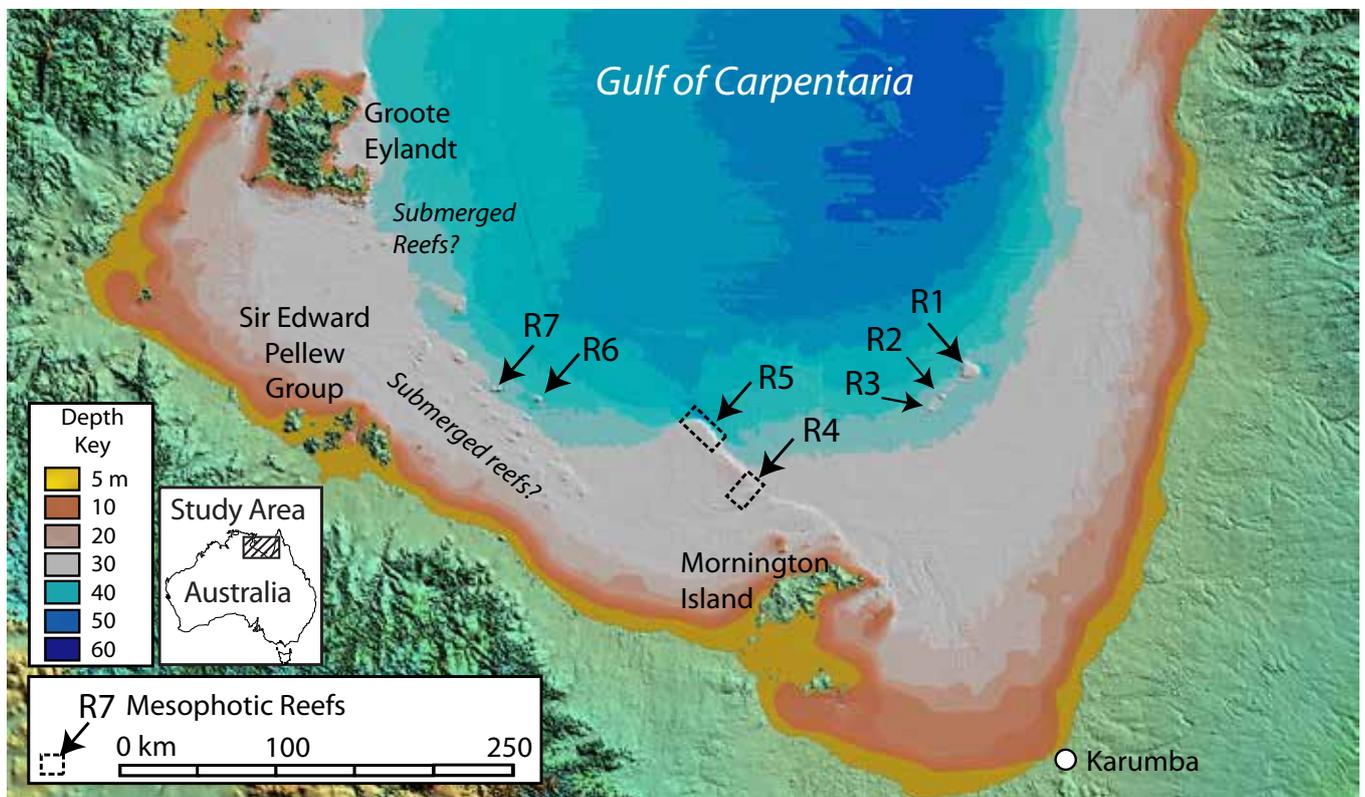


Figure 1. Location map of MCEs in the southern Gulf of Carpentaria, covering over 300 km² (although their full extent is unknown). Locations cited in the text are indicated.

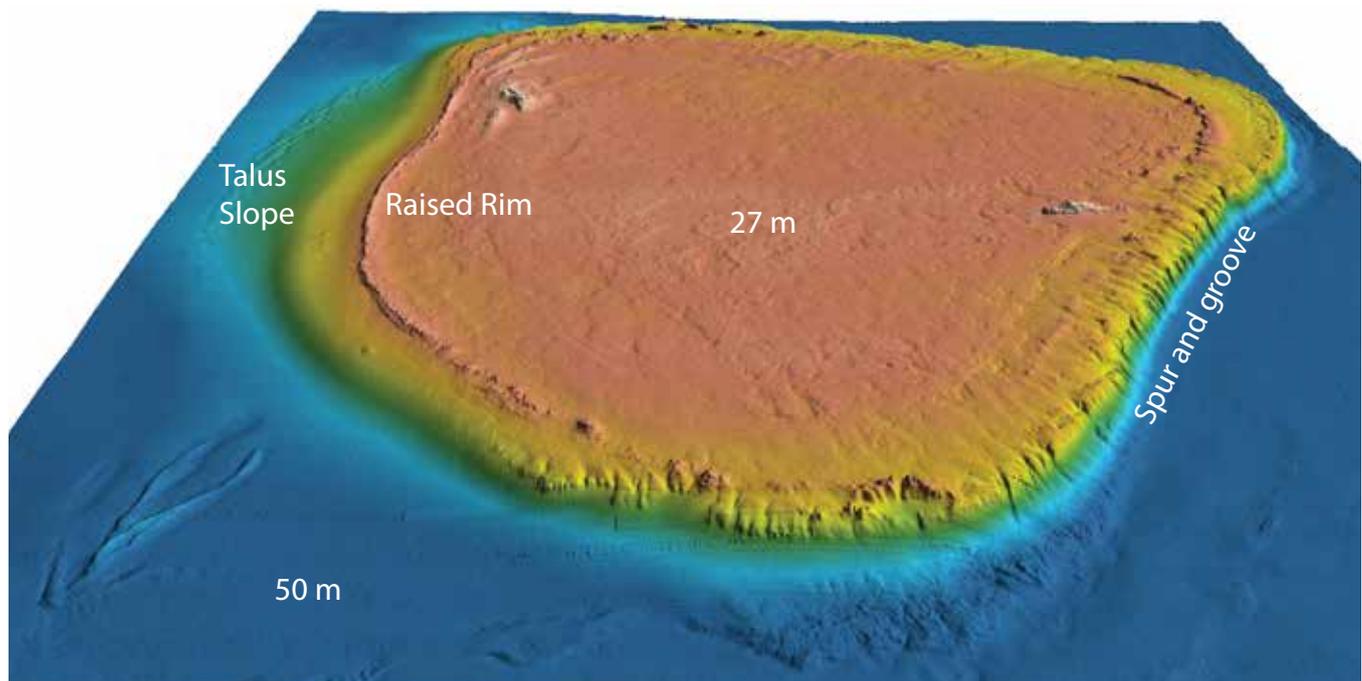


Figure 2. Three-dimensional view of submerged coral reef R1 in the Gulf of Carpentaria. The reef is approximately 10 km wide and covers 72 km². Water depths on the reef platform average 27 m, compared with 50 m in the surrounding areas. The reef exhibits classical reef geomorphology, including a raised rim, flat lagoon and spur and groove edges. A talus slope on the southern edge of the reef is attributed to the transport of cyclone sediment (Harris and Heap 2009).

R1, R3 and R6. Late Holocene reef growth has been measured only on Reef R6, which could indicate that part of this reef has regenerated, while the other reefs have not.

Since circa 8 kyr BP, coral growth has not resulted in the deposition of significant amounts of framework reef limestone, and the reefs have remained submerged 14 to 30 m below present sea level. The relatively thin veneer of Holocene limestone has been bored by benthic animals and the reef limestone has become cemented to form local hard ground deposits. Elsewhere, there is no evidence of any Holocene reef deposition, which implies either local absence of reef growth (non-deposition) and/or erosion. Interestingly, Holocene reef growth was not always located on the reef crests (e.g. Reefs R4 and R5). The typical pattern of growth is initiation on the slightly raised marginal rims and then, soon after, growth within the central platform and crests. The underlying Pleistocene limestone is exposed at the surface at many locations, and hence the morphology of the reefs is mostly relict, and is the product of several episodes of reef growth during the Pleistocene.

A number of factors could have limited regional reef development, including the rate of reef growth relative to sea level rise, water temperature variations, changes in water turbidity, and/or a reduction in larval dispersion due to changes in water circulation (e.g. Montaggioni 2005). Tropical cyclones regularly impact the Gulf of Carpentaria region and substantial talus sediment deposits have accumulated against the down-drift side of the patch reefs (Harris and Heap 2009). Cyclones and their associated sediment transport events (and turbidity) may also limit regional reef growth.

The Gulf of Carpentaria mesophotic reefs R1 to R5 are programmed to receive protection by the Australian government, by being included within a Commonwealth Marine Reserve (Department of Environment 2015). However, until the current review of the marine reserves by the Australian government is completed, the MCEs are not protected. Moreover, the MCEs around the Sir Edward Pellew Group (i.e., Reefs R6 and R7) are not included in the proposed Commonwealth Marine Reserve.

3.8. Hawaiian Archipelago, USA

Samuel E. Kahng, Hawai'i Pacific University, USA

MCEs occur along the entire Hawaiian Archipelago, which consists of high volcanic islands and associated reefs, submerged banks, atolls and seamounts spanning 2,500 km from the Big Island (18.5°N) to Kure Atoll (28°N; Kahng and Maragos 2006, Fletcher et al. 2008, Rooney et al. 2008; Figure 1). This archipelago provides a unique natural laboratory for studying ecological and geological processes associated with coral reefs. Located in the oligotrophic Central North Pacific Ocean, the Hawaiian Archipelago has the most isolated coral reef ecosystem in the world (Grigg 1988). As a result, Hawai'i exhibits relatively low diversity of coral species, but exceptionally high levels of marine endemism, both in terms of the percentage of species and their numerical abundance (Eldredge and Evenhuis 2003, DeMartini and Friedlander 2004, Kerswell 2006, Grigg et al. 2008).

The Hawaiian Islands share a common geological history, having been formed over the Hawaiian hotspot as the Pacific plate moved northwest towards the Aleutian Trench (Grigg 1982, 1988, Fletcher et al. 2008, Rooney et al. 2008). Wide insular island shelves at mesophotic depths surround most of the islands and atolls, providing substantially more potential habitat for MCEs than shallow-water coral reefs (Parrish and Boland 2004, Locker et al. 2010, Rooney et al. 2010). At mesophotic depths, large monospecific aggregations of corals and macroalgae are commonly observed over spatial scales of 10s to 100s of meters (Kahng and Kelley 2007, Kahng et al. 2010, Spalding 2012).

Common massive and branching shallow-water corals (i.e., *Porites*, *Pocillopora* and *Montipora*) dominate the coral

community structure to 50–60 m (Grigg 1983, Kahng and Kelley 2007, Rooney et al. 2010, Franklin et al. 2013). While these shallow-water corals persist to much deeper depths, their dominance on hard substrate appears to be replaced by other megabenthic organisms, including green and red macroalgae (e.g. *Halimeda*, *Ulva*, *Udotea*, *Cladophora*, *Codium*, *Avrainvillea*, *Peyssonnelia* and non-articulated corallines), plate corals (*Leptoseris* and *Pavona*), finely branched or plate-like morphs of the coral *Montipora capitata*, in areas of high current flow (Rooney et al. 2010), antipatharians (*Antipathes*, *Cirripathes*, *Myriopathes*, *Aphanipathes* and *Stichopathes*) and the invasive octocoral *Carijoa* spp. (Adey et al. 1982, Kahng and Grigg 2005, Webster et al. 2006, Spalding 2012, Luck et al. 2013, Wagner 2015).

Below 80 m, live benthic cover attenuates significantly, and obligate phototrophs of *Leptoseris* spp. dominate the coral community (Kahng 2006, Kahng and Kelley 2007, Rooney et al. 2010; Figure 2). Similar vertical zonation has also been recorded within the mesophotic macroalgae and antipatharian communities (Agegian and Abbott 1985, Wagner 2015). The 80–90 m depth range is also associated with a peak in diversity and a change in composition within the macroalgae community in the Main Hawaiian Islands (Spalding 2012).

Some common mesophotic species appear to be depth specialists (i.e., observed only below a given depth). In particular, *Leptoseris hawaiiensis* and two antipatharian species (*Aphanipathes verticillata* and *Stichopathes echinulata*) have been observed only below 80 m (Luck et al. 2013, Pochon et al. 2015, Wagner 2015). Several macroalgae species

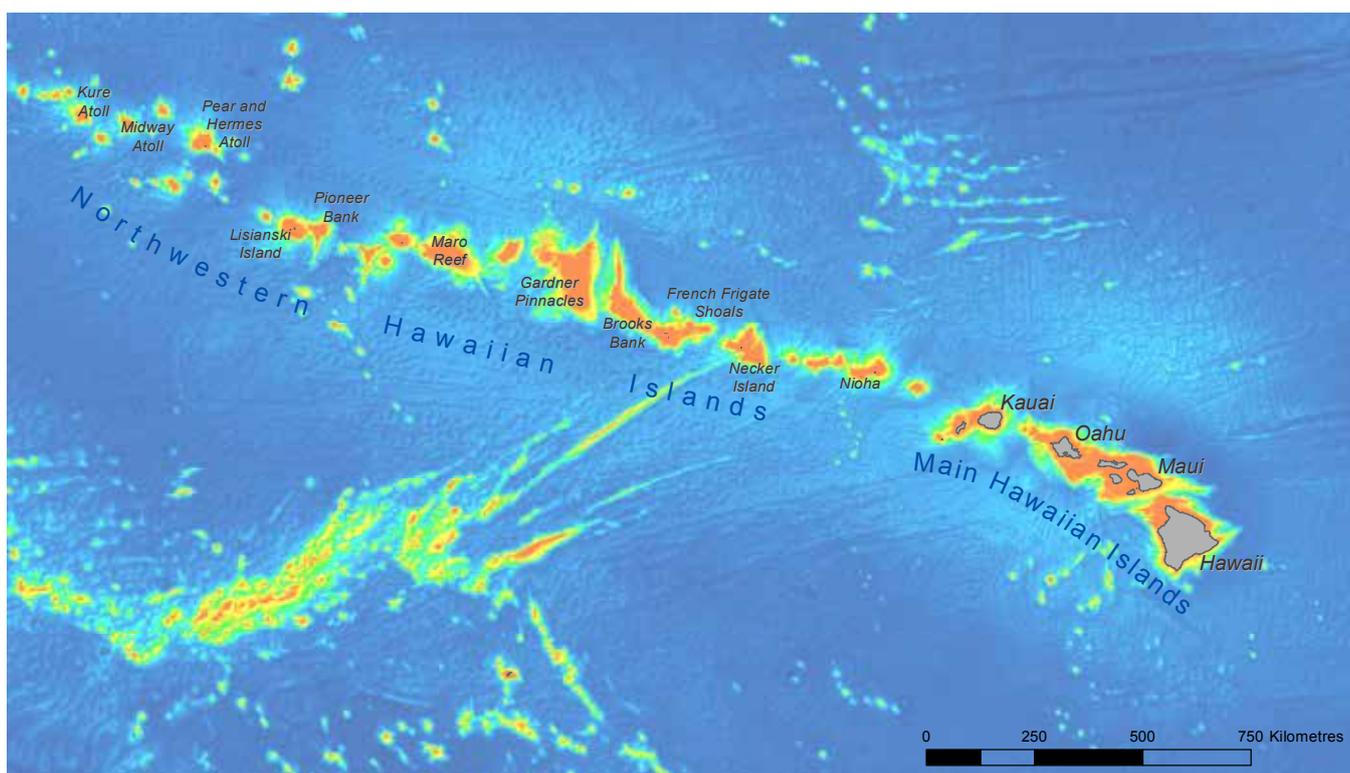


Figure 1. Map of the islands, atolls and submerged banks of the Hawaiian Archipelago.



Figure 2. The coral *Leptoseris* spp. dominates deeper MCEs in the 'Au'au Channel between Maui and Lāna'i in the Main Hawaiian Islands and provides habitat for fish, *Psuedanthias thompsoni* and *Cheato don milliaris* (photo NOAA's Hawai'i Undersea Research Laboratory; see Figure 1 for location).

also appear only below 40 m (Spalding 2012). The benthic organisms that dominate the lower mesophotic appear to be largely distinct from the shallow-water community, and some species exhibit special physiological adaptations (Kahng et al. 2012b, 2014). Based on limited data, growth rates for shallow-water corals (e.g. *Porites lobata*) decline with increasing depth, while growth rates of deep-water specialists (e.g. *Leptoseris hawaiiensis*) in the lower mesophotic appear moderate (Grigg 2006, Kahng 2013). Growth rates of obligate heterotrophic suspension-feeding organisms (e.g. *Antipathes griggi*) at mesophotic depths can be relatively rapid in areas of high current flow (Grigg 1976, Roark et al. 2006).

There are limited published data on mesophotic fish communities in Hawai'i. In general, fewer herbivores are found at mesophotic depths despite the presence of foliose macroalgae (Kosaki et al. 2012), and rates of fish endemism

are two times higher at mesophotic depths in comparison with shallow water (Kane et al. 2014). The majority (84 per cent) of fish species observed below 30 m are also found above 30 m. However, among all shallow and mesophotic species, only 46 per cent occur both shallower than 30 m and deeper than 60 m (Pyle pers. com.). Ecosystem connectivity between Hawai'i's mesophotic and shallow communities has not been studied in depth; however, a recent publication demonstrated that both vertical and horizontal connectivity exists for the endemic damselfish *Chromis verater* between shallow and mesophotic reefs across the archipelago (Tenggardjaja et al. 2014). Regular movement between shallow-water and mesophotic habitats has also been demonstrated for two common foraging predators, the Galapagos shark (*Carcharhinus galapagensis*) and the giant trevally (*Caranx ignobilis*), although a majority of their sustenance comes from shallow-water habitat (Hilting et al. 2013, Papastamatiou et al. 2015).

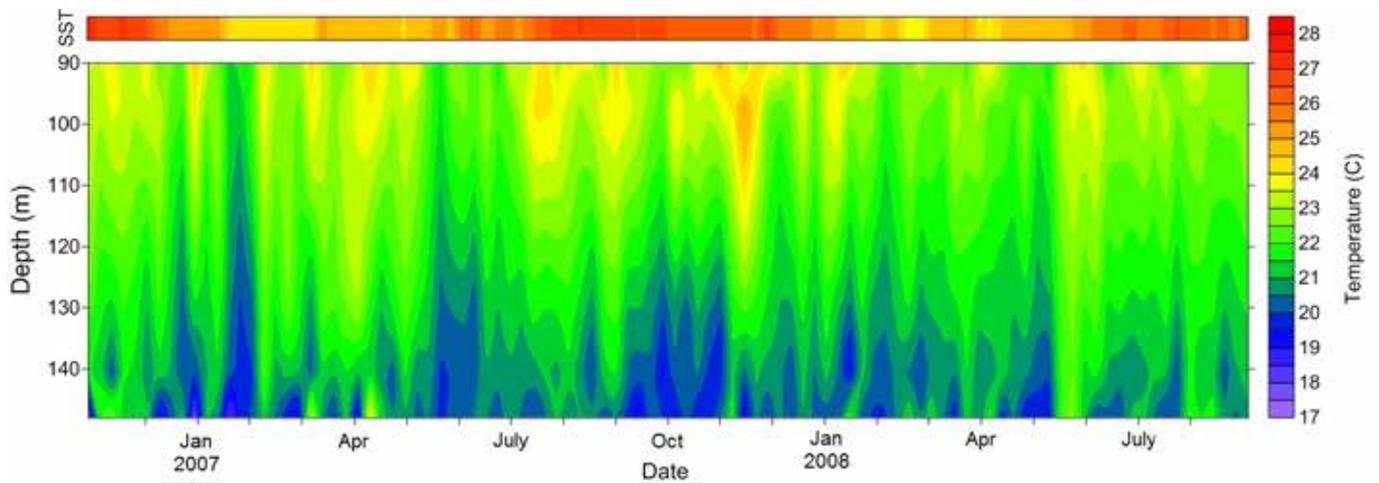


Figure 3. Temperature-depth contour from October 2006 to August 2008 in the 'Au'au Channel, between the islands of Lāna'i and Maui. The top bar represents sea surface temperature over the same time frame. Temperature recorded every 30 min at 90–150 m (reproduced from Kahng et al. 2012a; see Figure 1 for location).

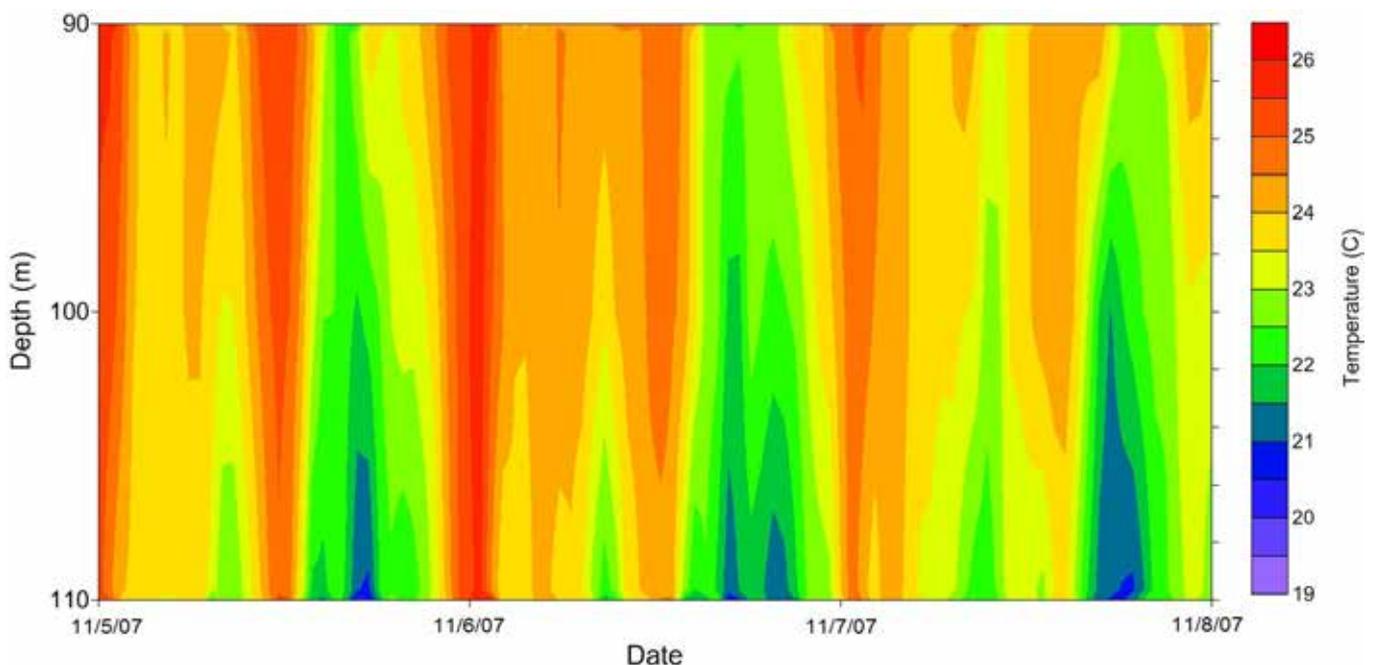


Figure 4. High resolution temperature-depth contour from 5–8 November 2006 in the 'Au'au Channel, between the islands of Lāna'i and Maui. Temperature recorded every 90 seconds at 90–110 m (see Figure 1 for location).

While the attenuation of light and wave stress with increasing depth are factors influencing community structure (reviewed in Kahng et al. 2010), thermal regime at the seafloor also changes significantly with increasing depth. Given Hawai'i's exposure to internal tides, MCEs with southwesterly exposures are subject to semidiurnal oscillations of the thermocline and propagation of internal waves along the insular island shelves (Merrifield et al. 2001, Merrifield and Holloway 2002). High-resolution monitoring of thermal regime from 90–150 m in the 'Au'au Channel, between the islands of Lāna'i and Maui, reveals that the lower mesophotic is decoupled from the predictable seasonality of sea surface temperature (Figure 3) and commonly experiences fluctuations of 5–7 °C within a diel cycle (Figure 4; Kahng et al. 2012a).

Due in part to the optically clear waters in Hawai'i, obligate zooxanthellate corals (e.g. *Leptoseris hawaiiensis* at 153 m)

and benthic macroalgae (e.g. *Cladophora* sp. at 212 m) have been reported from exceptional depths (Kahng and Maragos 2006, Kahng et al. 2012b, Spalding 2012). The maximum depth for zooxanthellate corals appears to occur at progressively shallower depths at higher latitudes along the archipelago (Table 1). Peak abundance of corals also occurs at shallower depths in the Northwestern Hawaiian Islands compared with the Main Hawaiian Islands at the lower latitudes (Rooney et al. 2010). For fishes in the Northwestern Hawaiian Islands, levels of endemism on MCEs appears to increase with latitude (Kane et al. 2014). Given the gradient in thermal regime with latitude along the archipelago (Kahng 2006), the depth limit for warm-water benthic organisms (both phototrophic and heterotrophic) are likely limited by lower temperatures at the northernmost islands (Kahng et al. 2012a). The lower mesophotic habitat at the northern end of the archipelago is almost certainly temperate and not subtropical.

Table 1. Deepest in situ observations of obligate zooxanthellate corals by island (see Figure 1 for location).

Deepest in situ observations of obligate zooxanthellate corals by island.			
Location	Latitude (°N)	Depth (m)	Reference
Hawai'i	19.5	153	Kahng and Maragos 2006
Maui Nui	21.0	131	Kahng and Maragos 2006
O'ahu	21.3	115	Blythe-Skyrme et al. 2013
Ni'ihau-Kaula	21.6	111	pers. obs., HURL P5-571
Kaua'i	21.9	110	pers. obs., HURL P4-223
French Frigate Shoals	23.7	77	Blythe-Skyrme et al. 2013
Pearl & Hermes	27.9	67	Luck et al. 2013
Midway	28.2	66	Luck et al. 2013
Kure	28.4	66	Luck et al. 2013

While MCEs in Hawai'i are subject to the same natural and anthropogenic disturbances as other MCEs (reviewed in Bongaerts et al. 2010a), Hawai'i's evolutionary isolation and low species diversity of shallow-water marine fauna likely increase its susceptibility to non-indigenous invasive species from underrepresented taxa (Stachowicz and Tilman 2005, Kahng 2006). At mesophotic depths in Maui Nui, the invasive octocoral *Carijoa riisei*, which is cryptic in shallow-water, has been reported to be dominating rugose substrate and overgrowing antipatharian and scleractinian fauna (Kahng and Grigg 2005, Kahng 2007). On the island of Oahu, the invasive green alga *Avrainvillea* sp. (first reported in 1981) has been

observed forming vast meadows to depths of 90 m (Peyton 2009, Spalding 2012). At French Frigate Shoals, the bluestripe snapper, *Lutjanus kasmira*, was recorded as the second most abundant fish at 30–90 m (Kane et al. 2014). Introduced to Oahu in 1955, it is prolific in shallow water across the archipelago (Friedlander et al. 2002, Gaither et al. 2013). Therefore, its abundance on mesophotic reefs in the Main Hawaiian Islands is probably significant. These reports demonstrate the potential susceptibility of Hawai'i's MCEs to biological invasions, which have been well documented in shallow-water and terrestrial ecosystems (U.S. Congress OTA 1993, Coles and Eldredge 2002, Eldredge and Carlton 2002, Smith et al. 2002).

3.9. Ryukyu Archipelago, Japan

Frederic Sinniger, University of Ryukyus, Japan

The Ryukyu Archipelago in Japan (Figure 1) hosts a large coral diversity, with species numbers comparable to those found in the Great Barrier Reef (Spalding et al. 2001). This diversity results directly from the influence of the Kuroshio Current, which brings warm tropical water from the Philippines and equatorial Pacific to the archipelago.

In the late 1960s, MCEs were reported in several locations off the Archipelago at depths of 30–102 m (Yamazato 1972). Although only limited samples were obtained and most coral identification relied on in situ visual observations, specimens of *Acropora longicyathus* (as *A. syringodes*), *Porites rus* (as *P. hawaiiensis*), *Dipsastrea speciosa* (formerly *Favia speciosa*), *Goniastrea* sp. and *Pachyseris speciosa* were collected in the

depth zone of 70–100 m. *Leptoseris scabra* and *Leptoseris* spp. were reported between 50 m to 100 m, with *L. scabra* extending no deeper than 70 m.

Recent studies indicate that several MCEs at the upper edge of the mesophotic zone (around 30 m depth) are characterized by high coral cover and the dominance of a single/few species. For example, a community dominated by *Acropora horrida* was found in Kume Island, while *Pachyseris foliosa* was dominant at an MCE in Okinawa Island (Kimura et al. 2011, White et al. 2013).

Low diversity and high cover examples can also be found in other depth ranges. For example, at 45–50 m depth in Amitori

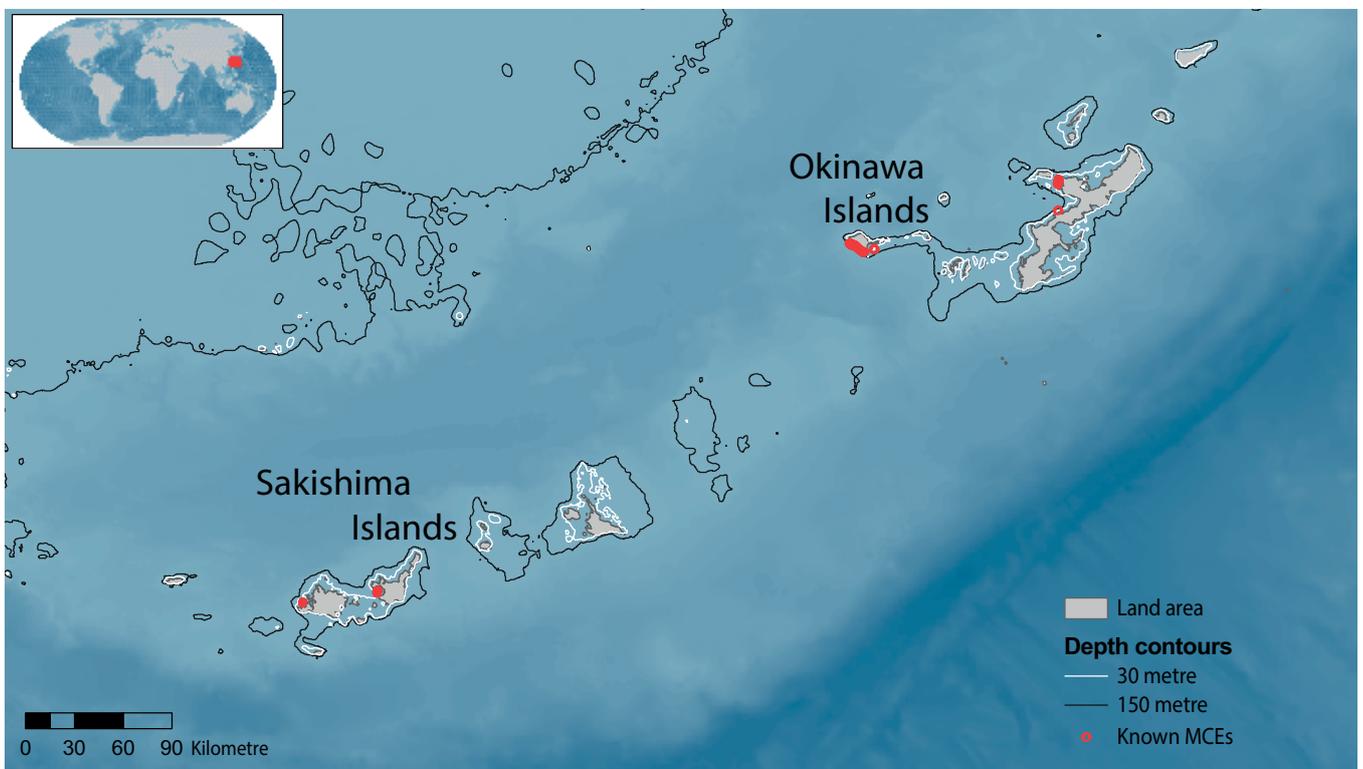


Figure 1. Location of MCEs of the Ryukyu Archipelago, Japan (source GRID-Arendal).

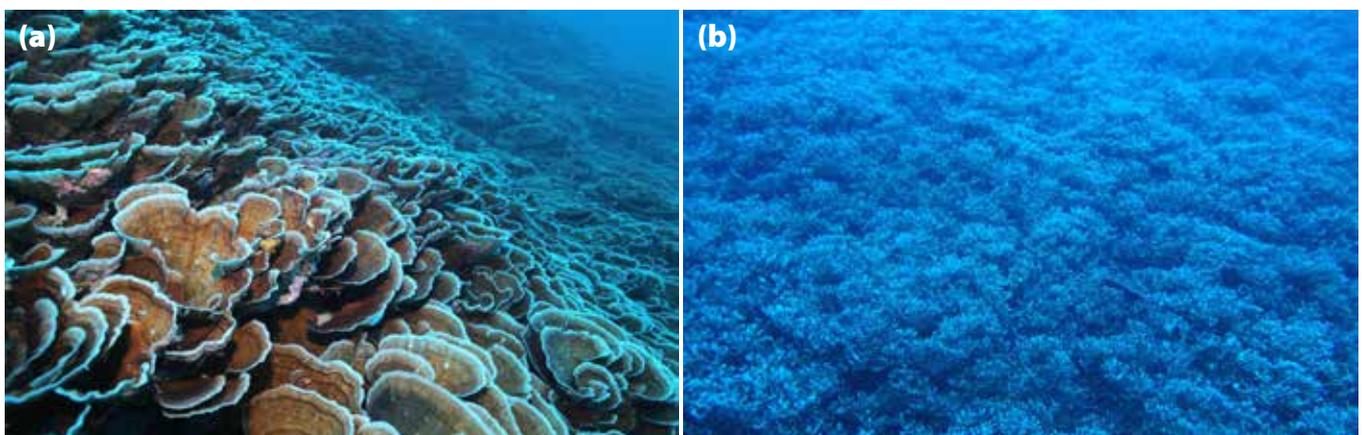


Figure 2. Dominant corals in Amitori Bay, Japan. (a) *Leptoseris amitoriensis* at 48 m (photo Giovanni Casari). (b) *Leptoseris papyracea* at 30 m (photo Frederic Sinniger).

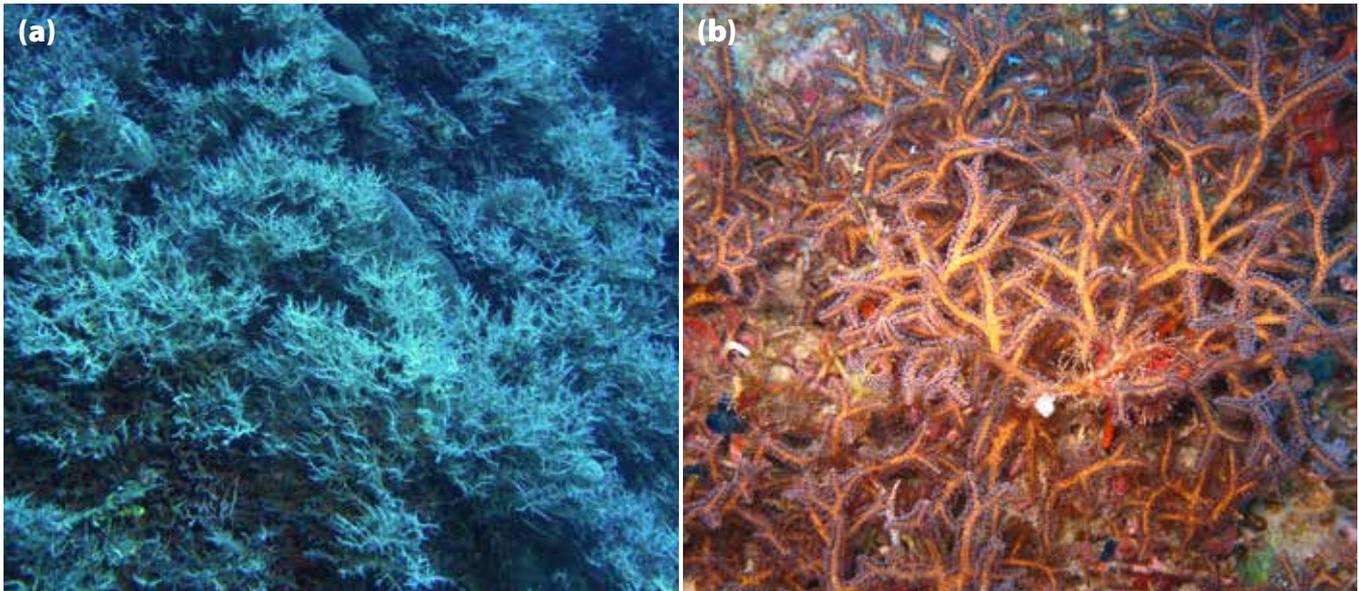


Figure 3. (a) *Seriatopora hystrix* in Amitori Bay, Japan at 30 m. (b) *Seriatopora hystrix* off Okinawa Island, Japan at 45 m (photos Frederic Sinniger).

Bay (Iriomote Island in the southern part of the Ryukyu Archipelago), *Leptoseris amitoriensis* is dominant (Veron 1990, Nishihira and Veron 1995), with only a few other species present (Figure 2a). This community also corresponds to the deepest edge of this MCE, as below 55 m sediment blankets the bottom and no coral communities have been observed. Above the *Leptoseris amitoriensis* stand, the upper edge of the mesophotic zone is dominated by *Leptoseris papyracea* (Figure 2b) and a transition towards *Seriatopora hystrix* and a more diverse shallow coral community (Figure 3a).

The recent discovery of a diverse MCE (Sinniger et al. 2013), dominated by species such as *Acropora tenella*, *Seriatopora hystrix*, *Pachyseris speciosa* and *Porites* sp. (Figure 4), contrasts with other less diverse MCEs described from the area (Kimura et al. 2011, White et al. 2013). This finding

of a deep healthy population of *S. hystrix* (Figure 3b), near a location where this species had disappeared from the shallow reefs following bleaching events (Sinniger et al. 2013), motivated further studies on the similarities between upper mesophotic and shallow reef coral fauna, as well as on the reproductive biology of corals found in local upper MCEs (e.g. Praselia et al. 2015). Although the connectivity between shallow and mesophotic populations of most species remains to be investigated, this finding is a good illustration of the potential of MCEs to serve as refugia in this location (see Chapter 5). Overall, MCEs in the region not only harbour a high diversity of coral species, but also a wide diversity of different ecosystems (i.e., ecosystems dominated by *Leptoseris*, *Acropora*, or *Pachyseris*). However, little is known about the factors influencing the coral diversity of specific MCEs and the distribution of these ecosystems.

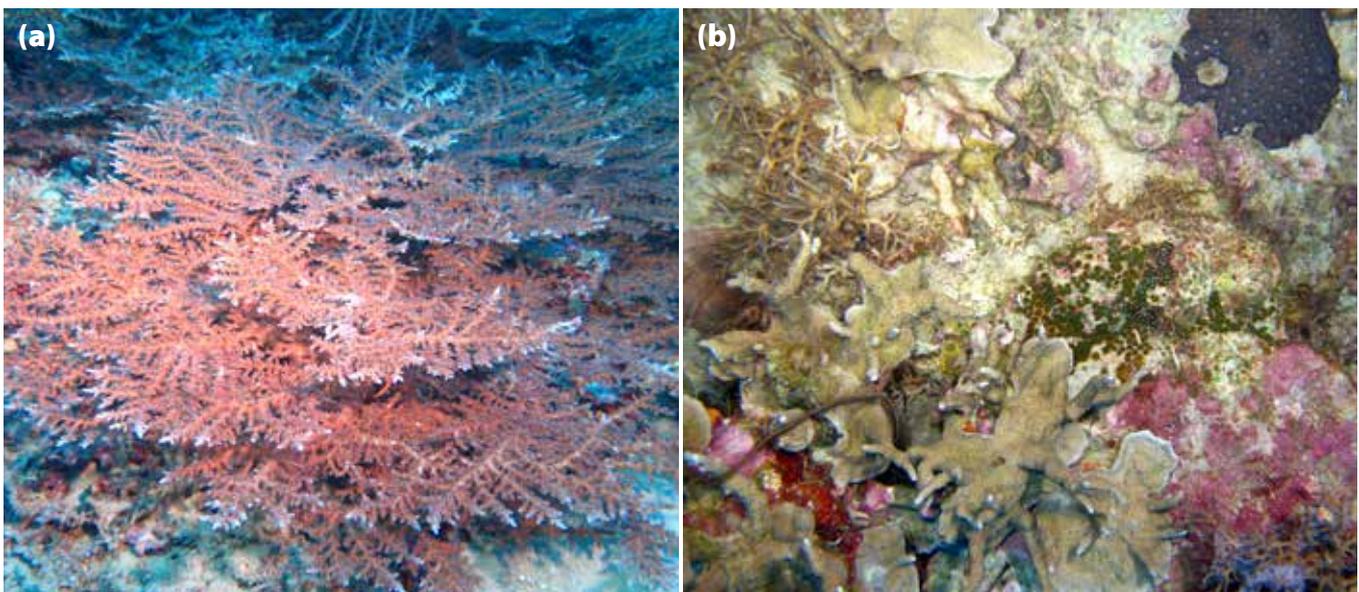


Figure 4. A diverse MCE off Okinawa Island, Japan was recently discovered (Sinniger et al. 2013). (a) *Acropora tenella* at 40 m. (b) *Porites* sp. along with *S. hystrix*, *P. speciosa*, *Dipsastrea* sp. and the zoantharian *Zoanthus sansibaricus* at 40 m (photos Frederic Sinniger).

3.10. La Parguera, Puerto Rico, USA

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David Ballantine, National Museum of Natural History, Smithsonian Institution and University of Puerto Rico at Mayagüez, USA

Ivonne Bejarano, University of Puerto Rico at Mayagüez, USA

Héctor Ruiz, University of Puerto Rico at Mayagüez, USA

Nikolaos Schizas, University of Puerto Rico at Mayagüez, USA

Wilford Schmidt, University of Puerto Rico at Mayagüez, USA

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Studies of the MCEs off La Parguera on the southwest coast of Puerto Rico have been focused along the insular slope, located approximately 10 km offshore (Figure 1). This area is located within the La Parguera Natural Reserve, an area under nominal management by the Puerto Rico Department of Natural and Environmental Resources (Schärer-Umpierre et al. 2014). The insular platform extending to the slope has an average depth of 20 m and supports an extensive development of coral reefs, seagrass beds and mangrove forests. The entire shelf and the shelf edge have karst topography (Morelock et al. 1977). The shelf break occurs at 20–35 m in depth and supports a barrier reef with spur and groove formations through which sand is transported over the shelf edge (Morelock et al. 1977). Deep buttresses are common between 45 and 65 m in depth, and a prominent terrace occurs at approximately 80–90 m. Below 90 m, a steep wall drops precipitously to 160 m (Sherman et al. 2010).

Geomorphology and geological processes strongly influence the distribution and development of MCEs off La Parguera. Along a 20 km stretch off La Parguera, only five sites were found to have well-developed MCEs (Figures 1 and 2). As with shallow coral reefs, sedimentation and bedload transport can restrict reef development. At mesophotic depths, sedimentation is generally low, but bedload transport down steep slopes plays a significant role, limiting extensive coral development to areas of topographic highs, where benthic organisms can settle and survive. Off La Parguera, southeast-facing slopes were exposed to direct wave impacts during past sea level rise. They consequently have a shallower slope and are less rugose. In contrast, southwest-facing slopes are steeper and have greater rugosity, which helps channel sediment away from coral outcrops. For this reason, well-developed MCEs off La Parguera were found only on southwest-facing slopes (Figure 1).

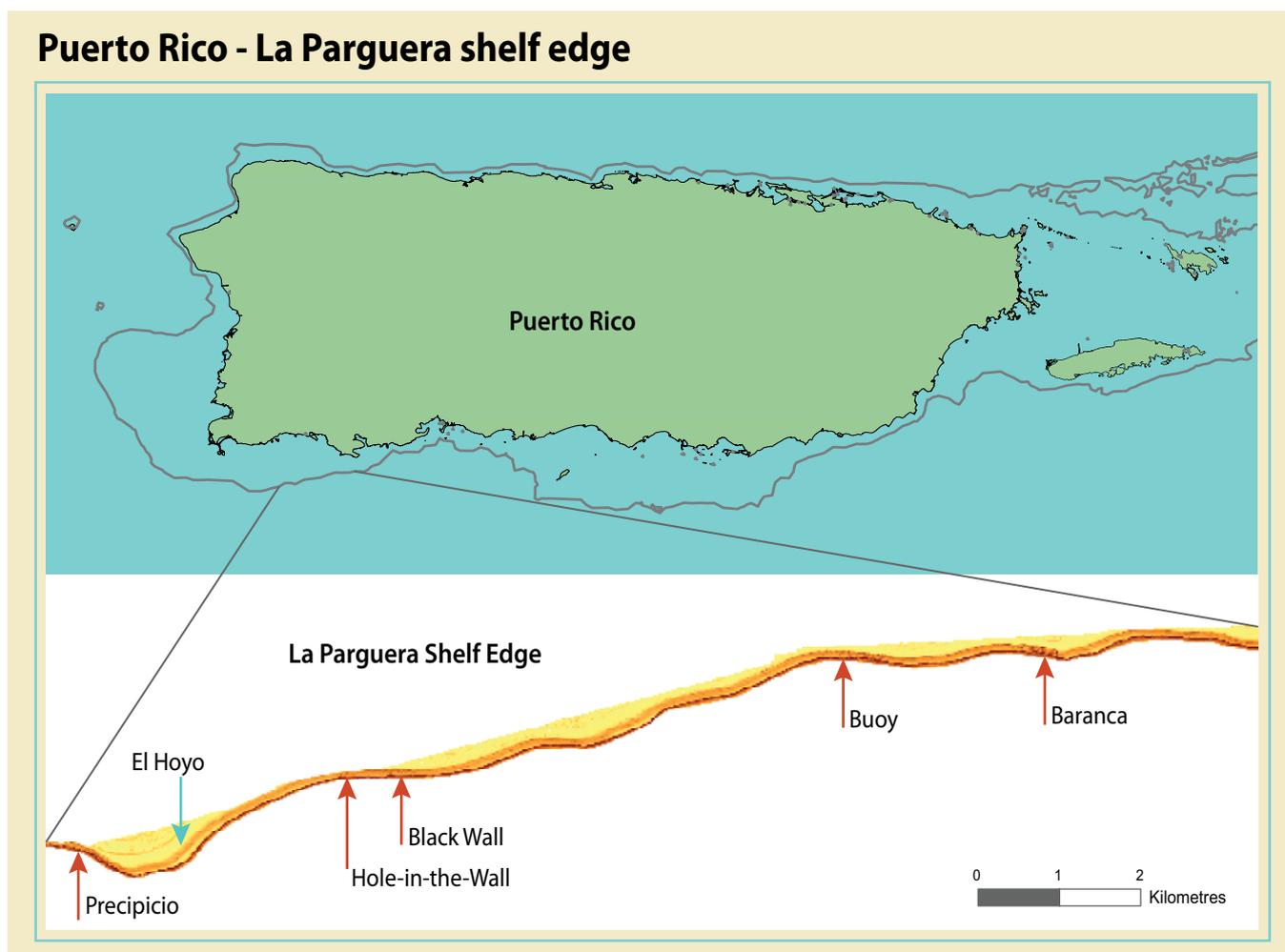


Figure 1. Shelf edge and upper insular slope off La Parguera, Puerto Rico. Red arrows show those sites containing well-developed MCEs. Primary study sites were Hole-in-the-Wall, a southwest-facing slope, and El Hoyo (blue arrow), a southeast-facing slope (sources Richard S. Appeldoorn and Clark Sherman http://www.noaanews.noaa.gov/stories2011/20110104_corals.html).

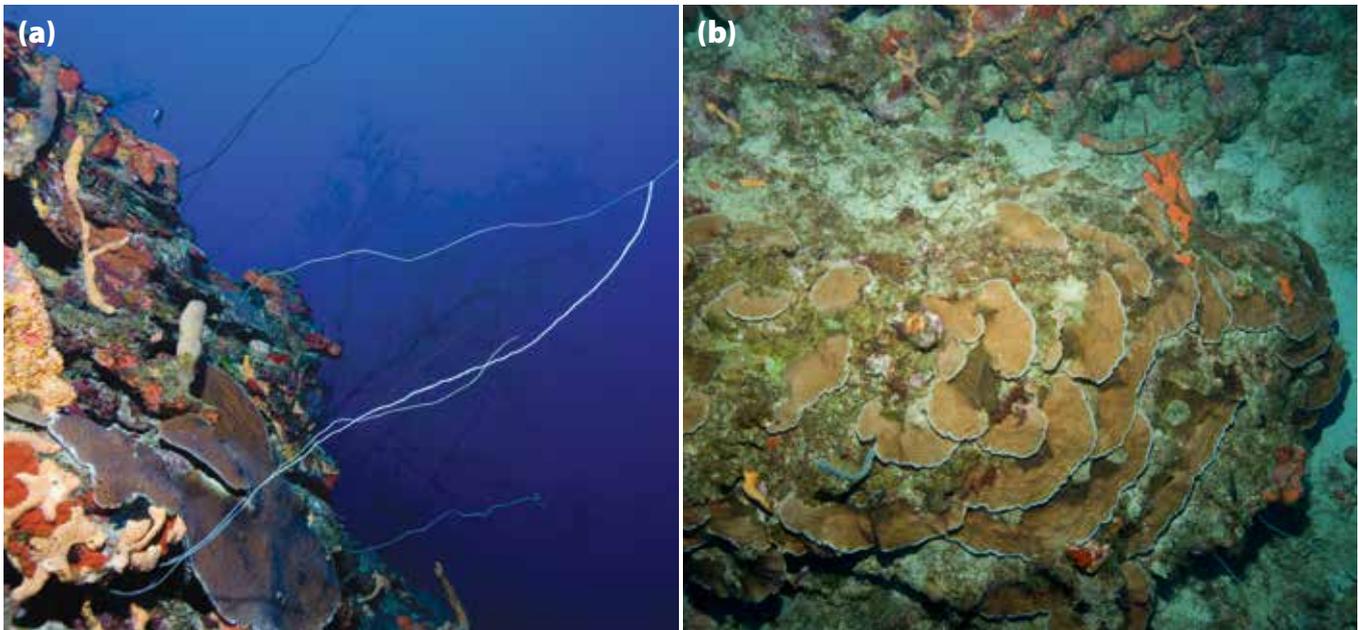


Figure 2. Well-developed MCEs off of La Parguera. (a) Mixed community atop a deep buttress at 45 m. (b) Large colony of *Undaria agaricites* (photos Héctor Ruiz).

MCEs off La Parguera are exposed to a highly energetic thermocline and high-amplitude incident internal waves. At 40 m, temperatures track seasonal surface temperatures, varying between 26 and 29.8° C. Exceptions occur during the passage of particularly large amplitude internal waves. In one instance, a series of internal waves resulted in rapid temperature drops at 40 m of up to 3° C as the peak of the wave passed over the station. In contrast, at 80 m, temperatures are almost always lower than surface temperatures, particularly during the summer. During autumn and winter, however, internal wave troughs can reach as deep as 80 m.

Both fish and benthic communities within MCEs are biologically diverse. Benthic cover is typically dominated by a diverse algal community, while sponges, scleractinian corals, black corals and gorgonians provide larger scale benthic structure. At 50–60 m, macroalgae comprise 55–60 per cent cover (Sherman et al. 2010). Among the macroalgae, coralline red algae and Peyssonneliaceae generally provide the most abundant cover. Corals and sponges only comprise about 6 per cent and 16 per cent cover, respectively. However, at 70 m, total algal cover is only 38 per cent (8 per cent non-calcareous algae), but corals increase to 27 per cent cover, with little change among sponges. In key locations, coral cover can be extensive, due to large agariciid colonies (Figure 2b), which are the dominant mesophotic corals off La Parguera.

MCEs are unique communities and there is a clear shift in species composition for both benthic organisms and fish with depth. For algal species, there is a fairly high similarity in species composition between 30 and 50 m (68 per cent). The species similarity between 30 and 70 m falls to 54 per cent, i.e., roughly half of the species are cosmopolitan at these depths. Some 20 species of red and green macroalgae are essentially restricted to the mesophotic realm, whereas no brown macroalgal species occurring within southwest Puerto Rico were observed to be depth restricted.

The composition of coral, octocoral and sponge species from 20 to 80 m changes as a function of depth. Shallower areas (shelf edge) are dominated by the coral family Faviidae (*Orbicella* species complex, *Colpophyllia* spp. and *Diploria* spp.), and the deeper communities by Agariciidae and *Madracis* spp. A total of 21 zooxanthellate scleractinian coral species were observed in mesophotic habitats, plus two azooxanthellate coral species (*Rhizosmilia maculata* and *Astrangia solitaria*) and two hydrocorals (*Millepora alcicornis* and *Stylaster roseus*). All but five coral species (*Agaricia undata*, *A. grahamae*, *Leptoseris caillieti*, *A. fragilis* and *Mycetophyllia reesi*) are common shallow-water dwellers. Coral diversity gradually drops with depth — from 45 species at the shelf break to 24 species at mesophotic depths. Of the species found at mesophotic depths (see Figure 3 for examples), species richness peaks between 40 and 60 m.

Mesophotic coral communities at depths greater than 50 m in La Parguera are not well-connected to shallow coral communities, as many shallow coral species decrease in abundance or are absent at these depths (Table 1). The major shallow reef-building corals, such as *Acropora* and *O. annularis* and *O. faveolata*, are not found at depths of 50 m or greater; *Montastraea cavernosa* does occur at depths greater than 80 m, but as small isolated colonies. In general, the coral community at 50 m or deeper is very distinct, particularly so for the dominant species, which are platy corals of the genera *Agaricia* and *Undaria*. For the shallow species present at mesophotic depths, their generally small size and scattered distribution further reduces the probability of spawning and fertilization (in non-brooders). Furthermore, genetic evidence based on the distribution of zooxanthallae clades (the photosynthetic algae associated with scleractinian corals) show distinct separation between corals from shallow and mesophotic depths (Schizas unpubl.).

There is a rapid decrease in the proportion of shallow fish species present with depth (Bejarano et al. 2014). Most of these species disappear at or above 60 m. Table 2 lists the top

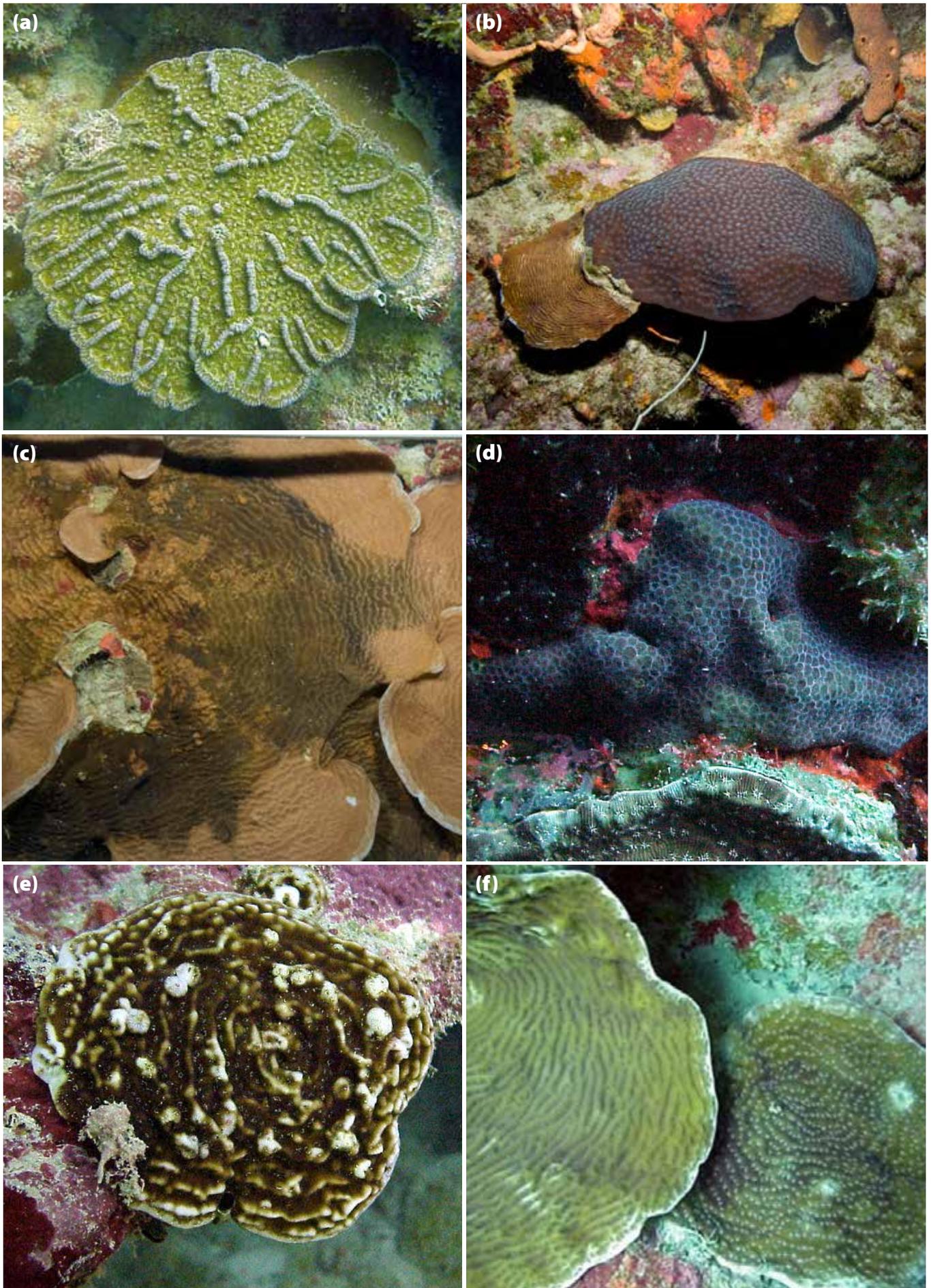


Figure 3. Coral species characteristic of mesophotic depths, especially ≥ 50 m off La Parguera, Puerto Rico. (a) *Mycetophyllia aliciae* (photo Ernesto Weil), (b) *M. reesi*, (c) *Agaricia undata*, (d) *Madracis pharensis*, (e) *A. fragilis* and (f) *A. grahamae*, left colony and *A. lamarcki*, right colony (photos Héctor Ruiz).

Table 1. Zooxanthellate scleractinian coral species observed below 50 m off La Parguera Puerto Rico.

Zooxanthellate scleractinian coral species observed below 50 metres - off La Parguera, Puerto Rico			
Agaricia lamarcki - Whitestar sheet coral	Undaria agaricites - Lettuce coral	Stephanocoenia intersepta - Blushing star coral	Scolymia cubensis - Artichoke coral
Agaricia undata* - Scroll plate coral	Leptoseris caillieti* - Deep thin lettuce coral	Siderastrea siderea - Massive starlet coral	Eusmilia fastigiata - Smooth flower coral
Agaricia grahamae* - Dimpled sheet coral	Orbicella franksi - Boulder star coral	Porites astreoides - Mustard hill coral	Dichocoenia stockesii - Elliptical star coral
Agaricia fragilis* - Fragile saucer coral	Montastraea cavernosa - Great star coral	Mycetophyllia aliciae - Knobby cactus coral	Mycetophyllia reesi* - Ridgeless cactus coral
Undaria humilis - Low relief lettuce coral	Madracis pharensis[#] - Star coral	* not common above 50 metres [#] both zooxanthellae and azooxanthellae forms	

Table 2. Rank of top four fish species occurring at mesophotic depths off La Parguera, Puerto Rico (Data from Bejarano et al. 2014).

Rank of top four fish in four depth zones		Depth in metres			
Species	Common name	40	50	60	70
<i>Coryphopterus personatus</i>	Masked goby	1	1	1	2
<i>Clepticus parrae</i>	Creole wrasse	2			
<i>Stegastes partitus</i>	Bicolor damselfish	3			
<i>Chromis insolata</i>	Sunshine fish	4	2	2	1
<i>Halichoeres garnoti</i>	Yellowhead wrasse		3	3	3.5
<i>Chromis cyanea</i>	Blue chromis		4		
<i>Serranus tortugarum</i>	Chalk bass			4	
<i>Chromis scotti</i>	Purple reef fish				3.5

species observed from 40 to 70 m. The most common and abundant species found only below 40 m is the sunshine fish, *Chromis insolata*, representing on average 23 per cent of the individuals within transects. Additional common species are *Liopropoma mowbrayi* (cave basslet), *Lutjanus buccanella* (blackfin snapper), *Prognathodes aculeatus* (longsnout butterflyfish) and *Sparisoma atomarium* (greenblotch

parrotfish). *Xanthichthys ringens* (sargassum triggerfish) is also common down to 60 m.

At 50 m or deeper, fish assemblages are dominated (in terms of density) by planktivores; dominance which progressively increases with depth. While constituting only 18 per cent of fish species, zooplanktivores make up over 80 per cent

of all fish in abundance. This is in contrast with shallower reefs, where zooplanktivores represent only 18 per cent of all fish. Herbivores are scarce at depths ≥ 50 m, reaching the upper but not the deeper portion of these ecosystems. In addition, the composition of piscivores changes from medium-sized species in shallow water to large species in deeper waters. Fish communities at mesophotic depths have a more complete trophic structure, with several large predators, such as black grouper (*Mycteroperca bonaci*), Cuba snappers (*Lutjanus cyanopterus*), dog snappers (*L. jocu*) and Caribbean reef sharks (*Carcharhinus perezii*) frequently observed, which are now rare at shallower depths. Deep MCEs also serve as important habitats for these and other protected species (Figure 6).

In contrast to corals, fish communities within MCEs ≥ 50 m are well-connected to shallow coral ecosystems. While fish

also show distinct differences in community structure with depth, there is substantial overlap, with 78 out of 85 species in MCEs found at both shallow (≤ 30 m) and mesophotic (≥ 40 m) depths. The most common connectivity pattern for fish (21 species) between shallow and mesophotic depths, including most commercially-important species (e.g. surgeonfish, parrotfish, snappers, groupers, grunts and barracuda) is through ontogenetic migration from nursery areas in shallow habitats, such as seagrass, mangroves, reefs and rocky shorelines.

Phototransects show that there is low disease prevalence at the community level (the mean is 6 per cent). However, in a one-year period, colonies of *A. undata* and *A. lamarcki* have shown signs of white syndrome (a coral disease resulting in rapid loss of tissue biomass, caused by an unknown pathogen) and permanent tissue mortality (see Chapter 4).

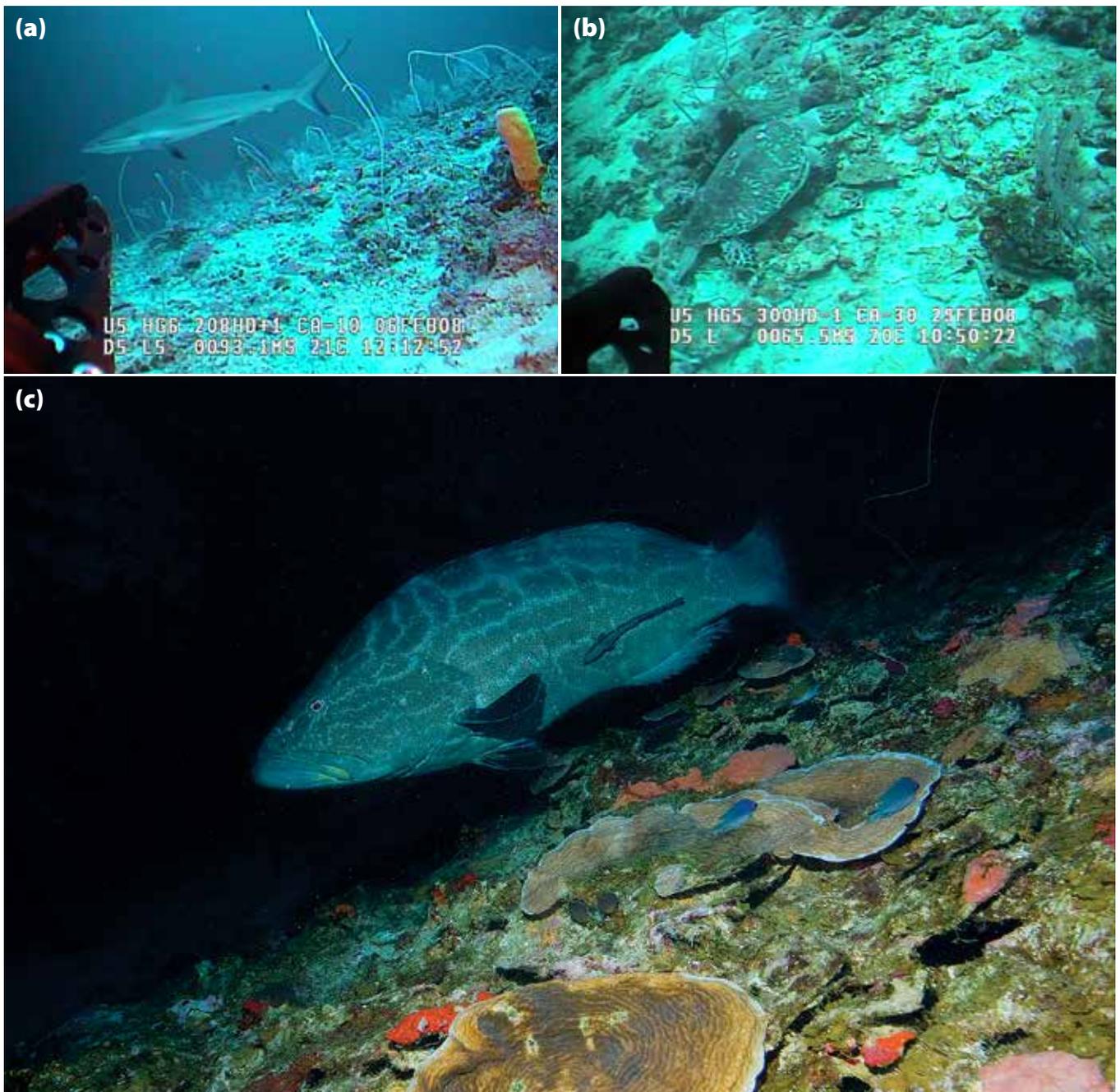


Figure 4sclerictinian. (a) Caribbean reef shark (photo Francisco Pagán), (b) hawksbill turtle (photo Francisco Pagán) and (c) black grouper observed at depths greater than 50 m (photo Héctor Ruiz).

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

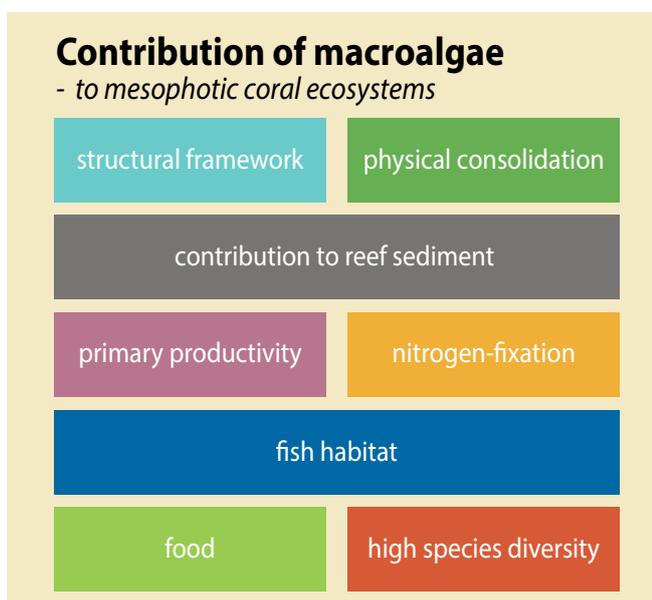


Figure 4.2. Contribution of macroalgae to MCEs.



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

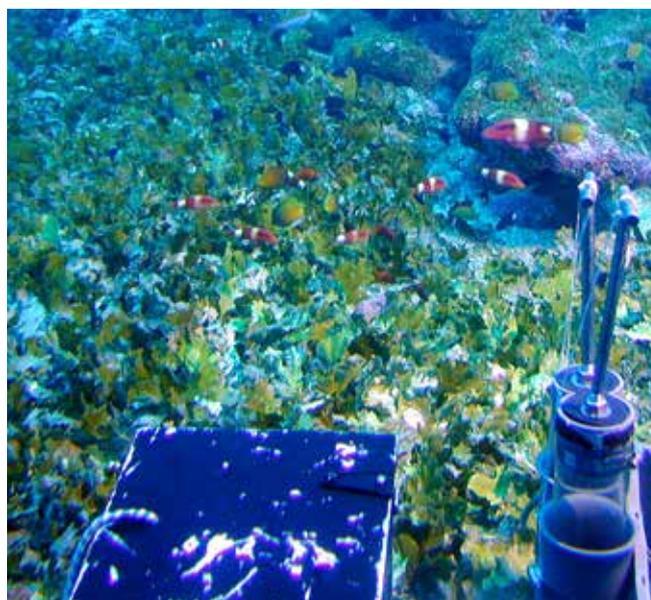


Figure 4.4. Foliose (leafy) algal beds are a common component of mesophotic assemblages in Hawai'i, USA. Dense beds of the green, sand-dwelling alga *Udotea* sp. surrounding a carbonate outcropping with pink crustose coralline and turf algae at 50 m off south O'ahu (photo NOAA's Hawai'i Undersea Research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

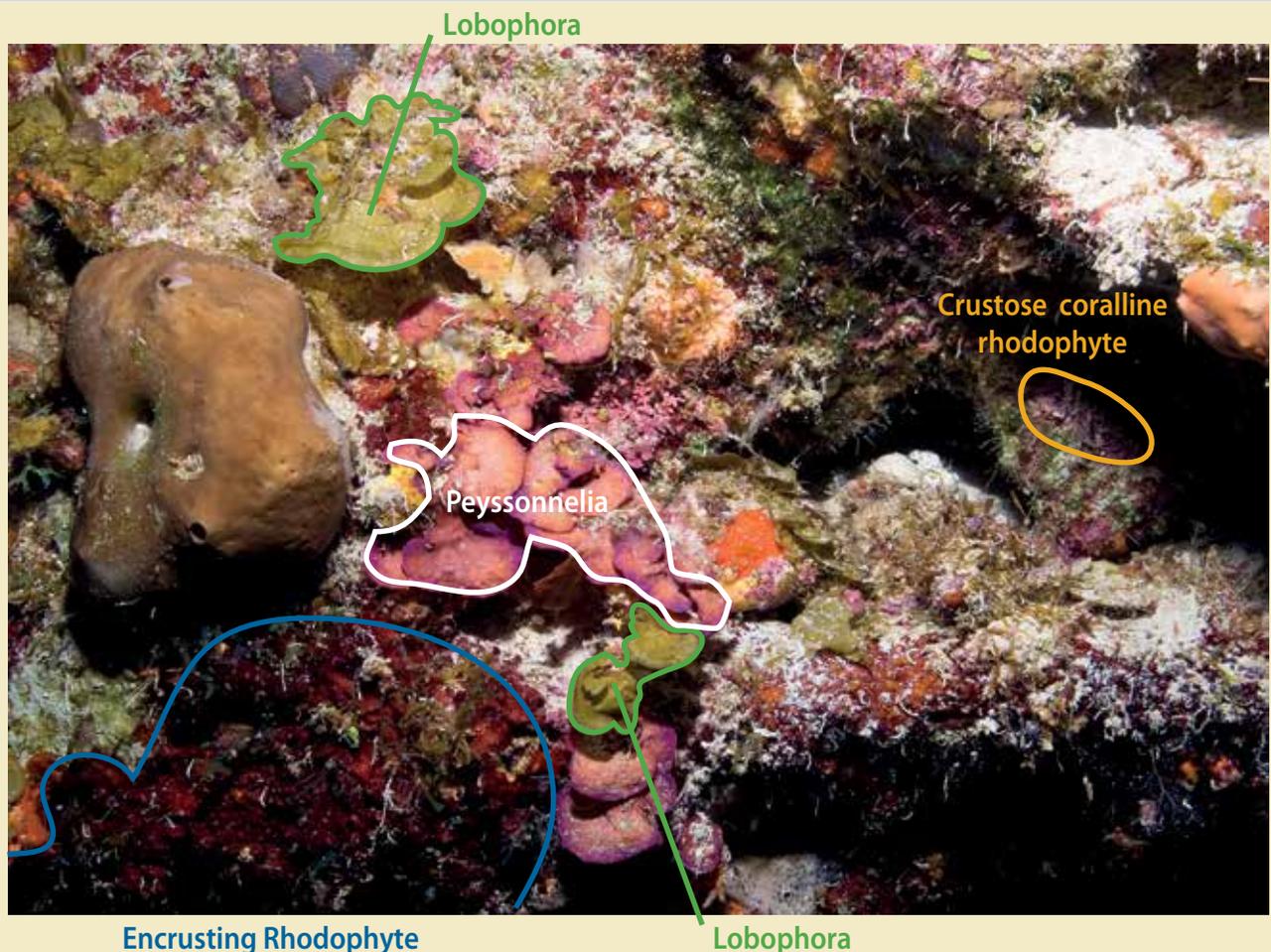


Figure 4.5. Algal dominated shelf-edge wall (65 m, La Parguera, Puerto Rico). Dominant macroalgae include: *Lobophora variegata*, *Peyssonnelia iridescens*, undescribed non-calcified encrusting rhodophyte and crustose coralline rhodophyte (photo Héctor Ruiz).

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

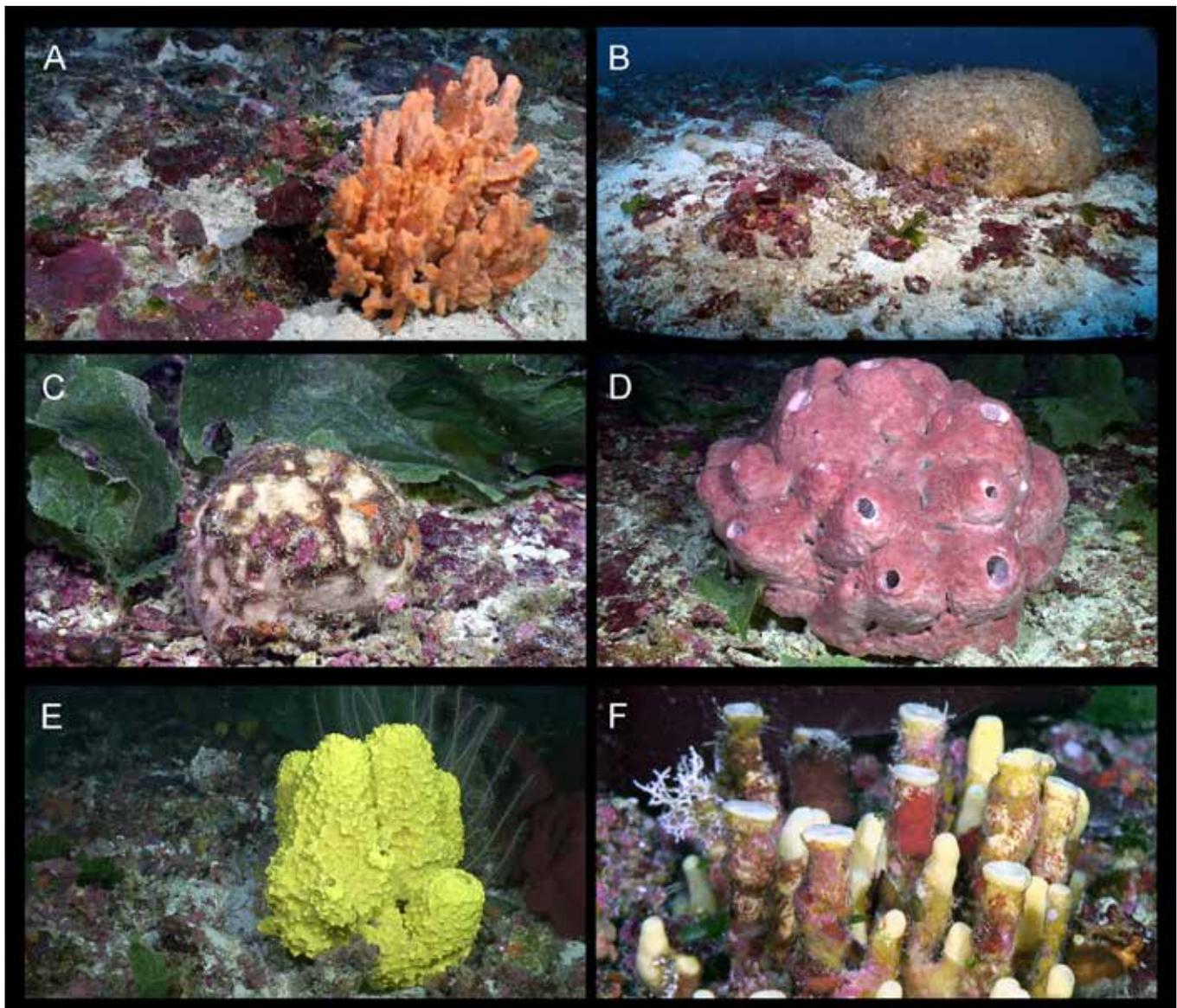


Figure 4.6. Sponges of Pulley Ridge off the southwest Florida shelf. Pulley Ridge is the deepest known light-dependent coral reef ecosystem off the continental United States at depths of 60–90 m. More than 100 distinct sponge “taxa” were photographed at Pulley Ridge. (a) Axinellidae, (b) *Spongisorites 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

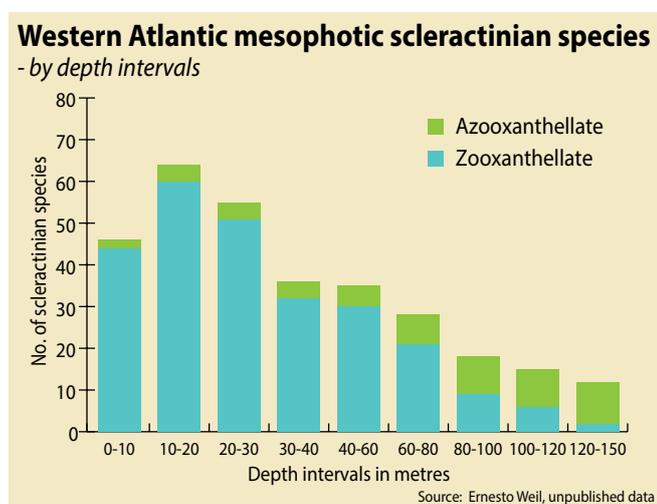


Figure 4.8. Relationship between the number of scleractinian coral species with and without zooxanthellae from shallow reefs to 150 m in the western Atlantic (Weil unpublished).

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

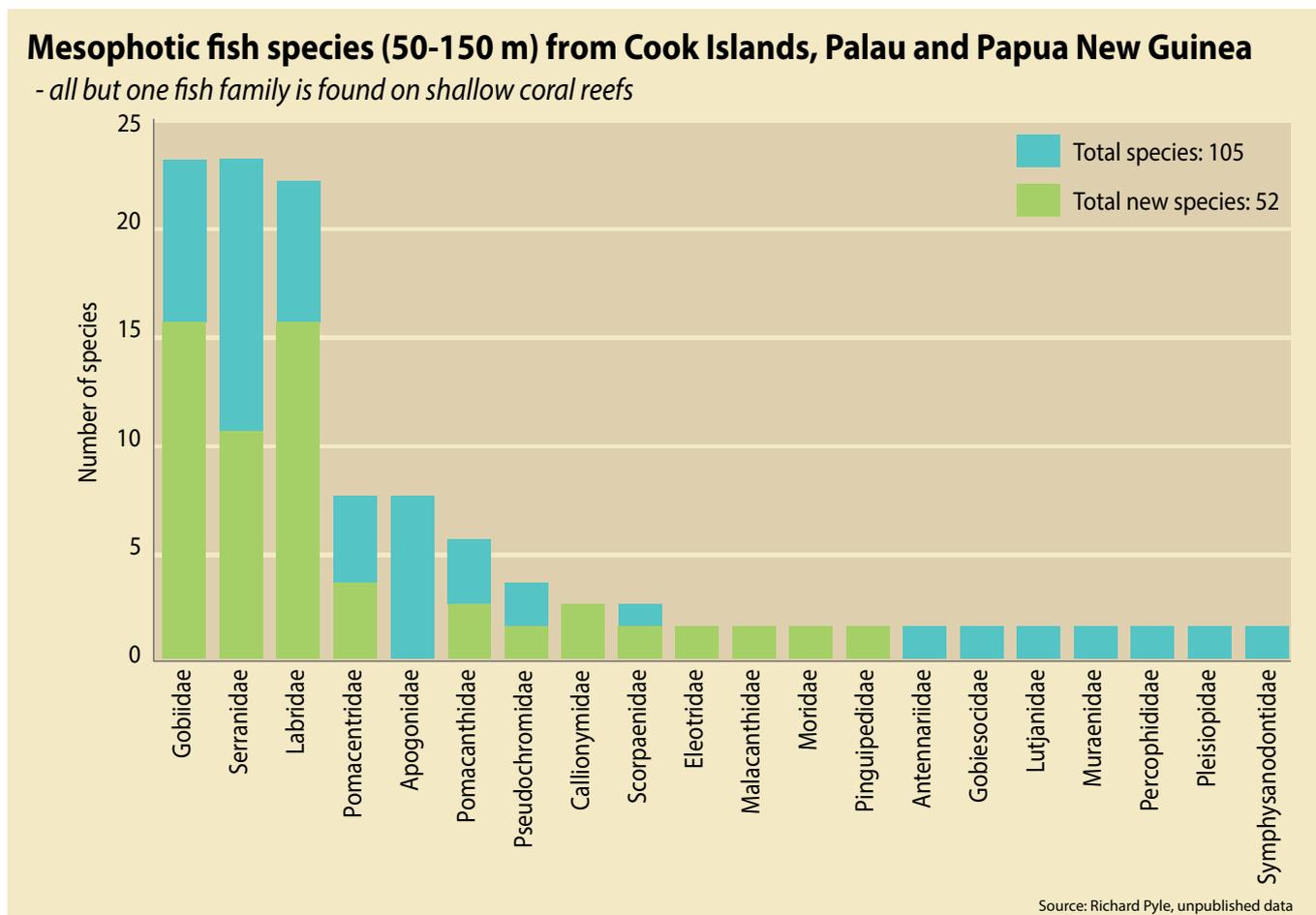


Figure 4.10. Total numbers of fish species within each family collected at depths of 50–150 m in the Cook Islands, Palau and Papua New Guinea, showing proportional numbers of new species. All but *Symphysanodontidae* (one specimen) are families characteristic of shallow coral reefs.

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

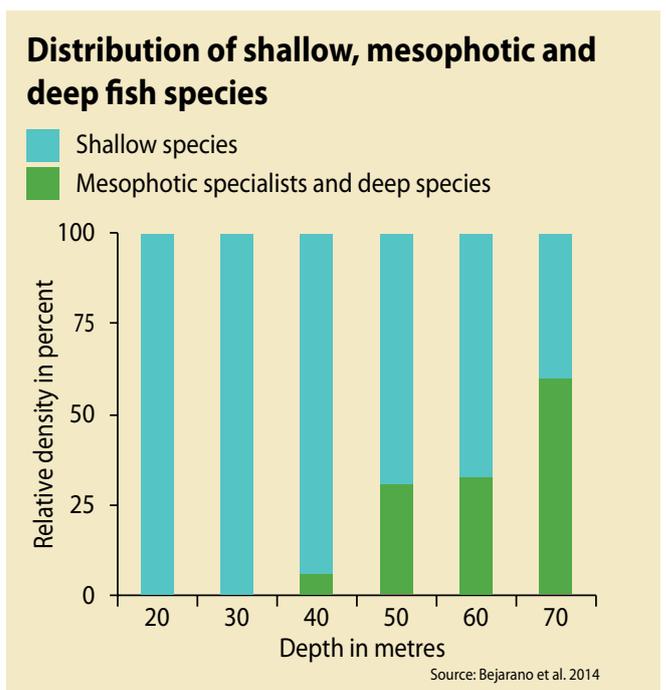


Figure 4.12. Proportion of shallow species vs. mesophotic specialist and deep species per depth, along a gradient from 20–70 m in Puerto Rico (Bejarano et al. 2014).

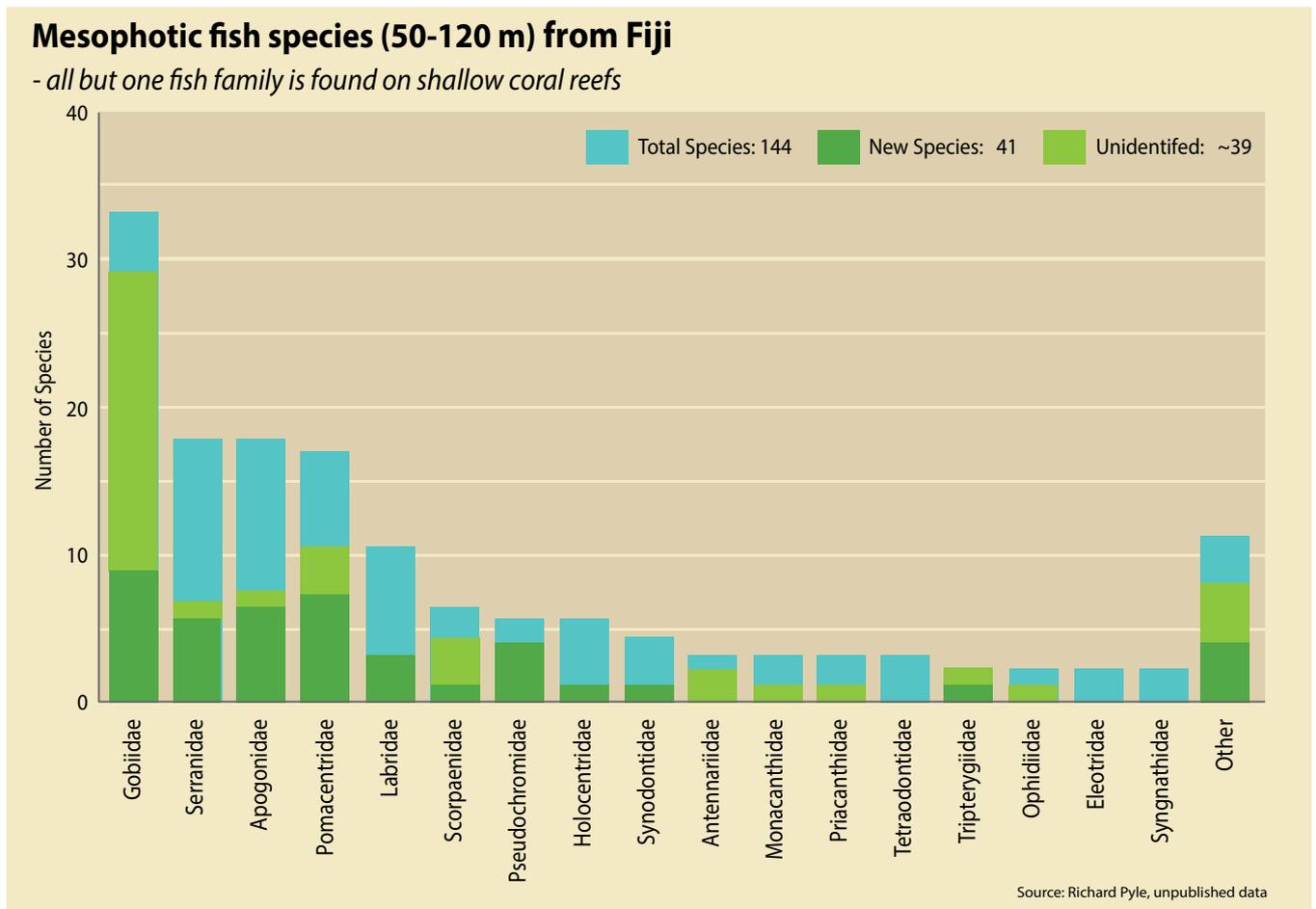


Figure 4.11. Total numbers of fish species within each family collected at depths of 50–120 m in Fiji, showing proportional numbers of new species and unidentified species (more than half of which are likely new species). All but Trachichthyidae (one specimen) are families characteristic of shallow coral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

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 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).

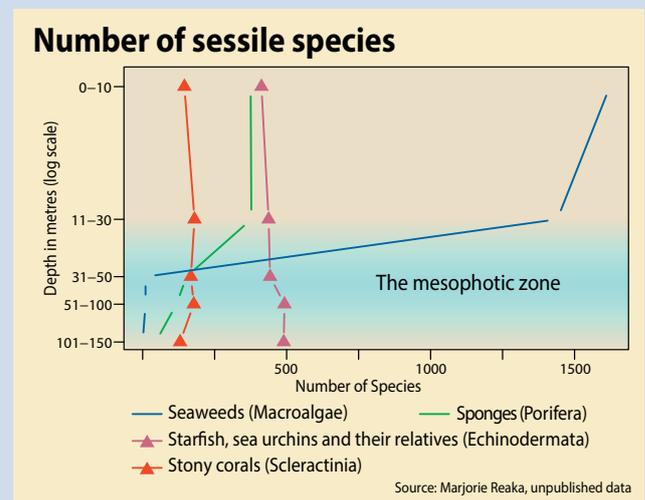


Figure 4.15. Number of sessile or relatively sessile species observed at different depths in the Gulf of Mexico. The vertical axis is a log scale for depth, and the biologically important zones that we wished to investigate are noted at the appropriate sites in log scale.

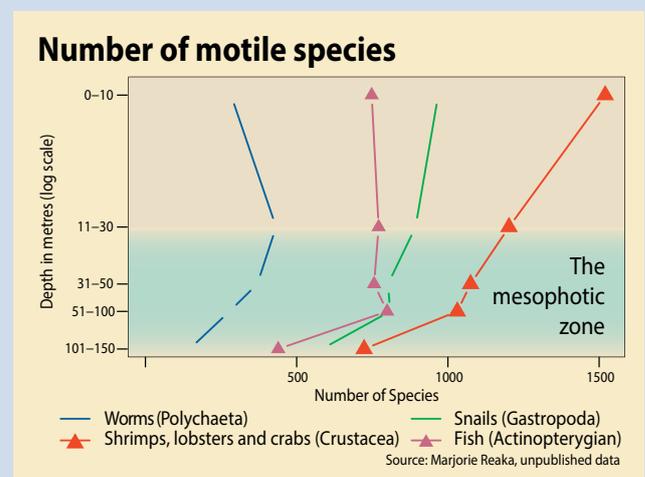


Figure 4.16. Number of motile species observed at different depths in the Gulf of Mexico. The vertical axis is as described for Figure 4.15.

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 %

Ecosystem services provided by mesophotic coral ecosystems

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5.1. Introduction

Ecosystem services are benefits provided to human societies by ecosystems — services such as regulating climate and weather, maintaining biodiversity and providing food and essential habitat (Costanza et al. 1997). As extensions of many shallow coral reef ecosystems, MCEs provide many of the well-documented ecosystem services associated with shallow coral reefs, as well as some services that may be unique to MCEs (Figure 5.1).

These ecosystem services include:

- habitat for economically- and ecologically-important species,
- a potential recovery source for shallow populations,
- employment in fishing, and to a lesser extent, recreation and tourism,
- new medicines and other natural products, and
- protection from coastal erosion and storms — submerged mesophotic reef banks that are close to land may possibly dampen long period swells and tsunamis.

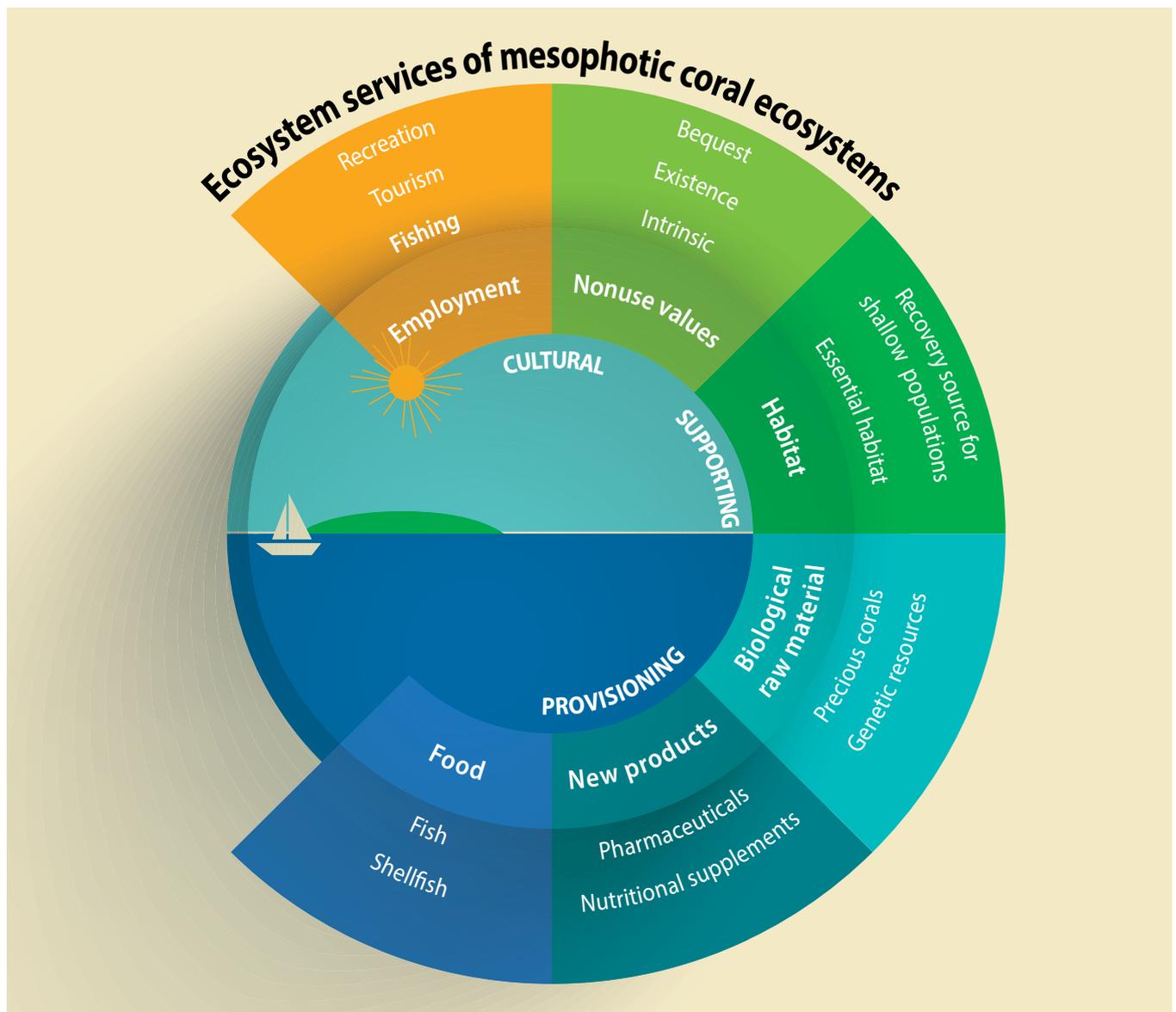


Figure 5.1. Summary of ecosystem services provided by MCEs.

5.2. Essential habitat

MCEs provide essential habitat for fish and other mobile species to spawn, shelter, feed and/or grow to maturity. Both mesophotic and shallow reefs enhance biodiversity through supporting fish in MCEs with significant connectivity to shallow areas, provide a refuge function from overexploitation that allows species to increase biomass, maintain higher numbers of species and individuals and support key ecological functions (e.g. predation and top-down control of community composition and maintenance of spawning stocks for fish settling in shallow reef ecosystems): all of which enhance overall system stability and resilience.

MCEs provide food and shelter for threatened species, such as sharks (Bejarano et al. 2014) and marine turtles (Appeldoorn et al. 2015), and serve as key habitat for a wide variety of fish, particularly large commercially-important snappers and groupers (Brokovich et al. 2008, Bejarano et al. 2014). Many commercially- and ecologically-important fish species have distributions that extend into mesophotic depths throughout the year, and still others are depth specialists found only in the deeper portion of the mesophotic zone (Brokovich et al. 2008, Bejarano et al. 2014). Mesophotic fish are generally easily exploited using traditional fishing gear (Sattar and Adam 2005, Wood et al. 2006), and in some areas, MCEs represent an opportunity for potential fishery expansion; while in others, there has already been a substantial depletion of commercially-important species (see Case Study Box, Chapter 6). MCEs can serve a critical role as a refuge area to protect species overexploited in shallower depths (Bejarano Rodríguez 2013) from fishing.

The essential role of MCEs in fish production and the maintenance of biodiversity is further illustrated by the large degree of connectivity between shallow reefs and MCEs. Mesophotic fish enhance this ecological connectivity following one or more strategies, including recruitment and residence across the full depth range, deep recruitment and upward migration, shallow recruitment and offshore migration, and migration to specific transient spawning aggregations (Bejarano Rodríguez 2013).

Many large-bodied coral reef fish form transient spawning aggregations on the edge of insular or continental shelves, sometimes at promontories, or along the sides or bottoms of channels. Individual fish may travel tens or even hundreds of kilometres to these aggregation sites (Bolden 2000, Nemeth et al. 2007). Transient spawning aggregation sites are typically at the edge of shelves and thus, depending on the species and local geomorphology, can occur in their entirety or in part within mesophotic depth ranges. For example, along the shelf edge south of St. Thomas, U.S. Virgin Islands, spawning aggregations have been documented for red hind (*Epinephelus guttatus*), yellowfin grouper (*Mycteroperca venenosa*) and

Nassau grouper (*E. striatus*). Depths ranged from 35–40 m on top of the shelf, although yellowfin and Nassau groupers can descend to 60 m during spawning (Nemeth 2005, Kadison et al. 2011). Similar depth ranges were reported for yellowfin, black (*M. bonaci*) and Nassau groupers at sites in the Mona Passage off western Puerto Rico (Schärer et al. 2012, 2014, Tuohy et al. 2015) that have similar depth profiles. The shelf break off the north coast of St. Thomas occurs much deeper (70–80 m) and spawning aggregations of several species have been reported by fishermen, including blackfin snapper (*Lutjanus bucanella*), a species limited to mesophotic and deeper depths (Ojeda-Serrano et al. 2007). Similarly, in the Indo-Pacific, spawning aggregations of the camouflage grouper (*E. polyphkadion*), brown marbled grouper (*E. fuscoguttatus*) and squaretail coral grouper (*Plectropomus areolatus*) occur typically in shallow depths (Rhodes and Sadovy de Mitcheson 2012), but have been reported to depths of 40 m (Rhodes 2012) for the former species and 50 m (Tamelander et al. 2008) for the latter two species. Off the west coast of Florida, the shelf-edge reefs are located at depths greater than 50 m and it is here that gag (*M. microlepis*) and scamp (*M. phenax*) groupers aggregate to spawn (Coleman et al. 1996, Koenig and Coleman 2012). Deeper still at 60–80 m is Pulley Ridge, a mesophotic reef in the Gulf of Mexico, where large red grouper (*E. morio*) spawn. Red groupers are nest builders, and scour out burrows 10 m in diameter that form oases for small reef fish (Reed et al. 2015). Each burrow has a single male or female grouper and multibeam sonar shows that these pits are very evenly spaced, at about 100 m apart. The breeding population within the Pulley Ridge marine protected area may exceed 130,000 burrows, not only providing unique habitat features, but also exporting larvae downstream to shallow reefs, such as the Florida Keys.

The occurrence of important transient spawning aggregations within mesophotic depths is probably not uncommon where the appropriate geomorphology exists. However, their distribution and numbers are probably underrepresented; owing to the difficulty in working at mesophotic depths and the general lack of depth information reported in many species accounts (see Chapter 12 in Sadovy de Mitcheson and Colin 2012 or www.scrfa.org). Fish aggregations have historically been overexploited by commercial fishers, even within mesophotic depths (e.g. Olsen and LaPlace 1978), and for many species, mesophotic aggregations are the only known sources of larvae left (Roberts 1996). Some transient aggregations are protected by temporary or permanent no-take restrictions (Nemeth 2005); however, the location and status of the vast majority of mesophotic aggregations are largely unknown and remain unregulated. These remarkable aggregations are a unique ecosystem service provided by MCEs; one that is critical to the continued recruitment of commercially- and ecologically-important fish species (Figure 5.2).

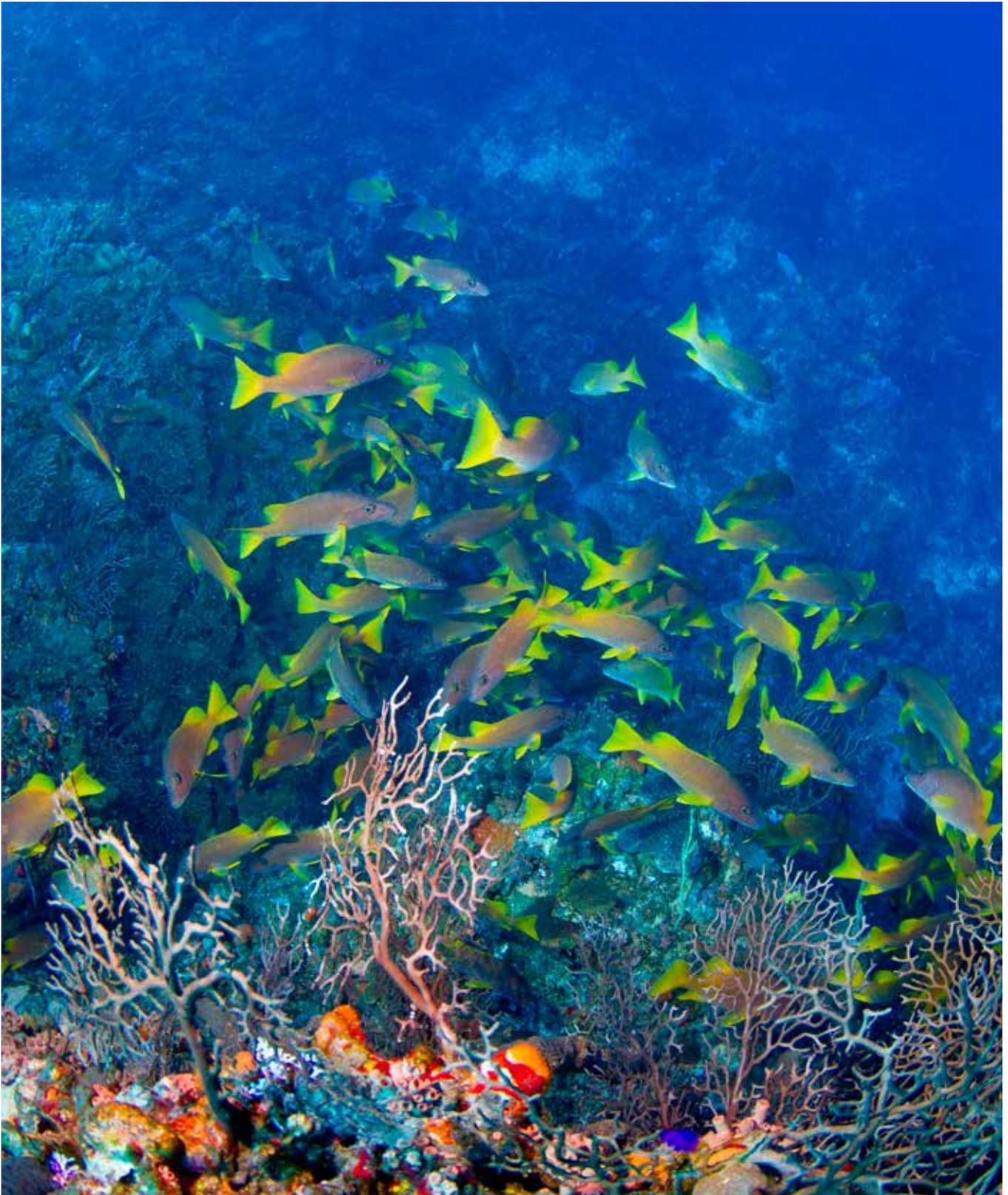


Figure 5.2. An aggregation of Schoolmaster Snappers (*Lutjanus apodus*) at Bajo de Sico, Puerto Rico, 50 m depth. Observed spawning aggregations of Schoolmaster Snappers in this area are known to consist of over 500 individuals (photo Héctor Ruiz, HJR Reefscaping).

5.3. Recovery source for shallow populations

MCEs may be a source of recovery and resilience for degraded or perturbed shallow populations, through the movement of adult individuals and the dispersal of larvae. At present, MCEs are considered to be buffered from many coastal and global stressors that are associated with shallow coral reef decline, and may in fact represent a refuge or refugia for specific species in specific locations. Indeed, some coral species have been found in higher densities on MCEs than on shallower reefs after periods of long-term decline or sudden local extinction on shallow reefs (Menza et al. 2008, Sinniger et al. 2013). For example, the common coral *Seriatopora hystrix* was thought to be extinct around Okinawa, Japan, following a severe global bleaching event in 1998, but has since been rediscovered at mesophotic depths (Sinniger et al. 2013). Refuge habitats that are capable of supporting populations of marine organisms throughout periods of stress must be sufficiently removed from stress, persistent in time and be connected through adult or larval migration to other habitats.

Many commercially-important fish species have depth-generalist distributions, and are found on both mesophotic and shallow coral reefs. It may be that adults of these species freely move between shallow reefs and MCEs, and could take refuge on mesophotic reefs during times of stress. Some of these mesophotic fish populations may be very important as refugia for coral reef fish under intense fishing pressure, since many fishing techniques (e.g. free diving) are not possible or are rendered more difficult at mesophotic depths (Bejarano et al. 2014, Lindfield et al. 2014).

Many corals are also depth-generalists; however, being sessile, adults cannot move to avoid stressful environmental conditions. There is evidence that the larvae of depth-generalist corals in the Caribbean can migrate into shallow habitat in some locations (Holstein et al. 2015). Evidence of this vertical migration, in the form of genetic population connectivity, has shown that vertical migration is location and species-specific (Bongaerts et al. 2010a, van Oppen et al. 2011, Slattery et al. 2011, Serrano 2013, Serrano et al. 2014) and that speciation may be occurring with depth in some scleractinian coral species (Bongaerts et al. 2013b, 2015a, Prada and Hellberg 2013). It is important to note that mesophotic coral species' ability to replenish shallow depths is limited to those species that are found in shallow waters (Bongaerts et al. 2010a).

Although the depth and isolation of MCEs has led to interest in their potential as refugia, coral communities on MCEs have been shown to be susceptible to disease (Smith et al. 2010), thermal (both warm and cold water) bleaching (Bongaerts et al. 2010a, Smith et al. 2015) sedimentation (Appeldoorn et al. 2015) and coral-algal phase-shifts potentially driven by invasive species (Lesser and Slattery 2011). Although the degree to which MCEs may serve as recovery sources for shallow coral reef communities remains uncertain, there is little doubt that these mesophotic communities are integrated components of larger marine metapopulations, and their conservation corresponds with the goals of coral reef conservation in general.

5.4. Tourists exploring the mesophotic zone

In recent years, the technology that has enabled scientists to explore areas of the ocean below scuba depths has become more accessible to the general public. Closed-circuit rebreathers that allow longer and deeper dives are being used by recreational divers. Tourists can now also explore the mesophotic zone in a submersible. Following in the footsteps of *DSV Alvin* and other research submersibles, companies are running submersible

dive tours (e.g. in Costa Rica, Honduras, Hawai'i and Curaçao). Tours to mesophotic depths and below are likely to increase, as researchers discover more about the deeper regions of the ocean and the infrastructure to visit these areas expands. Deep-sea tour operators are also helping to build our knowledge of the mesophotic zone, as they document their dives and analyse video footage for new species (Breedey and Guzman 2013).

5.5. Potential source of novel products

The collection of mesophotic reef organisms has been ongoing since the 1970s, resulting in many discoveries (including the drug discodermolide, a potent anti-tumour compound; Gunasekera et al. 1990), as well as other promising natural products (reviewed by Newman and Cragg 2007). Investigations in the waters around Palau have, for example, resulted in the publication of over 100 papers on marine natural products since 2004 (Faulkner et al. 2004). A number of the promising samples collected come from mesophotic depths (Qureshi et al. 2000, Sandler et al. 2006).

It is estimated that almost half of all drugs currently in use are sourced from natural products (Newman and Cragg 2012). Most of these have been derived from terrestrial plants, animals and microorganisms, but marine biotechnology is expanding, and will increasingly move out of the shallows and into deeper water. It is difficult to estimate the value of this industry at present, but it is probably safe to assume that potential future economic benefits could be very high (Newman and Cragg 2007).

Chapter 6.

Threats to mesophotic coral ecosystems and management options

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6.1. Introduction

MCEs are often considered to be buffered from many anthropogenic impacts known to directly affect shallow coral ecosystems, such as warm-water bleaching and tropical storms. Furthermore, by virtue of their depth, and in many cases their remote offshore locations, some MCEs are afforded greater protection from direct human impacts, such as overfishing and land-based runoff. However, there is increasing evidence to suggest that MCEs are vulnerable to

environmental disturbances, such as climate change impacts, overfishing, bottom fishing gear, capture of aquarium fish, precious coral trade, land-based pollution and invasive species (Table 6.1). Despite these threats, many MCEs are in good condition in comparison to their shallower counterparts. Strong management responses could mitigate at least some documented threats, thereby preventing future degradation of MCEs.

Table 6.1. Comparison of the major anthropogenic threats facing shallow-water reefs and MCEs.

Shallow-water coral reef ecosystems	Mesophotic coral ecosystems
<ul style="list-style-type: none">• Fishing (overfishing, destructive fishing with dynamite and poison and damage from lost fishing gear)• Thermal stress (bleaching) from ocean warming• Diseases• Pollution (land-based)• Invasive species• Tourism and recreation• Anchor damage• Coral mining (for aggregate and lime)• Coastal development• Marine aquarium trade	<ul style="list-style-type: none">• Fishing (overfishing and damage from lost fishing gear)• Thermal stress (bleaching) — reduced exposure to warm water stress• Diseases• Pollution — reduced exposure to land-based sources; exposed to deep-water sewage outfalls and dredging spoils• Invasive species• Tourism and recreation (reduced exposure)• Anchor damage (reduced exposure)• Coral mining (reduced to negligible exposure)• Marine aquarium trade• Oil and gas exploration• Cables and pipelines

6.2. Fisheries

The pressure from fisheries is considered by marine experts to be the greatest threat to all benthic habitats (Baker and Harris 2011). Fishing also represents a major threat to MCEs, both through the perturbation of trophic relationships and through physical damage to the reef structure. While in general, many MCEs have not been exploited to the same extent globally as shallower reefs (due in part to their relative geographic isolation and morphology, which impedes many fishing methods), overexploitation of shallower reefs and a resulting reduction in catches is leading to the expansion of fishing activities into MCEs.

Commercially-valuable fish species have been identified within MCEs, including species of high conservation concern (such as sharks and groupers). It has been suggested that following the onset of fishing, most commercially-valuable fish species suffer large population declines (Bejarano Rodríguez 2013, Williams et al. 2015). For example, many large-bodied grouper species form annual spawning aggregations at the edge of continental shelves, which — depending on the location — can occur at mesophotic depths (see Chapter 5.2 Essential habitat). The predictability in time and space of these grouper spawning aggregations have made them particularly vulnerable to overexploitation (De Mitcheson et al. 2008). As a result, many are now functionally extinct in large parts of their range. To combat this, Caribbean countries have instigated seasonal fisheries closures during spawning (Starr et al. 2007). In Cuba, fisheries studies have indicated that species with greater predictability in aggregation location and timing show greater declines in fisheries landings than species with less predictable and less concentrated aggregations (Claro et al. 2006).

As shallow reefs come under increasing pressure, many MCEs in areas accessible to artisanal fishing communities are likely to be fished. These fisheries often involve traditional fishing techniques, such as hook and line, which allow communities to catch mesophotic reef fish. For example in the Maldives, grouper are fished (mostly for export) down to 80 m using this technique (Sattar and Adam 2005). Similarly in Malaysia, where fishing is carried out from small boats, artisanal fishers use mostly hook and line, with a small number using longlines (Wood et al. 2006). Longlines are either deployed near the surface to catch pelagic fish such as tuna, or directly onto mesophotic reef slopes for demersal species, such as sharks and groupers (Wood et al. 2006). These techniques are fairly typical of many Southeast Asian mesophotic reef fisheries.

Satellite location systems and depth sounders allow easier identification of offshore MCEs as potential new fishing grounds. The arrival of even relatively established technologies into new areas can open up MCEs for fishing. For example, spearfishing in the Mariana Islands was traditionally limited to free diving on shallow reefs but following the introduction of scuba diving, fishing has expanded into the mesophotic zone (Myers 1993, Lindfield et al. 2014).

Trawling is a major threat to many mesophotic communities, with benthic trawl nets designed to be dragged close to the seafloor. In addition to destroying MCEs through the direct

impact of their large metal balls or plates on the bottom, trawls often stir up sediment that smothers corals, causing their death (Erftemeijer et al. 2012).

Documented examples of trawling impacts to MCEs are limited. Thus, to demonstrate the devastating effects that bottom trawling can have on MCEs, we must look to the azooxanthellate ivory tree coral reefs, *Oculina varicosa*, found at mesophotic depths off Florida, USA (70–90 m;

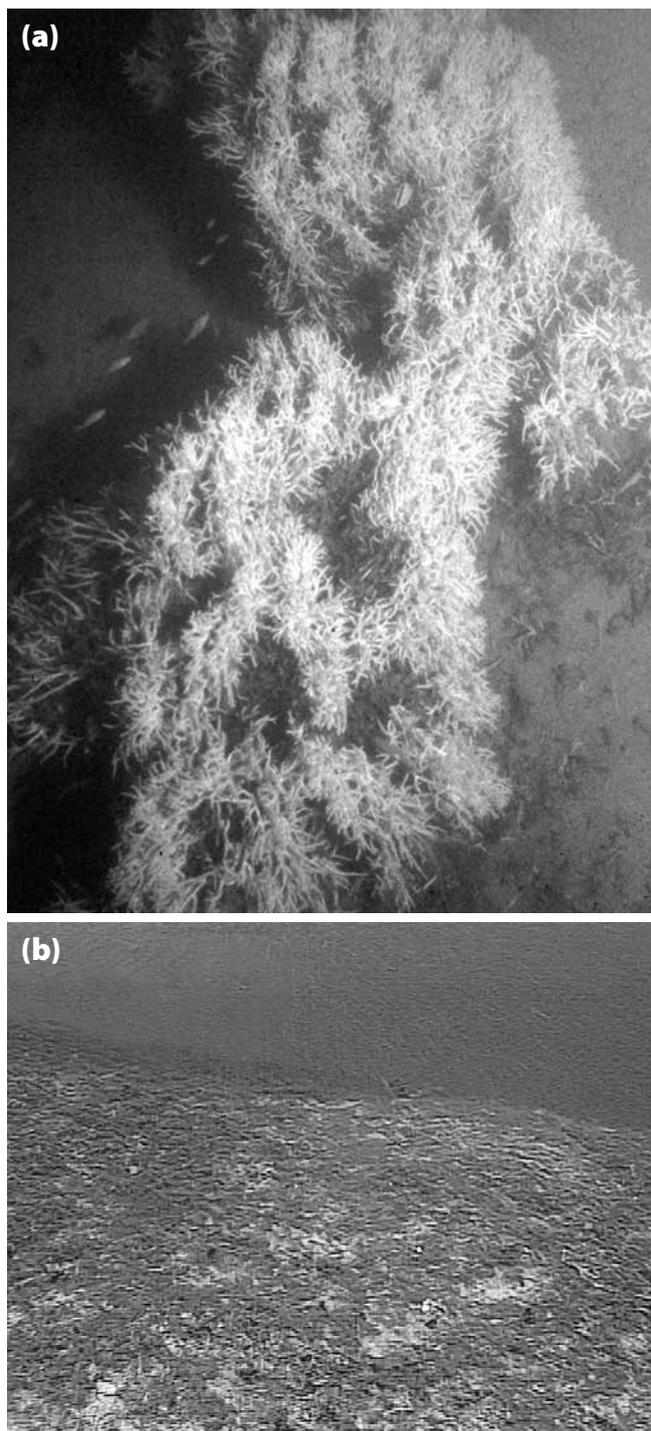


Figure 6.3. Deep-water *Oculina varicosa* off Cape Canaveral (67 m depth). (a) Historical photo from 1976, and (b) Same site in 2001 reduced to rubble from apparent bottom trawling (photos Reed et al. 2007, used with permission).

Koenig et al. 2005, Reed et al. 2007). The *Oculina* reefs were first discovered in the 1970s, with high coral cover and high densities of grouper spawning aggregations (Koenig et al. 2000). A small portion was set aside as a marine protected area in 1984, but the remaining reefs were left unprotected and open to trawling for rock shrimp. Chains were dragged through the reefs to provide tracks for the rock shrimp trawls. Submersible surveys showed the devastation caused by the trawls as the unprotected coral was crushed to rubble

(Figure 6.3; Reed et al. 2007). Live coral areas have over 70 species of fish, while the dead coral areas are virtually devoid of fish, with the few recorded being smaller bodied groups of low commercial value, such as damsels and butterflyfish (Koenig et al. 2000, 2005). This information led to the enactment of new legislation in 2015 that doubled the size of the *Oculina* marine protected area to approximately 600 nmi² and prohibits all bottom-tending gear, such as trawls, longlines and traps.

Commercially-important mesophotic fish in La Parguera, southwest Puerto Rico

The shallow reef fishery in La Parguera, Puerto Rico, is an important activity shaping the ecosystem. It has a direct impact on species, stocks and habitats present in the region (Valdés-Pizzini and Schärer-Umpierre 2014). Many commercially-important species that historically supported a productive fishery have significantly decreased over the last 50 years. For example, fishing pressure has resulted in the loss of large-bodied species and spawning aggregations (Kimmel 1985), the depletion of some species and reductions in body size (Kimmel 1985, Pittman et al. 2010). Keystone commercial species, such as the rainbow (*Scarus guacamaia*) and midnight (*S. coelestinus*) parrotfish and Nassau (*Epinephelus striatus*; Figure 6.1) and tiger (*Mycteroperca tigris*) groupers are no longer found in the area. Other commercially-important reef fish are less frequently observed (e.g. red hind, *E. guttatus*), and only the smaller grouper species are still common in shallow areas (e.g. graysby, *Cephalopholis cruentata*; Pittman et al. 2010). The low number of predators and the poor state of herbivores suggests that overfishing has impacted the food web (Guénette and Hill 2009, Pittman et al. 2010).

A recent study assessing the fish associated with MCEs off La Parguera found that many of these formally abundant species on the shelf are now only found, or are only present in abundance, off the steep insular slope at a depth of 60–70 m (Bejarano

et al. 2014). Some examples include the goliath grouper (*E. itajara*), black grouper (*M. bonaci*; Figure 6.2), yellowfin grouper (*M. venenosa*), rainbow parrotfish (*S. guacamaia*), nurse shark (*Ginglymostoma cirratum*), dog snapper (*Lutjanus jocu*), cubera snapper (*L. cyanopterus*) and Caribbean reef shark (*Carcharhinus perezii*). The more structurally complex MCEs have greater abundances of these species, as fish can shelter under steep overhangs and in caves and crevices.

The presence of many common shallow reef species at mesophotic depths (76 per cent of 103 species), the variability in fish assemblage composition, relative abundance and specific fish life stages suggest that connectivity occurs between shallow and mesophotic reefs via multiple mechanisms such as swimming, larval dispersal and ontogenetic and spawning migrations. Although shelf-edge MCEs support a richer and more diverse fishery resource than nearshore habitats, these areas are subject to a lower impact from fisheries due to their distance from the coast (10 km), steep sloping environment, narrow area and prevailing onshore winds and currents. The connectivity between the less-impacted MCEs and the shallow reefs of La Parguera may help to support the conservation of commercially fished species, by providing a refuge from the heavily exploited shallow-water areas.



Figure 6.1. Nassau grouper, *Epinephelus striatus*, on an MCE in La Parguera, Puerto Rico (photo Héctor Ruiz).



Figure 6.2. Black grouper, *Mycteroperca bonaci*, on an MCE in La Parguera, Puerto Rico at 62 m in depth. Many such large-bodied grouper species are now only found in high abundance on MCEs, due to overfishing on shallow reefs (photo Héctor Ruiz).

6.3. Climate change

Increasingly stressful conditions from natural and anthropogenic factors are producing significant population declines and community shifts in shallow coral reef communities. Increasing ocean temperatures as a consequence of increasing atmospheric carbon dioxide levels (IPCC 2014) have led to mass coral bleaching, an increase in the number and prevalence of diseases (produced by pathogens), and ocean waters becoming more acidic, which is predicted to severely affect growth and survivorship of calcifying marine organisms by mid-century (Hoegh-Guldberg et al. 2007, Hoegh-Guldberg and Bruno 2010, Pandolfi et al. 2011, van Hooidonk et al. 2013, Maynard et al. 2015). Bleaching and disease can cause substantial mortality in corals and can result in shifts in the composition and structure of coral communities over relatively short timescales (Miller et al. 2009, Weil et al. 2009a, b). Ocean acidification, a decrease in the pH level in seawater caused by increasing carbon dioxide levels, will reduce calcification rates in reef-building organisms, accelerate reef erosion problems and directly impact the

growth rates of coral and calcifying algae (Feely et al. 2004). Additionally, as ocean temperatures rise, it is expected that the intensity of tropical storms will increase (IPCC 2013), leading to increases in both direct (e.g. damaging storm waves) and indirect (e.g. sedimentation) impacts on MCEs.

There is little understanding of the extent of the impact of increasing ocean temperatures and carbon dioxide levels on MCEs due to the difficulties of sampling at depth and a lack of long-term monitoring records for most MCEs. Like shallow reefs, MCEs are likely to show considerable spatial variability in susceptibility to climate change, depending on factors such as local-scale environmental conditions, historical exposure to extreme conditions, and differing susceptibility to stressors among different reef species. Locations where long-term data do exist, including Palau and the U.S. Virgin Islands, provide valuable insights into environmental processes affecting MCEs that can help to guide monitoring, research and management programs. For example, from long-term datasets we have now

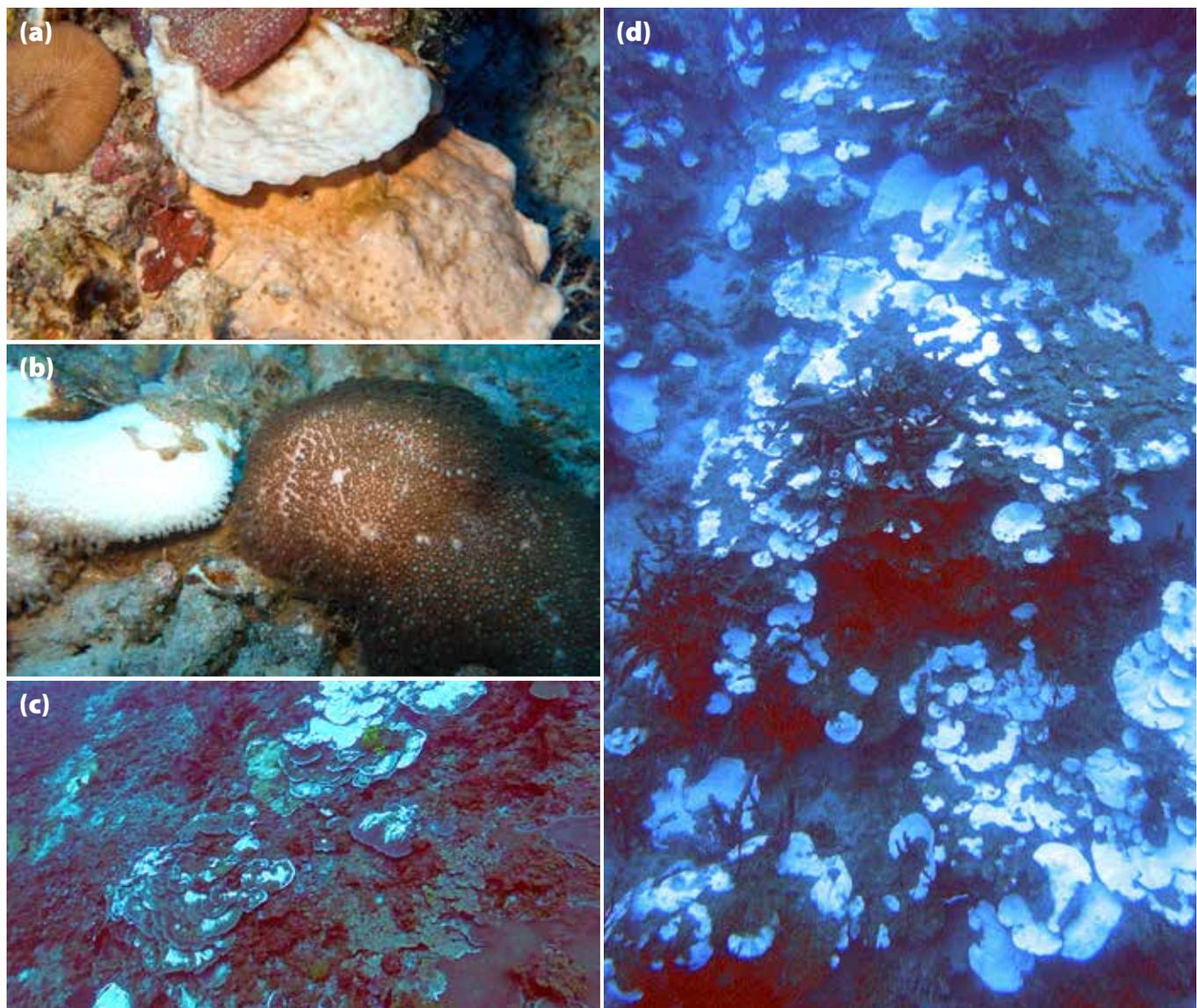


Figure 6.4. The loss of colour from these coral colonies is indicative of coral bleaching. (a) *Leptoseris* sp. in Palau at 90 m (photo Patrick L. Colin). (b) *Goniopora* sp. in Eilat, Israel at 60 m (photo Gal Eyal). (c) and (d) *Agaricia* sp. in the U.S. Virgin Islands at 60 m and 40 m, respectively (photos Tyler Smith).

learned that MCEs are not protected from all threats, and that oceanographic processes are perhaps more important than depth in terms of buffering corals from the impact of thermal stress (Neal et al. 2014, Nir et al. 2014).

6.3.1. Coral bleaching

MCEs are not immune to thermal stress (Neal et al. 2014) and coral bleaching. Coral bleaching, as evidenced by coral skeletons that are white or bleached in appearance, occurs when zooxanthellate corals become stressed and lose or expel their symbiotic algae (Figure 6.4). Corals can regain their algae and recover from coral bleaching, but prolonged stressful conditions may cause corals to die from starvation.

Coral bleaching often results from an interaction between high water temperatures and high light irradiance (Baird et al. 2009). The thresholds at which bleaching occurs vary among individual species, populations and geographic locations

(Baker et al. 2008). In some cases, previous exposure to stressors is also a factor effecting resilience. For example, corals that inhabit areas with fluctuating environmental conditions are often more tolerant than those from stable environments (Oliver and Palumbi 2011). The mechanisms influencing thermal tolerance include photo-protective pigments, a natural coral sunscreen (Salih et al. 2000), and switching of algal symbionts to more light-tolerant strains (Bongaerts et al. 2015b). However, since corals are thermally adapted or acclimated to their local environment, their ultimate response to fluctuating temperatures will be dictated by how quickly the external environment changes relative to their recent history (Oliver and Palumbi 2011). Such dependence is evident in the observed seasonal bleaching in mesophotic corals in the Red Sea as summer months bring higher light levels and temperatures (Nir et al. 2014). Consequently, as observed in the U.S. Virgin Islands (Smith et al. 2015), mesophotic corals may exhibit lower bleaching thresholds than corals in shallower habitats. However, other mesophotic corals occur in dynamic

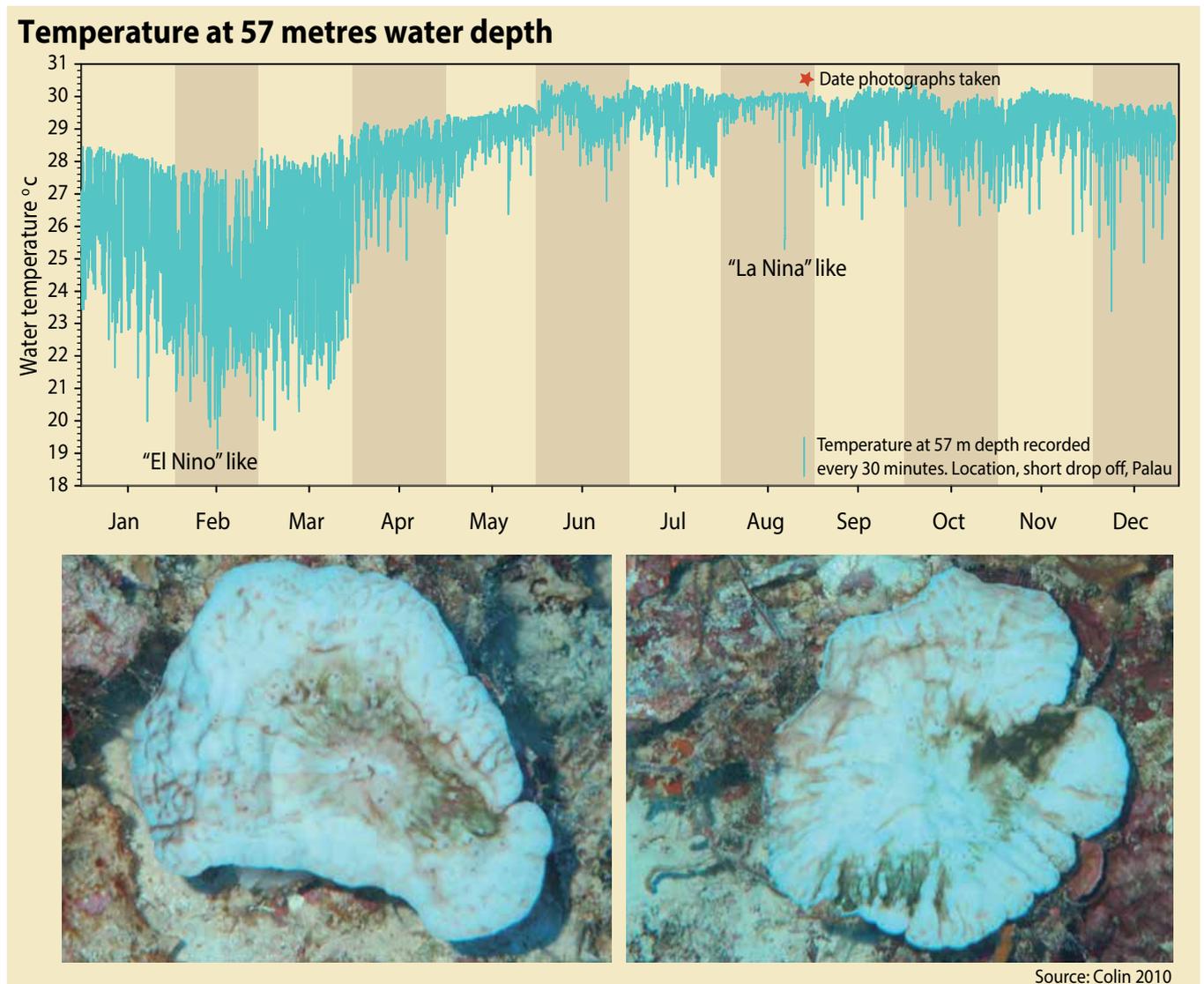


Figure 6.5. Temperature at 57 m in depth recorded every 30 minutes during 2010 off Palau. The rapid shift from a highly stratified El Niño type water column to a uni-thermal (at near 30°C) water column, with associated coral bleaching seen on the mesophotic reef (photos below graph). The bleached corals are platy agariciid corals within 30 m of the thermograph station. These and other similar corals did not survive the bleaching event of 2010 (photos Patrick L. Colin).



Figure 6.6. Examples of bleached and diseased coral colonies found in MCEs off La Parguera, Puerto Rico. (a) and (c) White plague-like signs were observed in agaricids. White band syndromes were observed in (b) *Agaricia grahamae* and (d) *Undaria agaricites*. (e) Bleaching was observed in *A. grahamae*. (f) Many coral colonies show signs of recent mortality (photos Héctor Ruiz).

environments exposed to large temperature fluctuations on daily or even hourly scales due to local-scale oceanographic factors such as internal waves. In these cases, the local oceanography could reduce the vulnerability of mesophotic corals to bleaching both through mitigating maximum temperatures and exposing corals to large fluctuations in temperature to which they have become adapted (e.g. Buerger et al. 2015). Water temperatures on MCEs may vary with changes in the depth of the thermocline, particularly due to the El Niño Southern Oscillation, upwelling and internal waves. Thermocline depth appears to exert a significant influence on MCEs, and a deepening of the thermocline associated with El Niño events has been implicated in bleaching of corals in Palau (Colin pers. obs.).

6.3.2. Impact of highly variable temperature regimes on mesophotic coral ecosystems

The El Niño Southern Oscillation is a naturally occurring phenomenon that produces varying ocean temperatures in the equatorial Pacific. It generally involves fluctuations between two phases (El Niño and La Niña) that can last for several seasons. For equatorial reefs in the Western Pacific, El Niño events are associated with cool surface waters, and shallow thermoclines and nutriclines. La Niña events cause the opposite effect, with warm surface waters, and deep thermoclines and nutriclines. This is in contrast to conditions in the Central and Eastern Pacific, where warmer than normal ocean temperatures are associated with El Niño and cooler than normal temperatures are associated with La Niña events. The oscillation between El Niño and La Niña conditions can lead to rapidly fluctuating conditions that may pose a serious threat to MCEs (Glynn and D’Croz 1990).

During a bleaching event in Palau in August 2010, constantly high temperatures to a depth of 90 m were observed for periods of hours to days (Figure 6.5). Overall, the 2010 bleaching event was moderate and limited in duration, so coral mortality was low (unlike the sustained bleaching event in 1998; Bruno et al. 2001).

6.3.3. Disease

Disease in corals and other organisms has increased in shallow coral reef ecosystems in the past decade along with increasing seawater temperatures (Burge et al. 2014). Such temperatures render organisms more susceptible to disease outbreaks, as well as bleaching events. Recent surveys of MCEs in Puerto Rico and the U.S. Virgin Islands indicate that mesophotic coral communities are indeed susceptible to biotic diseases (Smith et al. 2010, Weil unpubl. data — see Puerto Rico Case Study in Chapter 3) down to at least 100 m in depth. Coral bleaching and disease were observed in at least six of the 23 mesophotic scleractinian coral species in Puerto Rico (Figure 6.6) — *Agaricia undata*, *A. lamarcki*, *Undaria agaricites*, *Mycetophyllia aliciae*, *Montastraea cavernosa* and *Stephanocoenia intersepta*. Most of the “disease signs” observed fall into a general category known as “white syndromes” due to their characteristic white area of recent tissue-cleared skeletal material (Raymundo et al. 2008, Weil and Hooten 2008), with some signs resembling typical white plague disease (Figure 6.6). In 2014 at Pulley Ridge, an MCE in the eastern Gulf of Mexico, from a total of 7,329 individual plate corals (*Agaricia* spp. and *Helioseris cucullata*) counted from transect photos, 247 were noted to be bleached, partially bleached, totally bleached, partly dead, recently dead or diseased, resulting in 4 per cent morbidity of the total population measured (Reed et al. 2015).

A good example of white plague disease-like signs was observed in a single medium-sized (832 cm²) coral colony of *Mycetophyllia aliciae* at 55 m off La Parguera, Puerto Rico. This colony was healthy in October 2009, but showed white plague disease-like signs in December 2009, and was dead by March 2010 (Figure 6.7). Rate of tissue mortality varied approximately between 6–10 cm/month, one-third slower than the maximum tissue rate mortality reported for this disease type in shallower waters, but still faster than all other shallow coral diseases except black band disease (Weil 2004).



Figure 6.7. A time-series showing a colony of *Mycetophyllia aliciae* at 50 m off La Parguera, Puerto Rico that was (a) healthy in October 2009, (b) developed signs of white-plague-like disease and suffered rapid tissue mortality (white skeleton without tissue and secondary macroalgae colonization) and (c) was dead by March of 2010 (photos Héctor Ruiz).

6.3.4. Ocean acidification

Rising levels of carbon dioxide in the atmosphere — caused in large part by the burning of fossil fuels — has led to an increase in the levels of carbon dioxide in the ocean. Upon absorption of carbon dioxide, seawater becomes more acidic and its carbonate ions less abundant. As corals and other calcifying organisms require calcium carbonate to build skeletons and shells, increasing ocean acidification may inhibit growth (Langdon and Atkinson 2005, Albright et al. 2010, Fabricius et al. 2011). Ocean acidification can also impact organisms in other ways, such as the ability of fish to detect predators (Munday et al. 2014) and a decrease in coral settlement rates (Doropoulos et al. 2012). Perhaps the most consistent and pronounced effects of ocean acidification observed on coral reef ecosystems are enhanced rates of bioerosion (whereby hard substrata is eroded by living organisms; Andersson and Gledhill 2013).

Little information exists regarding the effects of ocean acidification on MCEs. One study, which examined the precious coral, *Corallium rubrum*, can be used as an example of what could happen to mesophotic corals as it occurs at mesophotic depths in the Mediterranean Sea. In controlled studies simulating ocean acidification conditions anticipated by the end of the century, *C. rubrum* exhibited reduced calcification and polyp activity (Cerrano et al. 2013). It has been suggested that calcification in the Mediterranean Sea may have already declined (by 50 per cent) as a consequence of anthropogenically-induced ocean acidification (Maier et al. 2012). In some regions, red corals are a component of MCEs; therefore, it is plausible that these populations will be directly impacted by ocean acidification over the course of the century.

6.3.5. Tropical storms

Hydrodynamic disturbances associated with storms (hurricanes in the Atlantic and Eastern Pacific, typhoons in the North Pacific and Indian Ocean and cyclones in the South Pacific) affect many coral reef regions, and play a significant role in structuring shallow reefs (Gardner et al. 2003, De'ath et al. 2012). Water velocities from storm waves (maximum orbital velocities) decline exponentially with depth, and MCEs are therefore afforded some protection from hydrodynamic disturbances (e.g. Woodley et al. 1981). However, organisms living in the upper mesophotic zone (30–50 m) may experience direct impacts from storms (White et al. 2013). Indirect effects of storms, such as debris avalanches, can affect MCEs (Harmelin-Vivien and Laboute 1986), while very severe storms can damage reefs to depths of at least 70 m (Bongaerts et al. 2013a). The typical plating and foliose morphologies of many mesophotic coral species leave them prone to degradation following physical disturbance. For example, significant impacts to large foliose coral communities combined with a large increase in rubble were detected on MCEs off Okinawa following a typhoon in 2012 (White et al. 2013). Submerged banks not exposed to breaking waves are likely to be less vulnerable than lower reef slopes (Roberts et al. 2015). In any case, predicted changes in the location, frequency and particularly the intensity of storms expected as ocean temperatures rise (IPCC 2013) will likely affect MCEs.

6.4. Sedimentation and pollution

Coral reefs normally require warm, clear, nutrient-poor water for development and survivorship (Veron 2000). For light-dependent organisms, anything that limits light penetration, such as sedimentation and turbidity, is going to have an impact on their survival. Sedimentation smothers corals causing energetic efficiency to be compromised (Riegl and Branch 1995), abrasion to coral tissues (Loya 1976b), impacts to calcification rates and coral growth, interference with feeding, photosynthesis of the symbiotic algae, respiration and settlement processes and fecundity of corals to be lowered (reviewed for shallow reefs

by Fabricius 2005). Sedimentation, nutrient enrichment and turbidity can also degrade both shallow and mesophotic coral reefs (Fabricius 2005, Vega-Thurber et al. 2013, Katz et al. 2015).

MCE environments adjacent to shallow reef systems are usually influenced by sediment from the shallow reefs above (Figure 6.8). MCEs further offshore can also be impacted by sediment, especially from anthropogenic origins (e.g. sewage outflows and dredge dump sites; Armstrong and Singh 2012, Appeldoorn et al. 2015).

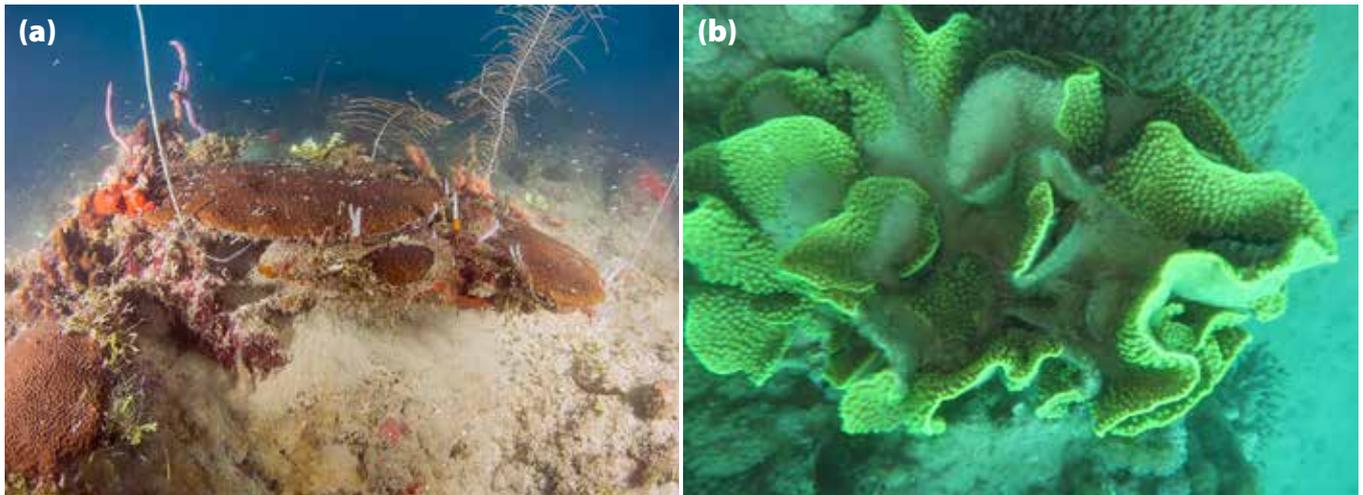


Figure 6.8. Sedimentation on mesophotic reefs. (a) Large, easily disturbed sediment beds surround MCEs at 50 m off the south shore of Utila, Honduras (photo Ally McDowell). (b) *Turbinaria* sp. at 40 m off Eilat, Israel, with sediment deposited within the foliose structure, smothering the coral polyps (photo Gal Eyal).

Anthropogenic stressors on MCEs in Ponce, Puerto Rico

MCEs located in a narrow insular shelf off the south coast of Puerto Rico are subject to a range of stressors such as outflow from several rivers, a sewage treatment plant with a deep sewer outfall, three deep dredge dump sites and shipping activities.

A study in 2010 (Appeldoorn et al. 2015) found the MCEs off Ponce received high rates of sedimentation and enriched ^{15}N (an indicator

of anthropogenic nitrogen) concentrations. The most impacted sites, which showed a progressive increase in sedimentation and a decline in live benthos, were located close to shore and associated with dredge disposal sites (Figure 6.9). Higher sedimentation rates and reduced light penetration resulted in poor MCE development, as well as shallower maximum depths at which mesophotic corals, algae and other photosynthetic organisms could survive.

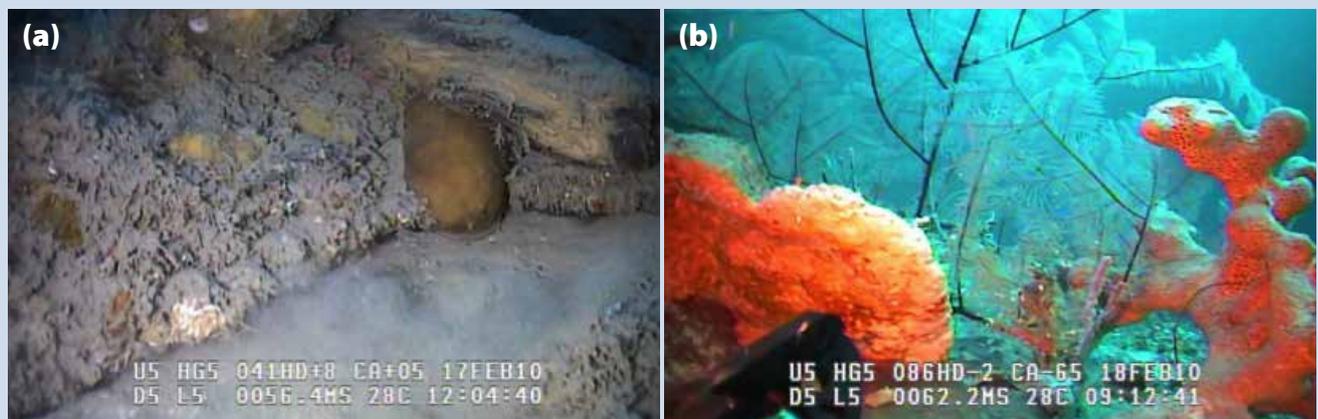


Figure 6.9. Remotely operated vehicle video footage from the area off Ponce, Puerto Rico. (a) An impacted site close to shore at a former dredge disposal site, Ratones at 56 m, showing heavy siltation over the reef structure (photo Francisco Pagán). (b) A less impacted offshore site, Caja de Muertos at 62 m, showing large sponges, black corals (*Antipathes* spp.) and an *Agaricia* sp. colony (photo Richard S. Appeldoorn).

6.5. Marine aquarium trade

The international marine aquarium trade involves the collection, breeding and supply of many shallow and mesophotic reef fish, corals and other invertebrates for home and public aquaria. Marine life in the trade is supplied from 40–45 countries (Rhyne et al. 2012). Estimates suggest that approximately 150 hard coral species and 1,500 fish species (across 50 families) are actively targeted by the marine aquarium trade (Wabnitz et al. 2003). Recent research has highlighted the role of the Philippines and Indonesia as the dominant global exporters, responsible for 55 per cent and 31 per cent, respectively, of all live fish imports into the United States for 2005 (Rhyne et al. 2012).

The United States imported approximately 11 million fish during the year 2004–2005 (Rhyne et al. 2012), and the European market is of a similar size (Wood 2001). This suggests a global trade of over 22 million fish annually. Currently, most monitoring of the marine aquarium trade is based on the Convention on International Trade in Endangered Species (CITES) permits or packing lists for international shipping of live fish.

It is unclear what proportion of the traded marine life is collected from MCEs. However, there is trade in mesophotic reef fish species with countries such as Japan, where there is an enthusiastic market for ‘rare’ mesophotic fish species. Traded mesophotic species include anthias (Subfamily: Anthiinae; Figure 6.10), dottybacks (Family: Pseudochromidae), butterflyfish (Family: Chaetodontidae), wrasse (Family: Labridae) and pygmy angelfish (Genus: *Centropyge*). In particular, within the pygmy angelfish, the Peppermint angelfish (*Centropyge boylei*) and the Narcosis angelfish (*Centropyge narcosis*) are highly prized (see case study). Mesophotic fish are commonly labelled as ‘rare’ by

the marine aquarium trade, but this is likely to reflect their limited supply due to the difficulties of collection rather than true ecological rarity. With current collection pressure quite dispersed over large reef areas, it is unlikely that the marine aquarium trade is having a large impact at mesophotic depths. However, populations of many mesophotic reef fish species lack quantitative assessments, making sustainable collection quotas hard to set.

As many mesophotic fish species in the aquarium trade have gas-filled swim bladders which expand and burst if fish are brought too rapidly to the surface (Munday et al. 2015), careful planning is required to bring them to the surface without injury. Traditionally, collectors have carefully punctured the swim bladder of the fish using a needle on ascent, though this may result in increased infection risk later. Many collectors still use ‘needling’ to bring collected fish to the surface (Figure 6.11), although, increasingly collectors are using decompression stops to allow fish time for gas to move out of the swim bladder during ascent. Work on Yellow Tang (*Zebrasoma flavescens*) on Hawaiian shallow reefs found that ‘needling’ to vent excess gas from the swim bladder reduced immediate mortality post-dive, but led to elevated serum cortisol (a proxy for fish stress), whereas the addition of decompression stops led to lower increases in serum cortisol (Munday et al. 2015).

In terms of scleractinian corals, it is unlikely that many are being collected from mesophotic depths, as most coral species in high commercial demand are found in greatest abundance on shallow reefs or reef slope environments less than 30 m in depth. With increased availability of advanced diving technologies, which allow access to greater depths, there could be an increase in demand for mesophotic species in the future.



Figure 6.10. Anthias, *Pseudanthias bimaculatus*, collected at 50 m in the Maldives for the marine aquarium trade (photo Elizabeth Wood).

Peppermint and Narcosis angelfish: jewels in the aquarium trade

The Peppermint (*Centropyge boylei*) and Narcosis (*Centropyge narcosis*) angelfish (Figure 6.12) are two of the most prized fish for home aquariums. They are both found in the Cook Islands, and the Peppermint angelfish has also been observed in French Polynesia. Peppermint angelfish have been recorded at depths of 55–120 m (Pyle et al. 2009), while Narcosis angelfish have been reported deeper at 100–120 m (Pyle and Myers 2010).

Both species ranges are likely to be severely underreported due to the difficulties in surveying these depths. Due to the rarity of collection in the marine aquarium trade, these species command extremely high prices. In 2012, private buyers offered up to US\$ 30,000 for a single Peppermint angelfish (Kaneshiro 2012), while a single Narcosis angelfish sold for US\$ 5,000 within seconds of being offered for sale online (Adams 2012).



Figure 6.12. (a) Peppermint angelfish (*Centropyge boylei*) and (b) the Narcosis angelfish (*Centropyge narcosis*) photographed at approximately 90 m in the Cook Islands (photos Richard Pyle).



Figure 6.11. Collector using a needle to puncture the swim bladder of an anthias, *Pseudanthias bimaculatus*, to prevent its swim bladder from bursting during ascent (photo Elizabeth Wood).

6.6. Precious coral fishery

Precious corals do not require sunlight and are generally referred to as deep-sea or cold-water corals. They are found all over the world, down to the deep ocean depths. However, the range of precious corals overlaps with MCEs, and in some areas, such as around Hawai'i, they can significantly contribute to habitat complexity and provide stabilization to substrates at mesophotic depths (Tsounis et al. 2010).

Many of the species used in jewellery manufacture, including the prized black coral *Antipathes griggi* (Figure 6.13), are

collected at mesophotic depths. In the past, trawling had been used to collect the corals (Tsounis et al. 2010). This practice has now been banned in most countries, limiting collection to less destructive and more selective harvesting methods, such as by divers and utilizing submersibles. Considering the ecological role of precious corals in some mesophotic habitats, it is important to ensure that harvesting is sustainably managed to maintain ecosystem functions (e.g. habitat complexity and substrate stabilisation) provided by precious corals.

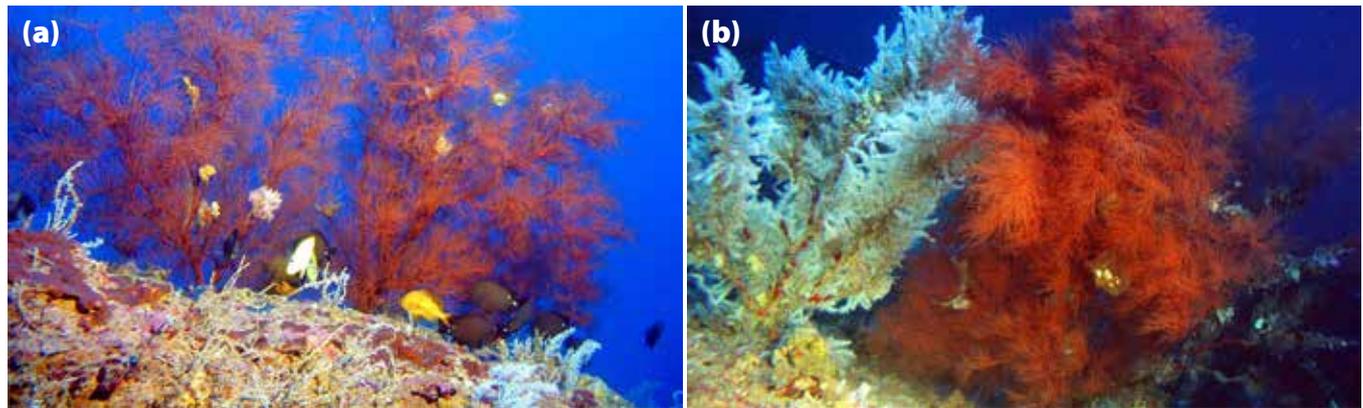


Figure 6.13. Black corals (*Antipatharia*) from mesophotic depths (70–100 m) in the 'Au'au Channel, Hawai'i located between the islands of Lāna'i and Maui (photos NOAA's Hawai'i Undersea Research Laboratory).

6.7. Invasive species

Invasive species are introduced species that are not native to a particular ecosystem. They may rapidly reproduce, causing detrimental ecological effects. Several invasive species have been recorded on MCEs, with the snowflake coral (*Carijoa riisei*), lionfish (*Pterois volitans* and *P. miles*) and green algae (*Avrainvillea* sp.) being best documented.

6.7.1. Snowflake coral

The invasive parasitic snowflake octocoral, *Carijoa riisei*, was first recorded on the island of O'ahu in Hawai'i in the 1960s. Native to the West Pacific, it is not clear how the snowflake

coral was first transported to Hawai'i (Concepcion et al. 2010). Since its arrival, the snowflake coral has spread around most of the Main Hawaiian Islands. It settles on black corals and smothers them (Figure 6.14; Kahng and Grigg 2005). In 2001, on the Maui Black Coral bed, it was found to cover more than 60 per cent of black corals at depths between 80–105 m and settle on the undersides of mesophotic scleractinian corals and overgrow them (Kahng and Grigg 2005). Like many invasive species, snowflake coral has a high reproductive rate. It employs continuous spawning of negatively buoyant eggs, as well as spreading vegetatively using 'runners' (Kahng et al. 2008).

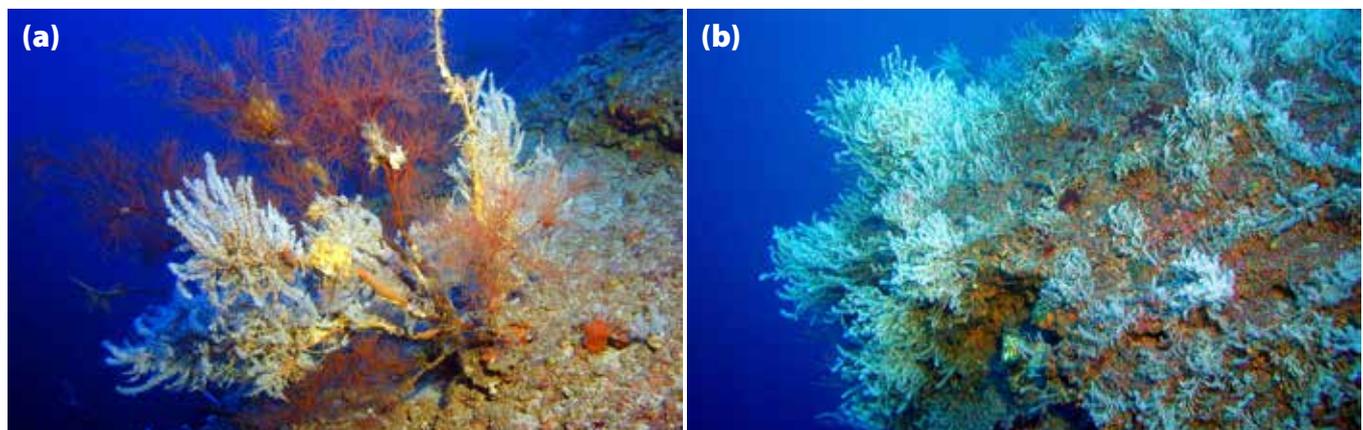


Figure 6.14. The 'Au'au Channel, Hawai'i at 70–100 m showing (a) the snowflake coral, *Carijoa riisei*, smothering a black coral colony and (b) a *C. riisei* dominated mesophotic habitat (photos NOAA's Hawai'i Undersea Research Laboratory).



Figure 6.15. Invasive lionfish (*Pterois volitans*) on a MCE at 60 m off Utila, Honduras (photo Ally McDowell).

6.7.2. Lionfish

Lionfish — *Pterois volitans* (Figure 6.15) and *P. miles* — originally native to the Indian and Pacific Oceans and Red Sea, are believed to have been introduced into waters around Florida, USA in the 1980s from home aquariums (Whitfield et al. 2002, Schofield 2009). Over the past decade they have rapidly spread, from their few initial sightings to colonizing shallow and mesophotic reef habitats across the Western Atlantic, where they can reach at least five times their natural population densities (Darling et al. 2011, Kulbicki et al. 2012). Their current Western Atlantic range stretches from Bermuda and North Carolina in the north, to Brazil in the south, encompassing the Caribbean Sea and Gulf of Mexico (Schofield 2009, 2010). Lionfish have been observed at 55 m in Puerto Rico (Bejarano et al. 2014), deeper than 100 m in the Bahamas (Lesser and Slattery 2011), 112 m in the northwestern Gulf of Mexico (Nuttall et al. 2014) and 120 m in Honduras (Schofield 2010).

Lionfish are voracious, gape-limited predators, feeding on a wide variety of fish and invertebrate species. As invasive species, their presence on reefs has been observed to cause declines in prey fish biomass of up to 65 per cent (Green et al. 2012) and to reduce native fish recruits by up to 79 per cent (Albins and Hixon 2008). Lionfish are highly successful invaders due to a combination of prey naivety (native prey species do not recognize lionfish as predators), a lack of predators, defensive venomous spines and a broad thermal tolerance (Morris et al. 2009). Furthermore, lionfish are highly fecund, spawning all year round at a maximum rate of once every 2–3 days (Gardner et al. 2015). Lionfish produce buoyant egg bundles, aiding dispersal and new site colonization by drifting in surface currents.

In addition to the direct effects on native reef fish and invertebrate abundance and recruitment, lionfish have also been linked with indirect MCE shifts. In the Bahamas, it is suggested that lionfish are associated with a shift in MCEs from coral- to algal-dominated states by altering the balance in the food chain, known as a trophic cascade. Lionfish feed upon mesophotic herbivorous and omnivorous fish, leading to a reduction in grazing pressure on the alga *Lobophora variegata*, and hence, an increase in algal abundance relative to corals and sponges occurs (Lesser and Slattery 2011, Slattery and Lesser 2014). Thus, the lionfish invasion may contribute to major MCE shifts over relatively short timescales of several years.

Lionfish exhibit ontogenetic migrations, with older lionfish found at greater depths on reef habitats (Claydon et al. 2012). Juvenile lionfish tend to use shallow reef environments, mangroves and seagrass beds as nursery grounds (Barbour et al. 2010, Claydon et al. 2012). It is likely that lionfish populations on MCEs form an extension of this ontogenetic migration, although this requires further research.

Current control measures for lionfish focus on hand culling with spears, often using dive volunteers (Figure 6.16). Culling is known to reduce the abundance of lionfish on shallow reefs (Frazer et al. 2012), and has been shown to aid the recovery of native shallow reef fauna (Green et al. 2014), although continuous culling is necessary to maintain low lionfish populations. There has been limited culling on MCEs, and there is no assessment of its effect. Across the Western Atlantic, the International Coral Reef Initiative has a regional lionfish strategy aimed at fostering collaboration between governments, scientists and reef-reliant industries in the management of lionfish.

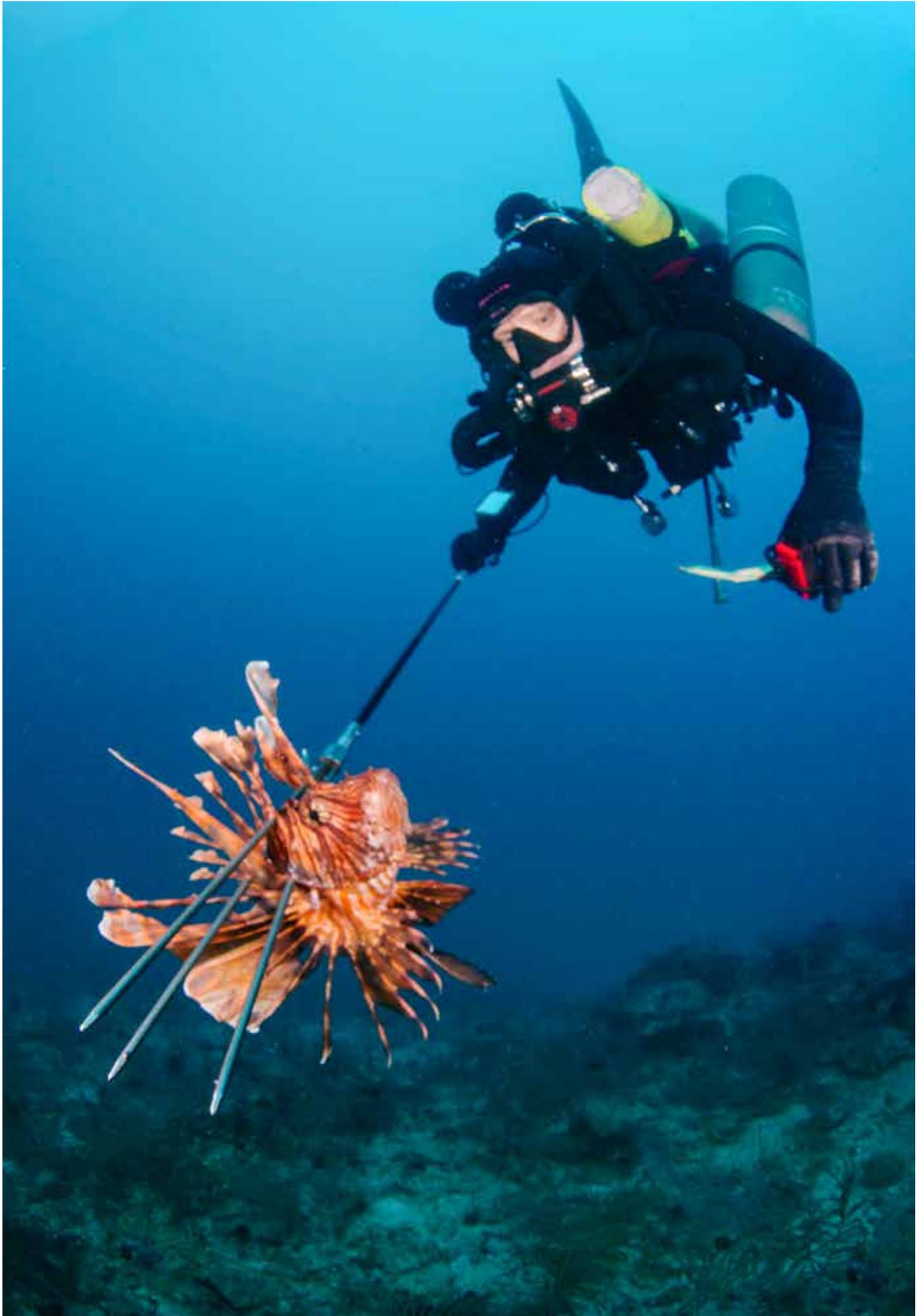


Figure 6.16. A diver using a closed-circuit rebreather to spear an invasive lionfish at 50 m off Utila, Honduras (photo Brian Sullivan).

Lionfish on the Pulley Ridge mesophotic reef in the Gulf of Mexico

Lionfish are now common throughout the Western Atlantic Ocean, the Gulf of Mexico and Caribbean. The first sightings in the Gulf of Mexico occurred in 2010, with lionfish populations having since increased dramatically on many shallow and mesophotic reefs. During submersible dives in 2010, only a few lionfish were documented along the West Florida Shelf MCEs in the Gulf of Mexico (Reed and Rogers 2011) and none were reported in the same region in 2003 (by a United States Geological Survey study). However, by 2013, a total of 703 lionfish were observed during remotely operated vehicle surveys at Pulley Ridge, a MCE (60–80 m depth) on the West Florida Shelf (Reed et al. 2014; Figure 6.17). Of the 33 1–km² blocks surveyed at Pulley Ridge, 72 per cent contained lionfish, most of which were associated with active red grouper, *Epinephelus morio*, burrows. Burrows (5–15 m in diameter) are excavated by red grouper and provide habitat and act as oases for many small reef fish and lionfish. From multibeam sonar maps of Pulley Ridge, over 136,000 red grouper burrows are visible in the region, providing the potential for tens of thousands of lionfish.



Figure 6.17. The invasive lionfish has been found in increasing numbers at red grouper burrows at Pulley Ridge at 70 m (photo John Reed, NOAA Coral Ecosystem Connectivity Expedition 2014).

6.7.3. The Green Alga *Avrainvillea* sp.

Avrainvillea sp., an invasive green alga (Figure 6.18) known for its propensity to displace native seagrass populations in the intertidal zone (Peyton 2009), was first reported in Hawai'i in 1981 in 13 m of water off Kahe Point, O'ahu (Brostoff 1989), and is now found offshore of O'ahu at depths to 90 m (Peyton 2009, Spalding 2012). Originally identified as *Avrainvillea amadelpha*, recent research suggests that this identification is incorrect and work is now underway to confirm the invasive alga's identity (A. Sherwood pers. com.).

The *Avrainvillea* sp. spread from its first collection site at Kahe Point to Maunalua Bay (50 km distance) within about six years (Brostoff 1989). Presently, the distribution of this species in Hawai'i extends along most of O'ahu's southern and western shores, and has been documented in a one-time collection from Kaua'i (Smith et al. 2002). The mechanism(s) of its rapid propagation is not known. The species' high abundance at mesophotic depths introduces the possibility that it may have originated in mesophotic waters and then moved into shallower waters (Spalding 2012).

Some species of *Avrainvillea* form dense mats on either hard or soft substrata. These mats sequester fine sediments under their holdfast structures (Littler et al. 2005), creating anoxic mounds of soft sediment in otherwise hard-substratum-dominated environments (H. Spalding pers. obs.). Within its natural range, members of the genus *Avrainvillea* have been found at mesophotic depths in Mauritius (*A. amadelpha*) at 90 m (Gepp and Gepp 1911) and on a Bahamian seamount (*A. levis*) at 125 m (Littler and Littler 1992). Despite its high abundance around west and south O'ahu, *Avrainvillea* sp. has not yet been found in the nearby 'Au'au Channel (located between the islands of Lāna'i and Maui), which contains extensive MCEs, and its competitive impact on dominant native mesophotic macroalgae, such as *Halimeda kanaloana* meadows in this region is unknown.

The high abundance and ability of *Avrainvillea* sp. to grow on a diversity of substrata types increases the likelihood of its transport between the islands by potential transfer on construction materials for underwater development, such as pipelines, or by attachment to boat anchors. Removal efforts for mesophotic populations of *Avrainvillea* sp. would be costly and difficult, highlighting the need to limit the spread of this highly adaptable and invasive algal species.



Figure 6.18. *Avrainvillea* sp., an invasive green alga at 50 m, is found offshore of O'ahu's southern and western shores from shallow to mesophotic depths. The diver is measuring the sediment depth under the algal mat. This species has the potential to transform a diverse, coral-dominated area into dense mats of macroalgae over anoxic mounds of sediment (photo Heather Spalding).

6.8. Management options

While some pressures on MCEs are global in origin, and require a global response, others are regional or local. It is important that measures to protect an individual MCE take an adaptive, ecosystem-based management approach to address the cumulative impacts, considering both global and local pressures. MCEs are vulnerable to the same threats and pressures as shallow coral reef ecosystems, but they are

rarely included in the design of marine spatial plans and marine protected areas. Lack of awareness about the existence of MCEs and a limited understanding of their spatial distribution are the main reasons for their exclusion from management plans. The good news is that many of the same management approaches used for shallow-water reefs can be used for MCEs (Table 6.2).

Table 6.2. Management options used for shallow-water reefs (Mumby and Steneck 2008) that could address comparable issues affecting MCEs.

Shallow-water coral reef ecosystems	Mesophotic coral ecosystems
<ul style="list-style-type: none"> • Fishing closures • Marine protected areas (MPAs) • Wastewater treatment and management to reduce pollution • Shipping industry guidelines to curb introduced species • Shipping industry guidelines to restrict discharge of oil • Ensure that international trade of reef species, and their parts and products is sustainable • Placement of fixed mooring buoys to reduce anchor damage • Tourism guidelines to reduce reef damage • Coral reef rehabilitation for damaged areas • Public education and involvement 	<ul style="list-style-type: none"> • Fishing closures • MPAs (MCEs are not considered in most countries) • Wastewater treatment and management to reduce pollution (potential) • Shipping industry guidelines to curb introduced species (potential) • Shipping industry guidelines to restrict discharge of oil (potential) • Ensure that international trade of mesophotic reef species, and their parts and products is sustainable (potential) • Placement of fixed mooring buoys to reduce anchor damage (potential) • Diving guidelines to reduce reef damage (potential) • Guidelines for oil and gas exploration, alternative energy, cables and pipelines (potential)

Understanding mesophotic coral ecosystems: knowledge gaps for management

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Patrick L. Colin, Coral Reef Research Foundation, Palau

7.1. Introduction

In comparison to their shallow-water counterparts, very little is known about MCEs. MCEs have been understudied, not due to their lack of importance, but because of the difficulty in accessing them with conventional technologies. The upper limit of the mesophotic zone, at 30–40 m, is too deep for scuba diving on air, while the lower limit of the mesophotic zone is too shallow for deep-diving technologies (e.g. submersibles and large remotely operated vehicles) to be used effectively and efficiently. Consequently, approximately two-thirds of light-dependent coral reef ecosystems remain largely unknown (Pyle 1996b, 2000, Feitoza et al. 2005, Puglise et al. 2009).

Although the study of MCEs has increased exponentially in the past 30 years — with the adoption of mixed-gas and closed-circuit rebreather scuba diving by scientists and the development of smaller remotely operated vehicles and autonomous underwater vehicles — there are still large gaps in our scientific knowledge. In 2008, the *First International Mesophotic Coral Ecosystems Workshop* (12–15 July in Jupiter, Florida, USA), organized by the U.S. National Oceanic and Atmospheric Administration and Geological Survey, brought together scientists and resource managers for the first time to discuss and review the state of knowledge regarding MCEs (Puglise et al. 2009, Hinderstein et al. 2010). The workshop resulted in three significant advances in improving our understanding of MCEs: (1) an agreed definition for MCEs (see text box), (2) a *Mesophotic Coral Ecosystem Research Strategy* (Figure 7.1), which identified critical management information needs (Puglise et al. 2009), and (3) a special MCE-themed section of the journal *Coral Reefs* (volume 29, number 2, pages 247–378) that reviewed what was known about these ecosystems (Hinderstein et al. 2010). By 2014, the MCE research community realized that there was a need for a *Second International Mesophotic Coral Ecosystems Workshop* to evaluate developments made in knowledge since 2008. Following the second workshop held by the Interuniversity Institute for Marine Sciences (26–31 October 2014 in Eilat, Israel), a special MCE-themed section of the journal *Coral Reefs* (volume 35, number 1) was developed, which highlights the latest MCE research efforts and identifies information gaps and priorities for future MCE research (Loya et al. 2016).

Mesophotic coral ecosystems definition

Mesophotic coral ecosystems are characterized by the presence of light-dependent corals and associated communities typically found at depths ranging from 30–40 m and extending to over 150 m in tropical and subtropical regions. The dominant communities providing structural habitat in the mesophotic zone can be comprised of coral, sponge, and algal species (Puglise et al. 2009, Hinderstein et al. 2010)

The two workshops made it abundantly clear that there is a growing body of work on the topic of MCEs and that the scientific community has made progress in gaining visibility for MCEs. This is best evidenced by searching peer-reviewed journals (using the Aquatic Sciences and Fisheries Abstracts database) for the term “mesophotic coral”. Search results show that before the first workshop was held in 2008, the term “mesophotic coral” was used only once, but it has been used in over 55 publications since 2008. This change is the direct result of scientists coalescing around the term MCEs for these ecosystems.

MCE visibility has improved within both the scientific and management communities, and scientists are making incremental improvements in our understanding of these ecosystems. However, there are still large gaps in our understanding of MCEs, especially in comparison with our knowledge of shallow reefs. The best way to close these information gaps is to focus research efforts on answering questions that are critical to enabling resource managers to make informed decisions about MCE protection and conservation. For MCEs, the most crucial information is what scientists refer to as “baseline information”. Key questions include: where are MCEs located? What controls where MCEs are found? What organisms are found in MCEs? What ecological role do MCEs play? What are the impacts from natural and anthropogenic threats on MCEs? Are MCEs connected to shallower reefs and can they serve as refuges for impacted shallow species?

7.2. Where are mesophotic coral ecosystems located?

MCEs have only been studied in a few places. As a rule of thumb, the best studied MCEs are also the most easily accessed by scientists and have infrastructure in place to support deep diving (e.g. a diving chamber and gas mixing facilities) and the use of undersea technologies (e.g. vessels with dynamic positioning for remotely operated vehicles and winches for launching heavy equipment). Thus, most work to date has been conducted in the Caribbean, the Gulf of Mexico, the Hawaiian Islands, the Red Sea, the main Palau Island group, Japan and the Great Barrier Reef. This has left major geographic gaps in our understanding of MCEs, particularly in the equatorial regions of the Indo-West Pacific (see Chapter 2, Figure 2.3). Large reef systems

in the “coral triangle” (Indonesia, the Philippines, Papua New Guinea and Solomon Islands), Micronesia, Polynesia and Melanesia, as well as the Maldives, the Chagos area, the Seychelles and the large banks of the central Indian Ocean, remain poorly documented. Knowledge of potential MCEs in the tropical regions off the west coast of Africa and the Pacific coasts of Mexico, Central America and South America remain a complete mystery.

Research Need: Locate where MCEs exist, with a priority in the equatorial regions of the Indo-West Pacific region, eastern Atlantic Ocean, and the Pacific coasts of Mexico, Central America and South America.

7.3. What controls where mesophotic coral ecosystems are found?

Like shallow coral reefs, MCEs are patchily distributed. Why well-developed MCEs are found in some areas and not others needs to be better understood. In La Parguera, Puerto Rico (see the case study in Chapter 3.10), scientists found only five well-developed MCEs within a 20 km stretch off the coast. Geological processes strongly influenced the siting of these MCEs, with the best developed ones located on topographic highs on steep southwest facing slopes where sedimentation was lowest. Meanwhile in Hawai'i, the best developed MCEs were found where there was clear water for deep light penetration and a submerged terrace located at the right depth for MCEs, forming a natural flume that improves water flow and enhances productivity (Costa et al. 2015, Pyle pers. com.).

Better knowledge of basic physical information on mesophotic reefs, particularly long-term datasets, would greatly enhance our ability to understand these ecosystems. Determining the role of water temperature, light levels, water currents, vertical water movements, sediment flux and turbidity coupled with high-resolution bathymetric data will help to better identify the parameters defining where MCEs are found, as well as to develop models to predict where MCEs are located. The use of models can help researchers and managers to identify priority areas with the potential to harbour MCEs, to ensure that limited funding for in situ research is targeted (Costa et al. 2015).

Research Need: Understand the geological and physical processes that control MCE distribution to enable us to predict where MCEs occur.

7.4. What ecological role do mesophotic coral ecosystems play and what organisms are found in them?

As we learned in Chapter 4, MCEs harbour complex and diverse assemblages of flora and fauna. Discoveries of flora and fauna that are new to science are common occurrences at mesophotic depths, and known species are being documented in new areas. The mantra for mesophotic scientists should be “The more we look, the more we find”. Because only a few areas have been studied, opportunities abound to enhance our knowledge of the breadth of organisms that inhabit MCEs. Species inventories are needed for understanding biodiversity in MCEs. This information must go beyond presence/absence data to include quantitative information on the number of individuals in order to determine population size for mobile species, and per cent cover for sessile species. Quantitative information will make it possible to calculate the degree of biodiversity and determine the number of unique or endemic species that occur in mesophotic habitats. In addition to quantitative information, collection and preservation of whole organisms along with genetic samples and in situ photographs are needed to enable species to be appropriately documented and identified.

Understanding which species are commonly found in MCEs will also help our understanding of relationships between species. Are there ecologically-important species, without whose presence the MCE ceases to function normally? How are these habitats utilized by species and does their utilization change over time? Are MCEs used by commercially- and/or ecologically-important species? All these questions are key to determining how to appropriately protect and conserve these ecosystems and yet, our understanding of them is limited and mostly relies on our knowledge of shallow coral reefs.

Research Need: Characterize MCE biodiversity to better understand, protect and conserve MCEs.

Research Need: Characterize community structure, including patterns of distribution and abundance.

Research Need: Understand the role of MCEs in supporting various life stages of living marine resources and the processes that regulate these ecosystems.

7.5. What are the impacts of natural and anthropogenic threats on mesophotic coral ecosystems?

Worldwide, shallow coral reef ecosystems are facing an array of natural and anthropogenic threats, including fishing, pollution, invasive species, climate change and extreme events (e.g. tropical cyclones), which are contributing to their decline (Wilkinson 2008). MCEs face similar threats, albeit to differing degrees. For light-dependent mesophotic organisms living at low light levels (1 per cent of that found at the sea surface), anything that inhibits light reaching the depths (e.g. sedimentation, turbidity or pollution) has a marked impact on their survival.

As we learned in Chapter 6, little is known or understood about the extent of the impact from natural and anthropogenic threats to MCEs. In many cases, our knowledge of these impacts is incidental. For example, in Puerto Rico, a single colony of the

knobby cactus coral, *Mycetophyllia aliciae*, was documented going from a healthy appearance to dead within five months. We know this because it happened within a research study's photographic time-series, but we don't know what caused it, or whether it occurred in only this coral colony or was found throughout colonies in the area. In general, the specific impacts from climate change and increasing carbon dioxide levels, fishing, pollution and invasive species and the effects of extreme events (such as tropical cyclones, earthquakes and tsunamis) on MCEs require documentation and study if resource managers are to address them in a meaningful way.

Research Need: Determine the anthropogenic and natural threats to MCEs and assess the ecological impacts and their subsequent recovery, if any, from them.

7.6. Are mesophotic coral ecosystems connected to shallow reefs and can they serve as refuges for impacted shallow species?

With the documented decline of shallow coral reefs, there has been strong interest in determining the level of ecosystem connectivity between shallow and mesophotic reefs. Ecosystem connectivity in the broadest sense is the exchange of materials (nutrients, organisms, and genes) between ecosystems. Connectivity can be further broken down into three types: genetic (exchange of genes and organisms), ecological (exchange of individuals) and oceanographic (water circulation patterns and material flow) connectivity.

The potential that MCEs may be ecologically or genetically connected to shallow reefs, and may serve as refugia for shallow reef species in decline from multiple natural and anthropogenic stressors, has brought hope to resource managers that all may not be lost. The 'deep reef refugia' hypothesis, first postulated in the mid-1990s, was based on the premise that MCEs may serve as a refuge or population source for replenishing shallow reef species being impacted by thermal stress induced by climate change (Glynn 1996). This hypothesis has since been expanded to also include serving as a refuge from fishing, pollution and other threats. The idea is that depth and distance from shore buffer or protect MCEs from the direct impacts associated with these threats, thereby allowing mesophotic populations to survive through disturbances primarily affecting shallow-water reefs, and reducing the likelihood that a species would be extirpated from a region by a severe disturbance event. In addition to serving as a refuge, a second premise of the hypothesis is that surviving populations could assist the recovery of shallower reefs by reseeding or replenishing shallower populations. Such

replenishment is dependent on a number of factors, including whether the same species are present at both depths, the extent of species adaptation at particular depths, and whether there is oceanographic connectivity between them.

Data on connectivity between shallow and mesophotic reefs is limited (Bongaerts et al. 2010a, Kahng et al. 2014). With the exception of a few studies, the validity of the deep reef refugia hypothesis can only be evaluated on known species distributions. Considering this, there is potential that many fish species are connected between shallow and mesophotic habitats, as has been shown for the threespot damselfish, *Chromis verater*, in the Hawaiian Islands (Tenggardjaja et al. 2014) using genetics, and for commercially-important snappers and groupers in the Caribbean (Bejarano et al. 2014). However, for coral species, the possibility of connectedness only exists for those living in the upper mesophotic zone (30–50 m) to mid-mesophotic zone (50–70 m) in clear waters, because the deeper mesophotic zone tends to be populated by coral species that are not found in shallow waters (Bongaerts et al. 2010a, Pochon et al. 2015). Determining the degree of connectivity of MCEs with shallow reefs and other MCEs for key sessile and mobile species is crucial to ensuring that effective management measures, such as marine protected areas (Lesser et al. 2009), are implemented.

Research Need: Understand the genetic, ecological and oceanographic connectivity of MCEs with shallow reefs and other MCEs.

Research Need: Determine whether MCEs can serve as refugia and reseed shallow reefs (or vice versa).

References

- Abbot, I.A. and Huisman, J.M. (2004). Marine green and brown algae of the Hawaiian Islands. Bishop Museum Press, Honolulu, Hawai'i, 259 p.
- Adams, J. (2012). Live Aquaria sells \$5000 narcosis angelfish almost immediately. Available from <http://reefbuilders.com/2012/10/18/liveaquaria-narcosis-angelfish/> [Accessed April 25, 2015].
- Adey, W.H., Townsend, R.A. and Boykins, W.T. (1982). The crustose coralline algae (Rhodophyta: Corallinaceae) of the Hawaiian Islands. *Smithsonian Contributions to Marine Science*, vol. 15, pp. 1-74.
- Agegian, C.R. and Abbott, I.A. (1985). Deep water macroalgal communities: a comparison between Penguin Bank (Hawaii) and Johnston Atoll. In: *Proceedings of the Fifth International Coral Reef Symposium*, vol. 5, pp. 47-50.
- Alamaru, A., Loya, Y., Brokovich, E., Yam, R. and Shemesh, A. (2009). Carbon and nitrogen utilization in two species of Red Sea corals along a depth gradient: insights from stable isotope analysis of total organic material and lipids. *Geochimica et Cosmochimica Acta*, vol. 73, No. 18, pp. 5333-5342.
- Albins, M.A. and Hixon, M.A. (2008). Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes. *Marine Ecology Progress Series*, vol. 367, pp. 233-238.
- Albright, R., Mason, B., Miller, M. and Langdon, C. (2010). Ocean acidification compromises recruitment success of the threatened Caribbean coral *Acropora palmata*. *Proceedings of National Academy of Sciences*, vol. 107, pp. 20400-20404.
- Alderslade, P. (2002). A new soft coral genus (Coelenterata: Octocorallia) from Palau. *The Beagle*, vol. 18, pp. 1-8.
- Allen, G.R. and Erdmann, M.V. (2014). Reef fishes of the East Indies, University of Hawai'i Press, Honolulu, 1292 p.
- Allen, G.R. and Randall, J.E. (1996). Three new species of wrasses (Labridae: *Cirrhilabrus*) from Papua New Guinea and the Solomon Islands. *Revue Française d'Aquariologie*, vol. 23, Nos. 3-4, pp. 101-111.
- Allen, G.R., Young, F. and Colin, P.L. (2006). *Centropyge abei*, a new species of deep-dwelling angelfish (Pomacanthidae) from Sulawesi, Indonesia. *Aqua*, vol. 11, No. 1, pp. 13-18.
- Amado-Filho, G.M., Moura, R.L., Bastos, A.C., Salgado, L.T., Sumida, P.Y., Guth, A.Z., Francini-Filho, R.B., Pereira-Filho, G.H., Abrantes, D.P., Brasileiro, P.S., Bahia, R.G., Leal, R.N., Kaufman, L., Kleypas, J.A., Farina, M. and Thompson, E.L. (2012). Rhodolith beds are major CaCO₃ bio-factories in the tropical South West Atlantic. *PLoS ONE*, vol. 7, e35171.
- Anati, D.A. (1974). Water transports in the Gulf of Aqaba. *Locéanographie physique de la Mer Rouge*, CNEXO publ. No. 2, pp. 165-173.
- Andersson, A.J. and Gledhill, D. (2013). Ocean acidification and coral reefs: effects on breakdown, dissolution, and net ecosystem calcification. *Annual Review of Marine Science*, vol. 5, pp. 321-348.
- Andrews, J.C., Dunlap, W.C. and Bellamy, N.F. (1984). Stratification in a small lagoon in the Great Barrier Reef. *Marine and Freshwater Research*, vol. 35, No. 3, pp. 273-284.
- Aponte, N.E. and Ballantine, D.L. (2001). Depth distribution of algal species on the deep insular fore reef at Lee Stocking Island, Bahamas. *Deep Sea Research Part I*, vol. 48, pp. 2185-2194.
- Appeldoorn, R., Ballantine, D., Bejarano, I., Carlo, M., Nemeth, M., Otero, E., Pagan, F., Ruiz, H., Schizas, N., Sherman, C. and Weil, E. (2015). Mesophotic coral ecosystems under anthropogenic stress: a case study at Ponce, Puerto Rico. *Coral Reefs*, In press, DOI 10.1007/s00338-015-1360-5.
- Arellano, S.M. and Fautin, D.G. (2001). Redescription and range extension of the sea anemone *Exocoelactis actinostoloides* (Wassilieff, 1908), with revision of genus *Exocoelactis* (Cnidaria, Anthozoa, Actinaria). *Zoosystema*, vol. 23, No. 4, pp. 645-657.
- Armstrong, R.A. and Singh, H. (2012). Mesophotic coral reefs of the Puerto Rico Shelf. In: Harris, P.T. and Baker, E.K. (eds.). *Seafloor geomorphology as benthic habitat*. Elsevier, London, pp. 365-374.
- Armstrong, R.A., Hanumant, S., Torres, J., Nemeth, R.S., Can, A., Roman, C., Eustice, R., Riggs, L. and Garcia-Moliner, G. (2006). Characterizing the deep insular shelf coral reef habitat of the Hind Bank marine conservation district (US Virgin Islands) using the Seabed autonomous underwater vehicle. *Continental Shelf Research*, vol. 26, pp.194-205.
- Armstrong, R.A., Singh, H., Rivero, S. and Gilbes, F. (2008). Monitoring coral reefs in optically-deep waters. In: *Proceedings of the 11th International Coral Reef Symposium*, Ft. Lauderdale, Florida, 7-11 July 2008, pp. 593-597.
- Aronson, R.B., Sebens, K.P. and Ebersole, J.P. (1994). Hurricane Hugo's impact on Salt River submarine canyon, St. Croix, U.S. Virgin Islands. In: Ginsburg, R.N. (ed.). *Proceedings of the Colloquium on Global Aspects of Coral Reefs: Health, Hazards, and History*, Miami: Rosenstiel School of Marine and Atmospheric Science, University of Miami, pp. 189-195.
- Ashcroft, M.B. (2010). Identifying refugia from climate change. *Journal of Biogeography*, vol. 37, No. 8, pp. 1407-1413.
- Baird, A.H., Bhagooli, R., Ralph, P.J. and Takahashi, S. (2009). Coral bleaching: the role of the host. *Trends in Ecology and Evolution*, vol. 24, No. 1, pp. 16-20.
- Bak, R.P.M., Nieuwland, G. and Meesters, E.H. (2005). Coral reef crisis in deep and shallow reefs: 30 years of constancy and change in reefs in Curacao and Bonaire. *Coral Reefs*, vol. 24, pp. 475-479.
- Baker, A.C., Glynn, P.W. and Riegl, B. (2008). Climate change and coral reef bleaching: an ecological assessment of long-term impacts, recovery trends and future outlook. *Estuarine, Coastal and Shelf Science*, vol. 80, pp. 435-471.
- Baker, E.K. and Harris, P.T. (2011). Habitat mapping and marine management. Seafloor geomorphology as benthic habitat-GeoHAB atlas of seafloor geomorphic features and benthic habitats, pp. 23-38.
- Baldwin, C.C. and Robertson, D.R. (2013). A new *Haptoclinus* blenny (Teleostei, Labrisomidae) from deep reefs off Curaçao, southern Caribbean, with comments on relationships of the genus. *Zookeys*, vol. 306, pp. 71-81.
- Baldwin, C.C. and Robertson, D.R. (2014). A new *Liopropoma* sea bass (Serranidae, Epinephelinae, Liopropomini) from deep reefs off Curaçao, southern Caribbean, with comments on depth distributions of western Atlantic liopropomins. *Zookeys*, vol. 409, pp. 71-92.
- Ballantine, D.L. and Aponte, N.E. (2002). A checklist of the benthic marine algae known to Puerto Rico, second revision. *Constancea* 83, online continuation of California Publications in Botany (1902-2002). Available from http://ucjeps.berkeley.edu/constancea/83/ballantine_aponte/checklist.html. [Accessed October 2015].
- Ballantine, D.L. and Aponte, N.E. (2003). An annotated checklist of deep-reef benthic marine algae from Lee Stocking Island, Bahamas (western Atlantic). I. Chlorophyta and Heterokontophyta. *Nova Hedwigia*, vol. 76, Nos. 1-2, pp. 113-127.
- Ballantine, D.L. and Aponte, N.E. (2005). An annotated checklist of deep-reef benthic marine algae from Lee Stocking Island, Bahamas. II. Rhodophyta. *Nova Hedwigia*, vol. 80, pp. 147-171.
- Ballantine, D.L., Ruiz, H. and Aponte, N.E. (2008). Changes to macroalgal species communities in shelf edge coral reef habitats in southwest Puerto Rico [abstract]. 11th International Coral Reef Symposium, 7-11 July 2008, Fort Lauderdale, Florida, pp. 424.
- Ballantine, D.L., Ruiz, H. and Aponte, N.E. (2010). Algal composition and dynamics in mesophotic coral reefs, southwest Puerto Rico [abstract]. 64th Annual Phycological Society of America Meeting, 10-13 July 2010, East Lansing, Michigan, Michigan State University.
- Ballantine, D.L., Ruiz, H. and Norris, J.N. (2015). Notes on the benthic marine algae of Puerto Rico. XI: new records including *Meredithia* (Kallymeniaceae, Rhodophyta) species. *Botanica Marina*, vol. 58, No. 5, pp. 355-365.
- Ballard, R.D. and Uchupi, E. (1970). Morphology and Quaternary history of the continental shelf of the Gulf Coast of the United States. *Bulletin of Marine Science*, vol. 20, No. 3, pp. 547-559.
- Barbour, A.B., Montgomery, M.L., Adamson, A.A., Díaz-Ferguson, E. and Silliman, B.R. (2010). Mangrove use by the invasive lionfish *Pterois volitans*. *Marine Ecology Progress Series*, vol. 401, pp. 291-294.
- Bare, A.Y., Grimshaw, K.L., Rooney, J.J., Sabater, M.G., Fenner, D. and Carroll, B. (2010). Mesophotic communities of the insular shelf at Tutuila, American Samoa. *Coral Reefs*, vol. 29, pp. 369-377.
- Beaman, R.J., Webster, J.M. and Wust, R.A.J. (2008). New evidence for drowned shelf edge reefs in the Great Barrier Reef, Australia. *Marine Geology*, vol. 247, Nos. 1-2, pp. 17-34.
- Bejarano Rodríguez, I. (2013). Deep reef fishes off La Parguera insular slope, Puerto Rico, and their connectivity with shallow reefs [dissertation]. University of Puerto Rico Mayagüez, Puerto Rico, 115 p.
- Bejarano, I., Appeldoorn, R.S. and Nemeth, M. (2014). Fishes associated with mesophotic coral ecosystems in La Parguera, Puerto Rico. *Coral Reefs*, vol. 33, No. 2, pp. 313-328.
- Bell, J.J., Davy, S.K., Jones, T., Taylor, M.W. and Webster, N.S. (2013). Could some coral reefs become sponge reefs as our climate changes? *Global Change Biology*, vol. 19, No. 9, pp. 2613-2624.
- Ben-Avraham, Z., Almagor, G. and Garfunkel, Z. (1979). Sediments and

- structure of the Gulf of Elat (Aqaba)-Northern Red Sea. *Sedimentary Geology*, vol. 23, pp. 239-267.
- Berman, T., Paldor, N. and Brenner, S. (2000). Simulation of wind-driven circulation in the Gulf of Elat (Aqaba). *Journal of Marine Systems*, vol. 26, pp. 349-365.
- Biton, E. and Gildor, H. (2011). The general circulation of the Gulf of Aqaba (Gulf of Eilat) revisited: The interplay between the exchange flow through the Straits of Tiran and surface fluxes. *Journal of Geophysical Research*, vol. 116, C08020.
- Blair, S.M. and Norris, J.N. (1988). The deep-water species of *Halimeda* Lamouroux (Halimedaceae, Chlorophyta) from San Salvador Island, Bahamas: species composition, distribution and depth records. *Coral Reefs*, vol. 6, pp. 227-36.
- Blyth-Skyrme, V.J., Rooney, J.J., Parrish, F.A. and Boland, R.C. (2013). Mesophotic coral ecosystems — potential candidates as essential fish habitat and habitat areas of particular concern. Pacific Islands Fisheries Science Center, National Marine Fisheries Science Center Administrative Report H-13-02, 53 p.
- Bohlke, J.E. and Chaplin, C.C.G. (1968). Fishes of the Bahamas and adjacent tropical waters. Livingston Publication Co., Wynnewood, Pennsylvania.
- Boland, R.C., Parrish, F.A. and Rooney, J.J. (2011). Fish communities of the mesophotic ecosystems in the Hawaiian Archipelago [abstract]. American Society of Limnology and Oceanography Aquatic Sciences Meeting, San Juan, Puerto Rico, Feb. 13-18, 2011.
- Bolden, S.K. (2000). Long-distance movement of a Nassau grouper (*Epinephelus striatus*) to a spawning aggregation in the central Bahamas. *Fishery Bulletin*, vol. 98, No 3, pp. 642-645.
- Bongaerts, P., Bridge, T.C.L., Kline, D.I., Muir, P.R., Wallace, C.C., Hoegh-Guldberg, O. and Beaman, R.J. (2011b). Mesophotic coral ecosystems on the walls of Coral Sea atolls. *Coral Reefs*, vol. 30, pp. 335-335.
- Bongaerts, P., Carmichael, M., Hay, K.B., Tonk, L., Frade, P.R. and Hoegh-Guldberg, O. (2015a). Prevalent endosymbiont zonation shapes the depth distributions of scleractinian coral species. *Royal Society Open Science*, vol. 2, No. 2, 140297.
- Bongaerts, P., Frade, P.R., Hay, K.B., Englebert, N., Latijnhouwers, K.R.W., Bak, R.P.M., Vermeij, M.J.A. and Hoegh-Guldberg, O. (2015b). Deep down on a Caribbean reef: lower mesophotic depths harbor a specialized coral-endosymbiont community. *Scientific Reports*, vol. 5, 7652.
- Bongaerts, P., Frade, P.R., Ogier, J.J., Hay, K.B., Van Bleijswijk, J., Englebert, N., Vermeij, M.J., Bak, R.P., Visser, P.M. and Hoegh-Guldberg, O. (2013b). Sharing the slope: depth partitioning of agariciid corals and associated *Symbiodinium* across shallow and mesophotic habitats (2-60 m) on a Caribbean reef. *BMC Evolutionary Biology*, vol. 13, 205.
- Bongaerts, P., Muir, P., Englebert, N., Bridge, T.C.L. and Hoegh-Guldberg, O. (2013a). Cyclone damage at mesophotic depths on Myrmidon Reef (GBR). *Coral Reefs*, vol. 32, No. 4, p. 935.
- Bongaerts, P., Ridgway, T., Sampayo, E.M. and Hoegh-Guldberg, O. (2010a). Assessing the 'deep reef refugia' hypothesis: focus on Caribbean reefs. *Coral Reefs*, vol. 29, No. 2, pp. 309-327.
- Bongaerts, P., Riginos, C., Hay, K.B., van Oppen, M.J.H., Hoegh-Guldberg, O. and Dove, S. (2011a). Adaptive divergence in a scleractinian coral: physiological adaptation of *Seriatopora hystrix* to shallow and deep reef habitats. *BMC Evolutionary Biology*, vol. 11, 303.
- Bongaerts, P., Riginos, C., Ridgway, T., Sampayo, E.M., van Oppen, M.J.H., Englebert, N., Vermeulen, F. and Hoegh-Guldberg, O. (2010b). Genetic divergence across habitats in the widespread coral *Seriatopora hystrix* and its associated *Symbiodinium*. *PLoS ONE*, vol. 5, e10871.
- Brakel, W.H. (1979). Small-scale spatial variation in light available to coral reef benthos: quantum irradiance measurements from a Jamaican reef. *Bulletin of Marine Science*, vol. 29, No. 3, pp. 406-413.
- Breedy, O. and Guzman, H.M. (2013). A new species of the genus *Eugorgia* (Cnidaria: Octocorallia: Gorgoniidae) from mesophotic reefs in the Eastern Pacific. *Bulletin of Marine Science*, vol. 89, No. 3, pp. 735-743.
- Bridge, T.C.L. and Guinotte, J.M. (2012). Mesophotic coral reef ecosystems in the Great Barrier Reef world heritage area: their potential distribution and possible role as refugia from disturbance. Great Barrier Reef Marine Park Authority, Townsville, 51 p.
- Bridge, T.C.L., Beaman, R.J., Done, T.J. and Webster, J.M. (2012a). Predicting the location and spatial extent of submerged coral reef habitat in the central Great Barrier Reef. *PLoS ONE*, vol. 7, No. 10, e48203.
- Bridge, T.C.L., Done, T.J., Beaman, R.J., Friedman, A., Williams, S.B., Pizarro, O. and Webster, J.M. (2011a). Topography, substratum, and benthic macrofaunal relationships on a tropical mesophotic shelf margin, central Great Barrier Reef, Australia. *Coral Reefs*, vol. 30, pp. 143-153.
- Bridge, T.C.L., Done, T.J., Friedman, A., Beaman, R.J., Williams, S.B., Pizarro, O. and Webster J.M. (2011b). Variability in mesophotic coral reef communities along the Great Barrier Reef, Australia. *Marine Ecology Progress Series*, vol. 428, pp. 63-75.
- Bridge, T.C.L., Fabricius, K.E., Bongaerts, P., Wallace, C.C., Muir, P.R., Done, T.J. and Webster J.M. (2012b). Diversity of Scleractinia and Octocorallia in the mesophotic zone of the Great Barrier Reef, Australia. *Coral Reefs*, vol. 31, pp. 179-189.
- Bridge, T.C.L., Grech, A.M. and Pressey, R.L. (2015). Factors influencing incidental representation of previously unknown features in marine protected areas. *Conservation Biology*, DOI: 10.1111/cobi.12557.
- Bridge, T.C., Hoey, A.S., Campbell, S.J., Muttaqin, E., Rudi, E., Fadli, N. and Baird, A.H. (2014). Depth-dependent mortality of reef corals following a severe bleaching event: implications for thermal refuges and population recovery. *F1000Research*, vol. 2, 187.
- Bridge, T.C., Hughes, T.P., Guinotte, J.M., and Bongaerts, P. (2013). Call to protect all coral reefs. *Nature Climate Change*, vol. 3, No. 6, pp. 528-530.
- Brokovich, E., Ayalon, I., Einbinder, S., Segev, N., Shaked, Y., Genin, A., Kark, S. and Kiflawi, M. (2010). Grazing pressure on coral reefs decreases across a wide depth gradient in the Gulf of Aqaba, Red Sea. *Marine Ecology Progress Series*, vol. 399, pp. 69-80.
- Brokovich, E., Einbinder, S., Shashar, N., Kiflawi, M. and Kark, S. (2008). Descending to the twilight zone: changes in coral reef fish assemblages along a depth gradient down to 65 m. *Marine Ecology Progress Series*, vol. 371, pp. 253-262.
- Brostoff, W.N. (1989). *Avrainvillea amadelpha* (Codiales, Chlorophyta) from Oahu, Hawaii. *Pacific Science*, vol. 43, pp. 166-69.
- Bruno, J., Siddon, C., Witman, J., Colin, P. and Toscano, M. (2001). El Niño related coral bleaching in Palau, western Caroline Islands. *Coral Reefs*, vol. 20, No. 2, pp. 127-136.
- Bryan, D.R., Kilfoyle, K., Gilmore, R.G. and Spieler, R.E. (2013). Characterization of the mesophotic reef fish community in south Florida, USA. *Journal of Applied Ichthyology*, vol. 29, pp. 108-117.
- Buerger, P., Schmidt, G., Wall, M., Held, C. and Richter, C. (2015). Temperature tolerance of the coral *Porites lutea* exposed to simulated large-amplitude internal waves (LAIW). *Journal of Experimental Marine Biology and Ecology*, vol. 471, pp. 232-239.
- Burge, C.A., Eakin, C.M., Friedman, C.S., Froelich, B., Hershberger, P.K., Hoffman, E.E., Petes, L.E., Prager, K.C., Weil, E., Willis, B.L., Ford, S.E. and Harvell, C.D. (2014). Climate change influences on marine infectious diseases: implications for management and society. *Annual Review of Marine Science*, vol. 6, pp. 249-277.
- Cairns, S.D. (2000). A revision of the shallow-water azooxanthellate Scleractinia of the western Atlantic. *Studies of the Natural History of the Caribbean Region*, vol. 75, pp. 1-231.
- Carlson, B.A., McKibben, J.N. and DeGruy, M.V. (1984). Telemetric investigation of vertical migration of *Nautilus belauensis* in Palau. *Pacific Science*, vol. 38, No. 3, pp. 183-188.
- Cerrano, C., Cardini, U., Bianchelli, S., Corinaldesi, C., Pusceddu, A. and Danovaro, R. (2013). Red coral extinction risk enhanced by ocean acidification. *Scientific Reports*, vol. 3, 1457.
- Chalker, B.E. and Dunlap, W.C. (1983). Bathymetric adaptations of reef-building corals at Davies Reef, Great Barrier Reef, Australia. II. Light saturation curves for photosynthesis and respiration. *Journal of Experimental Marine Biology and Ecology*, vol. 73, pp. 37-56.
- Chan, Y.L., Pochon, X., Fisher, M.A., Wagner, D., Concepcion, G.T., Kahng, S.E., Toonen, R.J. and Gates, R.D. (2009). Generalist dinoflagellate endosymbionts and host genotype diversity detected from mesophotic (67-100 m depths) coral *Leptoseris*. *BMC Ecology*, vol. 9, 21.
- Claro, R., Sadovy, Y., Lindeman, K.C. and García-Cagide, A.R. (2006). Effects of fishing on spawning aggregations in Cuba strongly influenced by fish and fisher behaviour and fish habitat [abstract]. In: Proceedings of the 59th Annual Gulf and Caribbean Fisheries Institute, vol. 59, pp. 453-454.
- Claydon, J., Calosso, M.C. and Traiger, S.B. (2012). Progression of invasive lionfish in seagrass, mangrove and reef habitats. *Marine Ecology Progress Series*, vol. 448, pp. 119-129.

- Coffroth, M.A. and Santos, S.R. (2005). Genetic diversity of symbiotic dinoflagellates in the genus *Symbiodinium*. *Protist*, vol. 156, No. 1, pp. 19-34.
- Coleman, F.C., Koenig, C.C. and Collins, L.A. (1996). Reproductive styles of shallow-water groupers (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. *Environmental Biology of Fishes*, vol. 47, pp. 129-141.
- Coles, S. and Eldredge, L. (2002). Nonindigenous species introductions on coral reefs: a need for information. *Pacific Science*, vol. 56, pp. 191-209.
- Colin, P.L. (1974). Observation and collection of deep-reef fishes off Jamaica and British Honduras. *Marine Biology*, vol. 24, pp. 29-38.
- Colin, P.L. (1976). Observation of deep reef fishes in the Tongue-of-the-Ocean, Bahamas. *Bulletin of Marine Science*, vol. 26, pp. 603-605.
- Colin, P.L. (1978). Caribbean reef invertebrates and plants. T.F.H. Publications, Neptune, New Jersey.
- Colin, P.L. (1999). Palau at depth. *Ocean Realm Magazine*, pp. 77-87.
- Colin, P.L. (2009). Marine Environments of Palau, Indo-Pacific Press, San Diego, 414 p.
- Colin, P.L., Devaney, D.M., Hillis-Colinvaux, L., Suchanek, T.H. and Harrison, J.T. (1986). Geology and biological zonation of the reef slope, 50-360 m depth at Eniwetok Atoll, Marshall Islands. *Bulletin of Marine Science*, vol. 38, pp. 111-128.
- Concepcion, G.T., Kahng, S.E., Crepeau, M.W., Franklin, E.C., Coles, S.L. and Toonen, R.J. (2010). Resolving natural ranges and marine invasions in a globally distributed octocoral (genus *Carijoa*). *Marine Ecology Progress Series*, vol. 401, pp. 113-127.
- Costa, B., Kendall, M.S., Parrish, F.A., Rooney, J., Boland, R.C., Chow, M., Lecky, J., Montgomery, A. and Spalding, H. (2015). Identifying suitable locations for mesophotic hard corals offshore of Maui, Hawai'i. *PLoS ONE*, vol. 10, No. 7, e0130285.
- Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P. and van den Belt, M. (1997). The value of the world's ecosystem services and natural capital. *Nature*, vol. 387, pp. 253-260.
- Cross, V.A., Twichell, D., Halley, R., Ciembronowicz, K., Jarrett, B., Hammar-Klose, E., Hine, A., Locker, S. and Naar, D. (2005). GIS compilation of data collected from the Pulley Ridge deep coral reef region. USGS Open-File Report 2005-1089.
- Culter, J., Ritchie, K., Earle, S., Guggenheim, D., Halley, R., Ciembronowicz, K., Hine, A., Jarrett, B., Locker, S. and Jaap, W. (2006). Pulley reef: a deep photosynthetic coral reef on the West Florida Shelf, USA. *Coral Reefs*, vol. 25, No. 2, 228.
- Darling, E.S., Green, S.J., O'Leary, J.K. and Côté, I.M. (2011). Indo-Pacific lionfish are larger and more abundant on invaded reefs: a comparison of Kenyan and Bahamian lionfish populations. *Biological Invasions*, vol. 13, No.9, pp. 2045-2051.
- Darnell, R.M. (1990). Mapping of the biological resources of the continental shelf. *American Zoologist*, vol. 30, pp. 15-21.
- Darnell, R.M. and Defenbaugh, R.E. (1990). Gulf of Mexico: Environmental overview and history of environmental research. *American Zoologist*, vol. 30, pp. 3-6.
- Darwin, C. (1889). The structure and distribution of coral reefs. Smith, Elder, and Co., London.
- Davies, P.S. (1977). Carbon budgets and vertical zonation of Atlantic reef corals. In: Proceedings of the Third International Coral Reef Symposium, vol. 1, pp. 391-396.
- De'ath, G., Fabricius, K.E., Sweatman, H. and Puotinen, M. (2012). The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proceedings of the National Academy of Sciences*, vol. 109, No. 44, pp. 17995-17999.
- de Goeij, J.M., Moodley, L., Houtekamer, M., Carballeira, N.M. and van Duyl, F.C. (2008). Tracing ¹³C-enriched dissolved and particulate organic carbon in the bacteria-containing coral reef sponge *Halisarca caerulea*: evidence for DOM feeding. *Limnology and Oceanography*, vol. 53, No. 4, pp. 1376-1386.
- de Goeij, J.M., van Oevelen, D., Vermeij, M.J.A., Osinga, R., Middelburg, J., de Goeij, A.F.P.M. and Admiraal, W. (2013). Surviving in a marine desert: the sponge loop retains resources within coral reefs. *Science*, vol. 342, No. 6154, pp. 108-110.
- DeMartini, E.E. and Friedlander, A.M. (2004). Spatial patterns of endemism in shallow-water reef fish populations of the Northwestern Hawaiian Islands. *Marine Ecology Progress Series*, vol. 271, pp. 281-296.
- De Mitcheson, Y.S., Cornish, A., Domeier, M., Colin, P.L., Russell, M. and Lindeman, K.C. (2008). A global baseline for spawning aggregations of reef fishes. *Conservation Biology*, vol. 22, No. 5, pp. 1233-1244.
- Denis, V., De Palmas, S., Benzoni, F. and Chen, C.A. (2014). Extension of the known distribution and depth range of the scleractinian coral *Psammocora stellata*: first record from a Taiwanese mesophotic reef. *Marine Biodiversity*, pp. 1-2.
- Dennis, G.D. and Bright, T.J. (1988). Reef fish assemblages on hard banks in the Northwestern Gulf of Mexico. *Bulletin of Marine Science*, vol. 43, No. 2, pp. 280-307.
- Department of Environment. (2015). Gulf of Carpentaria Commonwealth Marine Reserve. <http://www.environment.gov.au/topics/marine/marine-reserves/north-gulf-of-carpentaria> [Accessed October 2015].
- Dinesen, Z., Bongaerts, P., Bridge, T., Kahng, S.E. and Luck, D.G. (2012). The importance of the coral genus *Leptoseris* to mesophotic coral communities in the Indo-Pacific [poster]. 12th International Coral Reef Symposium, Cairns, Australia, Available from [Accessed October 2015].
- Doropoulos, C., Ward, S., Diaz-Pulido, G., Hoegh-Guldberg, O. and Mumby, P.J. (2012). Ocean acidification reduces coral recruitment by disrupting intimate larval-algal settlement interactions. *Ecology Letters*, vol. 15, pp. 338-346.
- Drew, E.A. and Abel, K.M. (1988). Studies on *Halimeda*. I. The distribution and species composition of *Halimeda* meadows throughout the Great Barrier Reef Province. *Coral Reefs*, vol. 6, pp. 195-205.
- Duckworth, A.R. and Peterson, B.J. (2013). Effects of seawater temperature and pH on the boring rates of the sponge *Cliona celata* in scallop shells. *Marine Biology*, vol. 160, pp. 27-35.
- Duckworth, A.R., West, L., Vansach, T., Stubler, A. and Hardt, M. (2012). Effects of water temperature and pH on growth and metabolite biosynthesis of coral reef sponges. *Marine Ecology Progress Series*, vol. 462, pp. 67-77.
- Eldredge, L. and Carlton, J. (2002). Hawaiian marine bioinvasions: a preliminary assessment. *Pacific Science*, vol. 56, pp. 211-212.
- Eldredge, L.G. and Evenhuis, N.L. (2003). Hawaii's biodiversity: a detailed assessment of the numbers of species in the Hawaiian Islands. Records of the Hawaii biological survey for 2001-2002. *Bishop Museum Occasional Papers*, vol. 76, pp. 1-28.
- Englebert, N., Bongaerts, P., Muir, P.R., Hay, K.B. and Hoegh-Guldberg, O. (2014). Deepest zooxanthellate corals of the Great Barrier Reef and Coral Sea. *Marine Biodiversity*, vol. 45, No. 1, pp. 1-2.
- Enriquez, S., Méndez, E.R. and Prieto, R.I. (2005). Multiple scattering on coral skeletons enhances light absorption by symbiotic algae. *Limnology and Oceanography*, vol. 50, No. 4, pp. 1025-1032.
- Ertfemeijer, P.L.A., Riegl, B., Hoeksema, B.W. and Todd, P.A. (2012). Environmental impacts of dredging and other sediment disturbances on corals: a review. *Marine Pollution Bulletin*, vol. 64, No. 9, pp. 1737-1765.
- Eyal, G. (2012). Ecology and Taxonomy of mesophotic communities in Israel (Red Sea and Mediterranean) [M.S. thesis]. Tel Aviv University. Irsael 64 p.
- Eyal, G., Eyal-Shaham, L., Cohen, I., Tamir, R., Ben-Zvi, O., Sinniger, F. and Loya, Y. (2016). *Euphyllia paradivisa*, a successful mesophotic coral in the northern Gulf of Eilat/Aqaba, Red Sea. *Coral Reefs*, vol. 35, In Press, DOI: 10.1007/s00338-015-1372-1.
- Eyal, G., Eyal-Shaham, L. and Loya, Y. (2011). "Teeth-anchorage": sleeping behavior of a Red Sea filefish on a branching coral. *Coral Reefs*, vol. 30, No. 3, p. 707.
- Fabricius, K.E. (2005). Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine Pollution Bulletin*, vol. 50, pp. 125-146.
- Fabricius, K.E. and Alderslade, P.P. (2001). Soft corals and sea fans: a comprehensive guide to the tropical shallow water genera of the central-west Pacific, the Indian Ocean and the Red Sea. Australian Institute of Marine Science, Townsville, 264 p.
- Fabricius, K.E., Alderslade, P., Williams, G., Colin P.L. and Golbuu Y. (2007). Octocorallia in Palau, Micronesia: Effects of biogeography and coast influences on local and regional biodiversity. In: Kayane, H., Omori, M., Fabricius, K., Verheij, E., Colin, P., Golbuu, Y. and Yukihira, Y. (eds.). Coral reefs of Palau, Palau International Coral Reef Center, pp. 79-91.
- Fabricius, K.E., Langdon, C., Uthicke, S., Humphrey, C., Noonan, S., De'ath, G., Okazaki, R., Muehlehner, N., Glas, M.S. and Lough, J.M. (2011). Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations. *Nature Climate Change*, vol. 1, pp. 165-169.
- Falkowski, P.G. and Raven, J.A. (2007). Aquatic photosynthesis. Princeton University Press, Princeton, New Jersey, 488 p.
- Falkowski, P.G., Jokieli, P.L. and Kinsey, R.R. (1990). Irradiance and corals. In: Dubinsky, Z. (ed.). Ecosystems of the World 25: Coral reefs. Elsevier, Amsterdam, pp. 89-107.
- Faulkner, D. and Chesher, R. (1979). Living corals. Clarkson N. Potter Inc., New York, 310 p.
- Faulkner, D.J., Newman, D.J. and Cragg, G.M. (2004). Investigations of the marine flora and fauna of the Islands of Palau. *Natural Product Reports*, vol. 21, No. 1, pp. 50-76.
- Fautin, D.G. and den Hartog, J.C. (2003). An unusual sea anemone from

- slope depths of the tropical west Pacific: range extension and redescription of *Isactinernus quadrilobatus* Carlgren, 1918 (Cnidaria, Actiniaria: Actineridae). *Zoologische Verhandlungen*, vol. 345, pp. 103-116.
- Feely, R., Sabine, C.L., Lee, K., Berelson, W., Kleypas, J., Fabry, V.J. and Millero, F.J. (2004). Impact of CO₂ on CaCO₃ system in the oceans. *Science*, vol. 305, pp. 362-366.
- Feitoza, B.M., Rosa, R.S. and Rocha, L.A. (2005). Ecology and zoogeography of deep-reef fishes in Northeastern Brazil. *Bulletin of Marine Science*, vol. 76, No 3, pp. 725-742.
- Felder, D.L. and Camp D.K. (2009). Gulf of Mexico origin, waters, and biota. Volume 1, Biodiversity. Texas A&M University Press. 1393 p.
- Fine, M., Gildor, H. and Genin, A. (2013). A coral reef refuge in the Red Sea. *Global Change Biology*, vol. 19, No. 12, pp. 3640-3647.
- Fletcher, C., Bochicchio, C., Conger, C., Engels, M., Feirstein, E., Frazer, N., Glenn, C., Grigg, R., Grossman, E. and Harney, J. (2008). Geology of Hawaii Reefs. In: Riegl, B.M. and Dodge, R.E. (eds.). *Coral Reefs of the USA*. Springer, pp. 435-488.
- Focke, J. and Gebelein, C. (1978). Marine lithification of reef rock and rhodolites at a fore-reef slope locality off Bermuda. *Geologie en Mijnbouw*, vol. 57, pp. 163-171.
- Frade, P.R., Englebert, N., Faria, J., Visser, P.M. and Bak, R.P.M. (2008). Distribution and photobiology of *Symbiodinium* types in different light environments for three colour morphs of the coral *Madracis pharensis*: is there more to it than total irradiance? *Coral Reefs*, vol. 27, No. 4, pp. 913-925.
- Franklin, E.C., Jokiel, P.L. and Donahue, M.J. (2013). Predictive modeling of coral distribution and abundance in the Hawaiian Islands. *Marine Ecology Progress Series*, vol. 481, pp. 121-132.
- Frazer, T.K., Jacoby, C.A., Edwards, M.A., Barry, S.C. and Manfrino, C.M. (2012). Coping with the lionfish invasion: can targeted removals yield beneficial effects? *Reviews in Fisheries Science*, vol. 20, No. 4, pp. 185-191.
- Freudenthal, H.D. (1962). *Symbiodinium* gen. nov. and *S. microadriaticum* sp. nov., a zooxanthella: taxonomy, life cycle, morphology. *Journal of Protozoology*, vol. 9, pp. 45-52.
- Fricke, H. W., and Knauer, B. (1986). Diversity and spatial pattern of coral communities in the Red Sea upper twilight zone. *Oecologia*, vol. 71, No. 1, pp. 29-37.
- Fricke, H.W. and Schuhmacher, H. (1983). The depth limits of Red Sea stony corals: an ecophysiological problem (a deep diving survey by submersible). *Marine Ecology*, vol. 4, pp. 163-194.
- Friedlander, M., Parrish, J.D. and DeFelice, R.C. (2002). Ecology of the introduced snapper *Lutjanus kasmira* (Forsskal) in the reef fish assemblage of a Hawaiian bay. *Journal of Fish Biology*, vol. 60, pp. 28-48.
- Gaither, M.R., Bowen, B.W. and Toonen, R.J. (2013). Population structure in the native range predicts the spread of introduced marine species. *Proceedings of the Royal Society B: Biological Sciences*, vol. 280, 20130409.
- García-Sais, J.R. (2010). Reef habitats and associated sessile-benthic and fish assemblages across a euphotic-mesophotic depth gradient in Isla Desecheo, Puerto Rico. *Coral Reefs*, vol. 29, pp. 277-288.
- García-Sais, J.R., Castro, R.L., Sabater, J.C. and Carlo, M. (2004). Monitoring of coral reef communities from Isla de Vieques, Puerto Rico. Final Report submitted to the Department of Natural and Environmental Resources of Puerto Rico, San Juan, Puerto Rico, 118 p.
- García-Sais, J.R., Williams, S.M., Sabater-Clavell, J., Esteves, R. and Carlo, M. (2014). Mesophotic benthic habitats and associated reef communities at Lang Bank, St. Croix, USVI. Caribbean Fishery Management Council, San Juan, Puerto Rico, 69 p.
- Gardner, P.G., Frazer, T.K., Jacoby, C.A. and Yanong, R.P. (2015). Reproductive biology of invasive lionfish (*Pterois* spp.). *Frontiers in Marine Science*, vol. 2, 7.
- Gardner, T.A., Cote, I.M., Gill, J.A., Grant, A. and Watkinson, A.R. (2003). Long-term region-wide declines in Caribbean corals. *Science*, vol. 301, pp. 958-960.
- Gavio, B. and Fredericq, S. (2005). New species and new records of offshore members of the Rhodymeniales (Rhodophyta) in the northern Gulf of Mexico. *Gulf of Mexico Science*, vol. 1, pp. 58-83.
- Genin, A., Lazar, B. and Brenner, S. (1995). Vertical mixing and coral death in the Red Sea following the eruption of Mount Pinatubo. *Nature*, vol. 377, pp. 507-510.
- Gepp, A. and Gepp, E.S. (1911). The Codiaceae of the Siboga Expedition including a monograph of *Flabellariae* and *Udoteae* (No. 62). EJ Brill.
- Gilmartin, M. (1960). The ecological distribution of the deep water algae of Eniwetok Atoll. *Ecology*, vol. 41, No. 1, pp. 210-221.
- Glynn, P.W. (1996). Coral reef bleaching: facts, hypotheses and implications. *Global Change Biology*, vol. 2, pp. 495-509.
- Glynn, P.W. and D'Croz, L. (1990). Experimental evidence for high temperature stress as the cause of El Niño-coincident coral mortality. *Coral Reefs*, vol. 8, pp. 181-191.
- Goreau, T.F. and Goreau, N.I. (1973). The ecology of Jamaican coral reefs. II. Geomorphology, zonation and sedimentary phases. *Bulletin of Marine Science*, vol. 23, pp. 399-464.
- Goreau, T.F. and Land, L.S. (1974). Fore-reef morphology and depositional processes, north Jamaica. In: Laporte, L.F. (ed.). *Reefs in time and space*. Society of Economic Paleontologists and Mineralogists, Special Publication, vol. 18, pp. 77-89.
- Goreau, T.F. and Wells, J.W. (1967). The shallow-water scleractinian of Jamaica: revised list of species and their vertical distribution range. *Bulletin of Marine Science*, vol. 17, No. 2, pp. 442-453.
- Gori, A., Viladrich, N., Gili, J.M., Kotta, M., Cucio, C., Magni, L., Bramanti, L. and Rossi, S. (2012). Reproductive cycle and trophic ecology in deep versus shallow populations of the Mediterranean gorgonian *Eunicella singularis* (Cap de Creus, northwestern Mediterranean Sea). *Coral Reefs*, vol. 31, No. 3, pp. 823-837.
- Gourlay, M.R. and Colleter, G. (2005). Wave-generated flow on coral reefs — an analysis for two-dimensional horizontal reef-tops with steep faces. *Coastal Engineering*, vol. 52, No. 4, pp. 353-387.
- Graham, M.H., Kinlan, B.P., Druehl, L.D., Garske, L.E. and Banks, S. (2007). Deep-water kelp refugia as potential hotspots of tropical marine diversity and productivity. *Proceedings of the National Academy of Sciences*, vol. 104, pp. 16576-16580.
- Green, S.J., Akins, J.L., Maljković, A. and Côté, I.M. (2012). Invasive lionfish drive Atlantic coral reef fish declines. *PLoS ONE*, vol. 7, No. 3, e32596.
- Green, S.J., Dulvy, N.K., Brooks, A.M., Akins, J.L., Cooper, A.B., Miller, S. and Côté, I.M. (2014). Linking removal targets to the ecological effects of invaders: a predictive model and field test. *Ecological Applications*, vol. 24, No. 6, pp. 1311-1322.
- Grigg, R.W. (1965). Ecological studies of black coral in Hawaii. *Pacific Science*, vol. 19, pp. 244-260.
- Grigg, R.W. (1976). Fisheries management of precious and stony corals in Hawaii. UNIH-SEAGRANT-TR77-03. University of Hawaii Sea Grant, Honolulu, 48 p.
- Grigg, R.W. (1982). Darwin Point: A threshold for atoll formation. *Coral Reefs*, vol. 1, pp. 29-34.
- Grigg, R.W. (1983). Community structure, succession and development of coral reefs in Hawaii. *Marine Ecology Progress Series*, vol. 11, pp. 1-14.
- Grigg, R.W. (1984). Resource management of precious corals. *Marine Ecology*, vol. 5, No. 1, pp. 57-74.
- Grigg, R.W. (1988). Paleogeography of coral reefs in the Hawaiian-Emperor Chain. *Science*, vol. 240, pp. 1737-1742.
- Grigg, R.W. (2006). Depth limit for reef building corals in the Au'au Channel, S.E. Hawaii. *Coral Reefs*, vol. 25, pp. 77-84.
- Grigg, R.W., Polovina, J., Friedlander, A.M. and Rohmann, S.O. (2008). Biology of coral reefs in the Northwestern Hawaiian Islands. In: Riegl, B.M. and Dodge, R.E. (eds.). *Coral Reefs of the USA*. Springer, pp. 573-594.
- Guénette, S. and Hill, R.L. (2009). A trophic model of the coral reef ecosystem of La Parguera, Puerto Rico: synthesizing fisheries and ecological data. *Caribbean Journal of Science*, vol. 45, pp. 317-337.
- Gulf of Mexico Fishery Management Council [GMFMC]. (2005). Final Generic Amendment Number 3 for addressing essential fish habitat requirements, Habitat Areas of Particular Concern, and adverse effects of fishing in the following Fishery Management Plans of the Gulf of Mexico: Shrimp Fishery of the Gulf of Mexico, Red Drum Fishery of the Gulf of Mexico, Reef Fish Fishery of the Gulf of Mexico, Coastal Migratory Pelagic Resources (Mackerels) in the Gulf of Mexico and South Atlantic, Stone Crab Fishery of the Gulf of Mexico, Spiny Lobster Fishery of the Gulf of Mexico and South Atlantic, Coral and Coral Reef Fishery of the Gulf of Mexico. Gulf of Mexico Fishery Management Council, Florida, 106 p.
- Gunasekera, S.P., Gunasekera, M., Longley, R.E. and Schulte, G.K. (1990). Discodermolide: a new bioactive polyhydroxylated lactone from the marine sponge *Discodermia dissoluta*. *The Journal of Organic Chemistry*, vol. 55, No. 16, pp. 4912-4915.
- Halley, R., Garrison, V., Ciembronowicz, K., Edwards, R., Jaap, W., Mead, G., Earle, S., Hine, A., Jarret, B. and Locker, S. (2003). Pulley Ridge — The United States' deepest coral reef. USGS Open-File Report 03-54, pp. 153-154.
- Hanisak, M.D. and Blair, S.M. (1988). The deep-water macroalgal community on the east Florida continental shelf. *Helgolander Meeresunters*, vol. 42, pp. 133-163.
- Harmelin-Vivien, M.L., and Laboute, P. (1986). Catastrophic impact of hurricanes on atoll outer reef slopes in the Tuamotu (French Polynesia). *Coral reefs*, vol. 5, No. 2, pp. 55-62.
- Harris, P.T. and Davies, P.J. (1989). Submerged reefs and terraces on the shelf edge of the Great Barrier Reef, Australia: morphology, occurrence and

- implications for reef evolution. *Coral Reefs*, vol. 8, pp. 87-98.
- Harris, P.T. and Heap, A. (2009). Cyclone-induced net sediment transport pathway on the continental shelf of tropical Australia inferred from reef talus deposits. *Continental Shelf Research*, vol. 29, pp. 2011-2019.
- Harris, P.T., Bridge, T.C.L., Beaman, R., Webster, J., Nichol, S. and Brooke B. (2013). Submerged banks in the Great Barrier Reef, Australia, greatly increase available coral reef habitat. *ICES Journal of Marine Science*, vol. 70, pp. 284-293.
- Harris, P.T., Heap, A.D., Marshall, J.F. and McCulloch, M.T. (2008). A new coral reef province in the Gulf of Carpentaria, Australia: colonisation, growth and submergence during the early Holocene. *Marine Geology*, vol. 251, pp. 85-97.
- Harris, P.T., Heap, A.D., Wassenberg, T. and Passlow, V. (2004). Submerged coral reefs in the Gulf of Carpentaria, Australia. *Marine Geology*, vol. 207, pp. 185-191.
- Hartman, W.D. (1969). New genera and species of coralline sponges (Porifera) from Jamaica. *Postilla*, vol. 137, pp. 1-39.
- Hartman, W.D. (1973). Beneath Caribbean reefs. *Discovery*, vol. 9, pp. 13-26.
- Hartman, W.D. and Goreau T.F. (1970). Jamaican coralline sponges: their morphology, ecology and fossil relatives. *Symposia of the Zoological Society of London*, vol. 25, pp. 205-243.
- Hayasaka, S., Oki, K., Suzuki, H. and Shinomiya, A. (1995). Environmental background of the habitat of *Nautilus belauensis* off the southeast coast of the Malakal Island, Palau. *Kagoshima University Research Center for the South Pacific, Occasional Papers*, No. 27, pp. 5-10.
- Heap, A. and Harris, P.T. (2008). Geomorphology of the Australian margin and adjacent sea floor. *Australian Journal of Earth Science*, vol. 55, pp. 555-584.
- Hilting, A.K., Currin, C.A. and Kosaki, R.K. (2013). Evidence for benthic primary production support of an apex predator-dominated coral reef food web. *Marine Biology*, vol. 160, pp. 1681-1695.
- Hinderstein, L.M., Marr, J.C.A., Martinez, F.A., Dowgiallo, M.J., Puglise, K.A., Pyle, R.L. and Appeldoorn, R. (2010). Theme section on "Mesophotic coral ecosystems: characterization, ecology, and management." *Coral Reefs*, vol. 29, No. 2, pp. 247-251.
- Hine, A.C., Halley, R.B., Locker, S.D., Jarrett, B.D., Jaap, W.C., Mallinson, D.J., Ciembronowicz, K.T., Ogden, N.B., Donahue, B.T. and Naar, D.F. (2008). Coral reefs, present and past, on the West Florida shelf and platform margin. In: Riegl, B.M. and Dodge R.E. (eds.). *Coral Reefs of the USA*. Springer, pp. 127-174.
- Hoegh-Guldberg, O. (1999). Climate change, coral bleaching and the future of the world's corals. *Marine and Freshwater Research*, vol. 50, pp. 839-866.
- Hoegh-Guldberg, O. and Bruno, J.F. (2010). The impact of climate change on the world's marine ecosystems. *Science*, vol. 328, pp. 1523-1528.
- Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E., Harvell, C.D., Sale, P.F., Edwards, A.J., Caldeira, K., Knowlton, N., Eakin, C.M., Iglesias-Prieto, R., Muthiga, N., Bradbury, R.H., Dubi, A. and Hatzigeorgis, M.E. (2007). Coral reefs under rapid climate change and ocean acidification. *Science*, vol. 318, pp. 1737-1742.
- Holmes, C.W. (1981). Late Neogene and Quaternary geology of the southwestern Florida shelf and slope. USGS Open-File Report 81-1029.
- Holstein, D.M., Paris, C.B., Vaz, A.C. and Smith, T.B. (2016). Modeling vertical coral connectivity and mesophotic refugia. *Coral Reefs*, vol. 35, In Press, DOI:10.1007/s00338-015-1339-2.
- Holstein, D.M., Smith, T.B., Gyory, J. and Paris, C.B. (2015). Fertile fathoms: deep reproductive refugia for threatened shallow corals. *Scientific Reports*, vol. 5, 12407.
- Hopley, D. (2006). Coral reef growth on the shelf margin of the Great Barrier Reef with special reference to the Pompey Complex. *Journal of Coastal Research*, vol. 22, pp. 150-158.
- Hopley, D., Smithers, S.G. and Parnell, K.E. (2007). The geomorphology of the Great Barrier Reef: development, diversity and change. Cambridge University Press, Cambridge, United Kingdom.
- Hubbard, D.K. (1989). The shelf-edge reefs of Davis and Cane Bays, Northwestern St. Croix, USVI. In: 12th Caribbean Geological Conference, Special Publication. no. 8, pp. 167-180.
- Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J.B.C., Kleypas, J., Lough, J.M., Marshall, P., Nystrom, M., Palumbi, S.R., Pandolfi, J.M., Rosen, B. and Roughgarden, J. (2003). Climate change, human impacts, and the resilience of coral reefs. *Science*, vol. 301, pp. 929-933.
- Huisman, J.M., Abbott, I.A. and Smith, C. (2007). Hawaiian reef plants. University of Hawaii Sea Grant College, Honolulu, 264 p.
- Intergovernmental Panel on Climate Change [IPCC]. (2013). Climate Change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., Qin, D., Plattner, G.K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V. and Midgley, P.M. (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, 1535 p.
- Intergovernmental Panel on Climate Change [IPCC]. (2014). Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 p.
- Irizarry-Soto, E. and Weil, E. (2009). Spatial and temporal variability in juvenile coral densities, survivorship and recruitment in La Parguera, southwestern Puerto Rico. *Caribbean Journal of Science*, vol. 45, pp. 269-281.
- Iryu, Y., Nakamori, T., Matsuda, S. and Abe, O. (1995). Distribution of marine organisms and its geological significance in the modern reef complex of the Ryukyu Islands. *Sedimentary Geology*, vol. 99, pp. 243-258.
- James, N.P. and Ginsburg, R. (1979). The seaward margin side of Belize barrier and atoll reefs. *International Association of Sedimentology, Special Publication*, vol. 3, 191 p.
- Jarrett, B.D., Hine, A.C., Halley, R.B., Naar, D.F., Locker, S.D., Neumann, A.C., Twichell, D., Hu, C., Donahue, B.T., Jaap, W.C., Palandro, D. and Ciembronowicz, K. (2005). Strange bedfellows — a deep water hermatypic coral reef superimposed on a drowned barrier island, southern Pulley Ridge, SW Florida platform margin. *Marine Geology*, vol. 214, pp. 295-307.
- Jensen, P.R., Gibson, R.A., Littler, M.M. and Littler, D.S. (1985). Photosynthesis and calcification in four deep-water *Halimeda* species (Chlorophyceae, Caulerpales). *Deep Sea Research Part A. Oceanographic Research Papers*, vol. 32, pp. 451-464.
- Jokiel, P.L., Rodgers, K.S., Kuffner, I.B., Andersson, A.J., Cox, E.F. and Mackenzie, F.T. (2008). Ocean acidification and calcifying reef organisms: a mesocosm investigation. *Coral Reefs*, vol. 27, pp. 473-83.
- Kadison, E., Nemeth, R., Brown-Peterson, N., Blondeau, J., Smith, T. and Calnan, J. (2011). Yellowfin grouper (*Mycteroperca venenosa*): reproductive biology, behavior and conservation of a large Caribbean grouper. *Proceedings of the Gulf and Caribbean Fisheries Institute*, vol. 63, pp. 157-160.
- Kahng, S.E. (2006). Ecology and ecological impact of an alien octocoral, *Carijia riisei*, in Hawaii [dissertation]. University of Hawai'i, 284 p.
- Kahng, S.E. (2007). Ecological impacts of *Carijia riisei* on black coral habitat. Report to Precious Coral Fishery Management Plan. NOAA Western Pacific Fishery Management Council, Honolulu, Hawaii, 5 p.
- Kahng, S.E. (2013). Growth rate for a zooxanthellate coral (*Leptoseris hawaiiensis*) at 90 m. *Galaxea, Journal of Coral Reef Studies*, vol. 15, pp. 39-40.
- Kahng, S.E. (2014). Unlocking the secrets of Hawaii's deep-water photosynthetic corals. *Reef Encounter*, vol. 29, No. 1, pp. 19-22.
- Kahng, S.E. and Grigg, R.W. (2005). Impact of an alien octocoral, *Carijia riisei*, on black corals in Hawaii. *Coral Reefs*, vol. 24, No. 4, pp. 556-562.
- Kahng, S.E. and Kelley, C. (2007). Vertical zonation of habitat forming benthic species on a deep photosynthetic reef (50-140 m) in the Au'au Channel, Hawaii. *Coral Reefs*, vol. 26, pp. 679-687.
- Kahng, S.E. and Maragos, J.E. (2006). The deepest zooxanthellate, scleractinian corals in the world? *Coral Reefs*, vol. 25, No. 2, p. 254.
- Kahng, S.E., Benayahu, Y., Wagner, D. and Rothe, N. (2008). Sexual reproduction in the invasive octocoral *Carijia riisei* in Hawaii. *Bulletin of Marine Science*, vol. 82, No. 1, pp.1-17.
- Kahng, S.E., Copus, J. and Wagner, D. (2014). Recent advances in the ecology of mesophotic coral ecosystems (MCEs). *Current Opinion in Environmental Sustainability*, vol. 7, pp. 72-81.
- Kahng, S.E., Garcia-Sais, J.R., Spalding, H.L., Brokovich, E., Wagner, D., Weil, E., Hinderstein, L. and Toonen, R.J. (2010). Community ecology of mesophotic coral reef ecosystems. *Coral Reefs*, vol. 29, No. 2, pp. 255-275.
- Kahng, S.E., Hochberg, E.J., Apprill, A., Wagner, D., Luck, D.G., Perez, D. and Bidigare R.R. (2012a). Efficient light harvesting in deep-water zooxanthellate corals. *Marine Ecology Progress Series*, vol. 455, pp. 65-77.
- Kahng, S.E., Wagner, D., Lantz, C., Vetter, O., Gove, J. and Merrifield, M. (2012b). Temperature related depth limits of warm-water corals. Proceedings of the 12th International Coral Reef Symposium, Cairns, Australia. 9C.
- Kajimura, M. (1987). Deep-water flora of benthic marine algae in the Oki Islands, Sea of Japan. *Botanica Marina*, vol. 30, pp. 373-385.
- Kakinuma, Y. (1995). Studies of *Nautilus belauensis* in Palau. *Kagoshima University Research Center of the South Pacific, Occasional Papers*, vol. 27, 105 p.
- Kane, C., Kosaki, R.K. and Wagner, D. (2014). High levels of mesophotic reef fish endemism in the Northwestern Hawaiian Islands. *Bulletin of Marine Science*, vol. 90, pp. 693-703.
- Kaneshiro, V. (2012). The \$30,000 Peppermint Angelfish at Waikiki Aquarium.

- Honolulu Magazine*. Available from <http://www.honolulumagazine.com/Honolulu-Magazine/May-2012/The-30000-Peppermint-Angelfish-at-Waikiki-Aquarium/> [Accessed April 25, 2015].
- Katz, T., Ginat, H., Eyal, G., Steiner, Z., Braun, Y., Shalev, S. and Goodman-Tchernov, B.N. (2015). Desert flash floods form hyperpycnal flows in the coral-rich Gulf of Aqaba, Red Sea. *Earth and Planetary Science Letters*, vol. 417, pp. 87-98.
- Keppel, G., Van Niel, K.P., Wardell-Johnson, G.W., Yates, C.J., Byrne, M., Mucina, L., Schut, A.G.T., Hopper, S.D. and Franklin, S.E. (2012). Refugia: identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography*, vol. 21, No. 4, pp. 393-404.
- Kerswell, A.P. (2006). Global diversity patterns of benthic marine algae. *Ecology*, vol. 87, pp. 2479-2488.
- Kimmel, J. (1985). A characterization of Puerto Rican fish assemblages [dissertation]. University of Puerto Rico at Mayagüez, Puerto Rico, 106 p.
- Kimura, T., Shimoike, K., Suzuki, G., Nakayoshi, I., Shioiri, A., Tabata, A., Tabata, Y., Fujita, Y., Zayas, Y., Yamano, H., Namizaki, N., Yokoi, K., Ogasawara, K. and Yasumura, S. (2011). Large scale communities of *Acropora horrida* in the mesophotic zone off Kume Island, Okinawa. *Journal of the Japanese Coral Reef Society*, vol. 13, pp. 43-45 (in Japanese).
- Kininmonth, S., Lemm, S., Malone, C. and Hartley, T. (2014). Spatial vulnerability assessment of anchor damage within the Great Barrier Reef World Heritage Area, Australia. *Ocean and Coastal Management*, vol. 100, pp. 20-31.
- Kirk, J.T.O. (1994). Light and photosynthesis in aquatic ecosystems. Cambridge University Press, New York, 500 p.
- Knudby, A., Kenchington, E. and Murillo, F.J. (2013). Modeling the distribution of *Geodia* sponges and sponge grounds in the northwest Atlantic. *PLoS ONE*, vol. 8, No. 12, e82306.
- Koenig, C.C. and Coleman, F.C. (2012). Chapter 12.7: Gag Grouper — *Mycteroperca microlepis*. In: Sadovy de Mitcheson, Y. and Colin, P.L. (eds.). Reef fish spawning aggregations: biology, research and management. Springer, New York, pp. 439-445.
- Koenig, C.C., Coleman, F.C., Grimes, C.B., Fitzhugh, G.R., Scanlon, K.M., Gledhill, C.T. and Grace, M. (2000). Protection of fish spawning habitat for the conservation of warm-temperate reef-fish fisheries of shelf-edge reefs of Florida. *Bulletin of Marine Science*, vol. 66, No. 3, pp. 593-616.
- Koenig, C.C., Shepard, A.N., Reed, J.K., Coleman, F.C., Brooke, S.D., Brushler, J. and Scanlon, K.M. (2005). Habitat and fish populations in the deep-sea *Oculina* coral ecosystem of the western Atlantic. *American Fisheries Society Symposium*, vol. 41, pp. 795-805.
- Kosaki, R.K., Kane, C. and Pyle, R.L. (2012). Trophic structure of mesophotic fish assemblages in the northwestern Hawaiian Islands [abstract]. 12th International Coral Reef Symposium, 9-13 July 2012, Cairns, Australia, pp. 208-209.
- Kuhlmann, D.H.H. (1983). Composition and ecology of deep water coral associations. *Helgoländer Meeresuntersuchungen*, vol. 36, pp. 183-204.
- Kulbicki, M., Beets, J., Chabanet, P., Cure, K., Darling, E., Floeter, S.R., Galzin, R., Green, A., Harmelin-Vivien, M., Hixon, M., Letourneur, Y., Lison de Loma, T., McClanahan, T., McIlwain, J., MouTham, G., Myers, R., O'Leary, J.K., Planes, S., Vigliola, L. and Wantiez, L. (2012). Distributions of Indo-Pacific lionfishes *Pterois* spp. in their native ranges: implications for the Atlantic invasion. *Marine Ecology Progress Series*, vol. 446, pp. 189-205.
- Labiosa, R.G., Arrigo, K.R., Genin, A., Monismith, S.G. and van Dijken, G. (2003). The interplay between upwelling and deep convective mixing in determining the seasonal phytoplankton dynamics in the Gulf of Aqaba: evidence from SeaWiFS and MODIS. *Limnology and Oceanography*, vol. 48, No. 6, pp. 2355-2368.
- Lang, J.C. (1974). Biological zonation at the base of a reef: observations from the submersible Nekton Gamma have led to surprising revelations about the deep fore-reef and island slope at Discovery Bay, Jamaica. *American Scientist*, vol. 62, pp. 272-281.
- Lang, J.C., Hartman, W.D. and Land, L.S. (1975). Sclerosponges: primary framework constructors on the Jamaican fore-reef. *Marine Research*, vol. 33, pp. 223-231.
- Langdon, C. and Atkinson, M. (2005). Effect of elevated pCO₂ on photosynthesis and calcification of corals and interactions with seasonal change in temperature/irradiance and nutrient enrichment. *Journal of Geophysical Research*, vol. 110, C09S07.
- Lehnert, H. and van Soest, R.W.M. (1999). More North Jamaican deep fore-reef sponges. *Beaufortia*, vol. 49, No. 12, pp. 141-169.
- Leichter, J.J. and Genovese, S.J. (2006). Intermittent upwelling and subsidized growth of the scleractinian coral *Madracis mirabilis* on the deep fore-reef of Discovery Bay, Jamaica. *Marine Ecology Progress Series*, vol. 316, pp. 95-103.
- Leichter, J.J., Stokes, M.D. and Genovese, S.J. (2008). Deep water macroalgal communities adjacent to the Florida Keys reef tract. *Marine Ecology Progress Series*, vol. 356, pp. 123-38.
- Leichter, J.J., Wankel, S., Paytan, A., Hanson, K., Miller, S. and Altabet, M.A. (2007). Nitrogen and oxygen isotopic signatures of subsurface nitrate seaward of the Florida Keys reef tract. *Limnology and Oceanography*, vol. 52, No. 3, pp. 1258-1267.
- Lesser, M.P. and Slattery, M. (2011). Phase shift to algal dominated communities at mesophotic depths associated with lionfish (*Pterois volitans*) invasion on a Bahamian coral reef. *Biological Invasions*, vol. 13, No. 8, pp. 1855-1868.
- Lesser, M.P. and Slattery, M. (2013). Ecology of Caribbean sponges: are top-down or bottom-up processes more important? *PLoS ONE*, vol. 8, No. 11, e79799.
- Lesser, M.P., Slattery, M. and Leichter, J.J. (2009). Ecology of mesophotic reefs. *Journal of Experimental Marine Biology and Ecology*, vol. 375, pp. 1-8.
- Lesser, M.P., Slattery, M., Stat, M., Ojimi, M., Gates, R.D. and Grotoli, A. (2010). Photoacclimatization by the coral *Montastraea cavernosa* in the mesophotic zone: light, food, and genetics. *Ecology*, vol. 91, No. 4, pp. 990-1003.
- Lindfield, S.J., McIlwain, J.L. and Harvey, E.S. (2014). Depth refuge and the impacts of SCUBA spearfishing on coral reef fishes. *PLoS ONE*, vol. 9, No. 3, e92628.
- Littler, D.S. and Littler, M.M. (1992). Systematics of *Avrainvillea* (Bryopsidales, Chlorophyta) in the tropical western Atlantic. *Phycologia*, vol. 31, No. 5, pp. 375-418.
- Littler, M.M. and Littler, D.S. (2012). Bloom of the giant *Anadyomene gigantodictyon* sp. nov. (Anadyomeniaceae, Cladophorales) from the outer slope (25-50 m) of the Belize Barrier Reef. *Journal of Phycology*, vol. 48, No. 1, pp. 60-63.
- Littler, M.M., Littler, D.S., Blair, S.M. and Norris, J.N. (1986). Deep-water plant communities from an uncharted seamount off San Salvador Island, Bahamas: distribution, abundance and primary productivity. *Deep-Sea Research*, vol. 33, pp. 881-892.
- Littler, M.M., Littler, D.S. and Brooks, B.L. (2005). Extraordinary mound building *Avrainvillea* (Chlorophyta): the largest tropical marine plants. *Coral Reefs*, vol. 24, p. 555.
- Littler, M.M., Littler, D.S. and Hanisak, M.D. (1991). Deep-water rhodolith distribution, productivity, and growth history at sites of formation and subsequent degradation. *Journal of Experimental Marine Biology and Ecology*, vol. 150, pp. 163-82.
- Locker, S., Armstrong, R., Battista, T., Rooney, J., Sherman, C. and Zawada, D. (2010). Geomorphology of mesophotic coral ecosystems: current perspectives on morphology, distribution, and mapping strategies. *Coral Reefs*, vol. 29, No. 2, pp. 329-345.
- Loya, Y. (1972). Community structure and species diversity of hermatypic corals at Eilat, Red Sea. *Marine Biology*, vol. 13, No. 2, pp. 100-123.
- Loya, Y. (1975). Possible effects of water pollution on the community structure of Red Sea corals. *Marine Biology*, vol. 29, No. 2, pp. 177-185.
- Loya, Y. (1976b). Effects of water turbidity and sedimentation on the community structure of Puerto Rican corals. *Bulletin of Marine Science*, vol. 26, No. 4, pp. 450-466.
- Loya, Y. (1976a). Recolonization of Red Sea corals affected by natural catastrophes and man-made perturbations. *Ecology*, vol. 57, pp. 278-289.
- Loya, Y. (2004). The coral reefs of Eilat-past, present and future: three decades of coral community structure studies. In: Coral health and disease. Springer Berlin Heidelberg, pp. 1-34.
- Loya, Y. (2007). How to influence environmental decision makers? The case of Eilat (Red Sea) coral reefs. *Journal of Experimental Marine Biology and Ecology*, vol. 344, No. 1, pp. 35-53.
- Loya, Y., Eyal, G., Treibitz, T., Lesser, M.P. and Appeldoorn, R. (2016). Theme section on mesophotic coral ecosystems: advances in knowledge and future perspectives. *Coral Reefs*, vol. 35, In Press, DOI 10.1007/s00338-016-1410-7.
- Loya, Y. and Rinkevich, B. (1980). Effects of oil pollution on coral reef communities. *Marine Ecology Progress Series*, vol. 3, No. 16, pp. 167-180.
- Luck, D.G., Forsman, Z.H., Toonen, R.J., Leicht, S.J. and Kahng, S.E. (2013). Polyphyly and hidden species among Hawaii's dominant mesophotic coral genera, *Leptoseris* and *Pavona* (Scleractinia: Agariciidae). *PeerJ*, vol. 1, e132.
- Ludt, W.B., Bernal, M.A., Bowen, B.W. and Rocha, L.A. (2012). Living in the past: phylogeography and population histories of Indo-Pacific wrasses (genus *Halichoeres*) in shallow lagoons versus outer reef slopes. *PLoS ONE*, vol. 7, No. 6, e38042.
- Macintyre, I.G. (1967). Submerged coral reefs, west coast of Barbados, West Indies. *Canadian Journal of Earth Sciences*, vol. 4, No. 3, pp. 461-474.
- Macintyre, I.G. (1972). Submerged reefs of eastern Caribbean. *AAPG Bulletin*, vol. 56, No. 4, pp. 720-738.
- Macintyre, I.G., Rutzler, K., Norris, J.N., Smith, K.P., Cairns, S.D., Bucher,

- K.E. and Steneck, R.S. (1991). An early Holocene reef in the western Atlantic: submersible investigations of a deep relict reef off the west coast of Barbados, W.I. *Coral Reefs*, vol. 10, pp. 167-174.
- Madin, J.S. and Madin, E.M.P. (2015). The full extent of the global coral reef crisis. *Conservation Biology*. In press, DOI: 10.1111/cobi.12564.
- Mah, C.L. (2003). *Astrosarkus idipi*, a new Indo-Pacific genus and species of Oreasteridae (Valvata: Asteroidea) displaying extreme endoskeletal reduction. *Bulletin of Marine Science*, vol. 73, No. 3, pp. 685-698.
- Mah, C.L. (2005). A phylogeny of *Iconaster* and *Glyphodiscus* (Echinodermata, Asteroidea, Valvata, Goniasteridae) with descriptions of four new species. *Zoosystema*, vol. 27, No. 1, pp. 137-161.
- Maier, C., Watremez, P., Taviani, M., Weinbauer, M.G. and Gattuso, J.P. (2012). Calcification rates and the effect of ocean acidification on Mediterranean cold-water corals. *Proceedings of the Royal Society B-Biological Sciences*, vol. 279, No. 1734, pp. 1716-1723.
- Manasrah, R.S., Al-Horani, F.A., Rasheed, M.Y., Al-Rousan, S.A. and Khalaf, M.A. (2006). Patterns of summer vertical and horizontal currents in coastal waters of the northern Gulf of Aqaba, Red Sea. *Estuarine, Coastal and Shelf Science*, vol. 69, pp. 567-579.
- Maragos, J.E. and Jokiel, P. (1986). Reef corals of Johnston Atoll: one of the world's most isolated reefs. *Coral Reefs*, vol. 4, pp. 141-150.
- Maynard, J., van Hooedonk, R., Eakin, C.M., Puotinen, M., Garren, M., Williams, G., Heron, S.F., Lamb, J., Weil, E., Willis, B. and Harvell, C.D. (2015). Projections of climate conditions that increase coral disease susceptibility and pathogen abundance and virulence. *Nature Climate Change*, vol. 5, pp. 688-694.
- Menza, C., Kendall, M. and Hile, S. (2008). The deeper we go the less we know. *Revista De Biologia Tropical*, vol. 56, pp. 11-24.
- Merrifield, M.A. and Holloway, P.E. (2002). Model estimates of M2 internal tide energetics at the Hawaiian Ridge. *Journal of Geophysical Research: Oceans*, vol. 107, pp. 5-1-5-12.
- Merrifield, M.A., Holloway, P.E. and Johnston, T. (2001). The generation of internal tides at the Hawaiian Ridge. *Geophysical Research Letters*, vol. 28, pp. 559-562.
- Miller, J., Muller, E., Rogers, C., Waara, R., Atkinson, A., Whelan, K.R.T., Patterson, M. and Witcher, B. (2009). Coral disease following massive bleaching in 2005 causes 60% decline in coral cover on reefs in the US Virgin Islands. *Coral Reefs*, vol. 28, pp. 925-937.
- Montaggioni, L.F. (2005). History of Indo-Pacific coral reef systems since the last glaciation: development patterns and controlling factors. *Earth Science Reviews*, vol. 71, pp. 1-75.
- Morelock, J., Schneiderman, N. and Bryant, W. (1977). Shelf reefs, southwestern Puerto Rico. *Studies in Geology*, vol. 4, pp. 17-25.
- Morris, J.A., Akins, J.L., Barse, A., Cerino, D., Freshwater, D.W., Green, S.J., Muñoz, R.C., Paris, C. and Whitfield, P.E. (2009). Biology and ecology of the invasive lionfishes, *Pterois miles* and *Pterois volitans*. In: Proceedings of the Gulf and Caribbean Fisheries Institute, vol. 61, pp. 409-414.
- Muir, P., Wallace, C., Bridge, T. and Bongaerts, P. (2015). Diverse staghorn coral fauna on the mesophotic reefs of northeast Australia. *PLoS ONE*, vol. 10, No. 2, e0117933.
- Mumby, P.J. and Steneck, R.S. (2008). Coral reef management and conservation in light of rapidly evolving ecological paradigms. *Trends in Ecology and Evolution*, vol. 23, pp. 555-563.
- Munday, E.S., Tissot, B.N., Heidel, J.R. and Miller-Morgan, T. (2015). The effects of venting and decompression on Yellow Tang (*Zebrasoma flavescens*) in the marine ornamental aquarium fish trade. *PeerJ*, vol. 3, e756.
- Munday, P.L., Cheal, A.J., Dixon, D.L., Rummer, J.L. and Fabricius, K.E. (2014). Behavioural impairment in reef fishes caused by ocean acidification at CO₂ seeps. *Nature Climate Change*, vol. 4, pp. 487-492.
- Muscatine, L. (1990). The role of symbiotic algae in carbon and energy flux in reef corals. In: Dubinsky, Z. (ed.). *Ecosystems of the World 25: Coral reefs*, Elsevier, Amsterdam, pp. 75-87.
- Myers, R.F. (1993). Guam's small-boat-based fisheries. *Marine Fisheries Review*, vol. 55, No. 2, pp. 117-128.
- Myers, R.F. (1999). *Micronesian reef fishes*, 3rd ed. Coral Graphics, Barrigada, 330 p.
- Nakao, Y. and Fusetani, N. (2010). Marine invertebrates: sponges. In: Liu, H.W. and Mander, L. (eds.). *Comprehensive Natural Products II*. Elsevier, Oxford, pp. 327-362.
- National Monitoring Program [NMP]. (2013). Israel's National Monitoring of the Gulf of Eilat, scientific reports and online data <http://www.iui-eilat.ac.il/NMP/Default.aspx> [Accessed October 2015].
- National Oceanic and Atmospheric Administration [NOAA]. (2014). *Endangered and Threatened wildlife and plants: final listing determinations on proposal to list 66 reef-building coral species and to reclassify Elkhorn and Staghorn corals*. 1104 p.
- Neal, B.P., Condit, C., Liu, G., dos Santos, S., Kahru, M., Mitchell, B.G. and Kline, D.I. (2014). When depth is no refuge: cumulative thermal stress increases with depth in Bocas del Toro, Panama. *Coral Reefs*, vol. 33, No. 1, pp. 193-205.
- Nemeth, R.S. (2005). Population characteristics of a recovering US Virgin Islands red hind spawning aggregation following protection. *Marine Ecology Progress Series*, vol. 286, pp. 81-97.
- Nemeth, R., Blondeau, J., Herzlieb, S. and Kadison, E. (2007). Spatial and temporal patterns of movement and migration at spawning aggregations of red hind, *Epinephelus guttatus*, in the U.S. Virgin Islands. *Environmental Biology of Fishes*, vol. 78, pp. 365-381.
- Newman, D.J. and Cragg, G.M. (2007). Natural products as sources of new drugs over the last 25 years. *Journal of Natural Products*, vol. 70, No. 3, pp. 461-477.
- Newman, D.J. and Cragg, G.M. (2012). Natural products as sources of new drugs over the 30 years from 1981 to 2010. *Journal of Natural Products*, vol. 75, No. 3, pp. 311-335.
- Nir, O., Gruber, D., Einbinder, S., Kark, S. and Tchernov, D. (2011). Changes in scleractinian coral *Seriatopora hystrix* morphology and its endocellular *Symbiodinium* characteristics along a bathymetric gradient from shallow to mesophotic reef. *Coral Reefs*, vol. 30, No. 4, pp. 1089-1100.
- Nir, O., Gruber, D.F., Shemesh, E., Glasser, E. and Tchernov, D. (2014). Seasonal mesophotic coral bleaching of *Stylophora pistillata* in the Northern Red Sea. *PLoS ONE*, vol. 9, No. 1, e84968.
- Nishihira, M. and Veron, J. (1995). *Hermatypic corals of Japan*. Kaiyusha, Tokyo (in Japanese).
- Nuttall, M.F., Johnston, M.A., Eckert, R.J., Embesi, J.A., Hickerson, E.L. and Schmahl, G.P. (2014). Lionfish (*Pterois volitans* [Linnaeus, 1758] and *P. miles* [Bennett, 1828]) records within mesophotic depth ranges on natural banks in the Northwestern Gulf of Mexico. *Bioinvasions Records*, vol. 3, No. 2, pp. 111-115.
- Ojeda-Serrano, E., Appeldoorn, R.S. and Ruiz-Valentín, I. (2007). Reef fish spawning aggregations of the Puerto Rican shelf. Final report to the Caribbean Coral Reef Institute. 31 p. http://ccri.uprm.edu/researcher/Ojeda/Ojeda_Final_Report_CCRI_SPAG%27s.pdf [Accessed October 2015].
- Oktyani, T. and Kurata, Y. (1995). An unusual molluscan assemblage containing *Perotrochus africanus teramachii* on the insular shelf of Palau Islands. *Venus*, vol. 57, No. 1, pp. 11-16.
- Olavo, G., Costa, P.A., Martins, A.S. and Ferreira, B.P. (2011). Shelf-edge reefs as priority areas for conservation of reef fish diversity in the tropical Atlantic. *Aquatic Conservation: Marine and Freshwater Ecosystems*, vol. 21, No. 2, pp. 199-209.
- Oliver, T.A. and Palumbi, S.R. (2011). Do fluctuating temperature environments elevate coral thermal tolerance? *Coral Reefs*, vol. 30, No. 2, pp. 429-440.
- Olsen, D.A. and LaPlace, J.A. (1978). A study of a Virgin Islands grouper fishery based on a breeding aggregation. In: Proceedings of the 31st Gulf Caribbean Fisheries Institute, vol. 3, pp. 130-144.
- Olson, J.B. and Kellogg, C.A. (2010). Microbial ecology of corals, sponges, and algae in mesophotic coral environments. *FEMS Microbial Ecology*, vol. 73, No. 1, pp. 17-30.
- Opresko, D. (2004). Revision of the Antipatharia (Cnidaria: Anthozoa). Part IV. Establishment of a new family, Aphanipathidae. *Zoologische Mededelingen*, vol. 78, No. 11, pp. 209-240.
- Pandolfi, J.M., Bradbury, R.H., Sala, E., Hughes, T.P., Bjorndal, K.A., Cooke, R.G., McArdle, D., McClenachan, L., Newman, M.J.H., Paredes, G., Warner, R.R. and Jackson, J.B.C. (2003). Global trajectories of the long-term decline of coral reef ecosystems. *Science*, vol. 301, pp. 955-958.
- Pandolfi, J.M., Connolly, S.R., Marshall, D.J. and Cohen, A.L. (2011). Projecting coral reef futures under global warming and ocean acidification. *Science*, vol. 333, No. 6041, pp. 418-422.
- Papastamatiou, Y., Meyer, C.G., Kosaki, R.K., Wallsgrove, N.J. and Popp, B.N. (2015). Movements and foraging of predators associated with mesophotic coral reefs and their potential for linking ecological habitats. *Marine Ecology Progress Series*, vol. 521, pp. 155-170.
- Parrish, F.A. and Boland, R.C. (2004). Habitat and reef-fish assemblages of banks in the Northwestern Hawaiian Islands. *Marine Biology*, vol. 144, pp. 1065-1073.
- Pawlik, J.R., McMurray, S.E., Erwin, P. and Zea, S. (2015a). A review of evidence for food limitation on Caribbean reefs. *Marine Ecology Progress Series*, vol. 519, pp. 265-283.
- Pawlik, J.R., McMurray, S.E., Erwin, P. and Zea, S. (2015b). No evidence for food limitation of Caribbean reef sponges: reply to Slattery & Lesser (2015). *Marine Ecology Progress Series*, vol. 527, pp. 281-284.
- Peyton, K.A. (2009). Aquatic invasive species impacts in Hawaiian soft

- sediment habitats [dissertation]. University of Hawaii at Mānoa, 138 p.
- Phillips, N.W., Gettleson, D.A. and Spring, K.D. (1990). Benthic biological studies of the southwest Florida shelf. *American Zoologist*, vol. 30, No. 1, pp. 65-75.
- Pinheiro, H.T., Goodbody-Gringley, G., Jessup, M.E., Sheperd, B., Chequer, A.D. and Rocha, L.A. (2016). Upper and lower mesophotic coral reef fish communities evaluated by underwater visual censuses in two Caribbean locations. *Coral Reefs*, vol. 35, In Press, DOI 10.1007/s00338-015-1381-0.
- Pitcher, R.C., Doherty, P.P., Arnold, P.P., Hooper, J.J. and Gribble, N.N. (2007). Seabed biodiversity on the continental shelf of the Great Barrier Reef World Heritage Area. AIMS/CSIRO/QM/QDPI CRC Reef Research Task Final Report, 320 p.
- Pittman, S.J., Hile, S.D., Jeffrey, C.F.G., Clark, R., Woody, K., Herlach, B.D., Caldwell, C., Monaco, M.E. and Appeldoorn, R. (2010). Coral reef ecosystems of Reserva Natural La Parguera (Puerto Rico): spatial and temporal patterns in fish and benthic communities (2001-2007). National Centers for Coastal Ocean Science, Center for Coastal Monitoring and Assessment, Silver Spring, MD. NOAA Technical Memorandum NOS NCCOS 107, 202 p.
- Polunin, N.V.C., Forsman, Z., Spalding, H., Padilla-Gamiño, J., Smith, C. and Gates, R. (2015). Depth specialization in mesophotic corals (*Leptoseris* spp.) and associated algal symbionts in Hawai'i. *Royal Society Open Science*, vol. 2, 140351.
- Porter, J.W. (1973). Ecology and composition of deep reef communities off the Tongue of the Ocean, Bahama Islands. *Discovery*, vol. 9, No. 1, pp. 3-12.
- Prada, C. and Hellberg, M.E. (2013). Long prereproductive selection and divergence by depth in a Caribbean candelabrum coral. *Proceedings of the National Academy of Sciences*, vol. 110, No. 10, pp. 3961-3966.
- Prasetia, R., Sinniger, F. and Harii, S. (2016). Gametogenesis and fecundity of *Acropora tenella* (Brook 1982) in a mesophotic coral ecosystem in Okinawa, Japan. *Coral Reefs*, vol. 35, In Press, DOI: 10.1007/s00338-015-1348-1.
- Puglise, K.A., Hinderstein, L.M., Marr, J.C.A., Dowgiallo, M.J. and Martinez, F.A. (2009). Mesophotic coral ecosystems research strategy: international workshop to prioritize research and management needs for mesophotic coral ecosystems, Jupiter, Florida, 12-15 July 2008. NOAA National Centers for Coastal Ocean Science, Center for Sponsored Coastal Ocean Research, and Office of Ocean Exploration and Research, NOAA Undersea Research Program, Silver Spring, MD. NOAA Technical Memorandum NOS NCCOS 98 and OAR OER 2., 24 p.
- Pyle, R.L. (1996a). How much coral reef biodiversity are we missing? *Global Biodiversity*, vol. 6, pp. 3-7.
- Pyle, R.L. (1996b). The twilight zone. *Natural History*, vol. 105, No. 11, pp. 59-62.
- Pyle, R.L. (2000). Assessing undiscovered fish biodiversity on deep coral reefs using advanced self-contained diving technology. *Marine Technology Society Journal*, vol. 34, No. 4, pp. 82-91.
- Pyle, R.L. (2005). Recent discoveries of new fishes inhabiting deep Pacific coral reefs, with biogeographic implications. 7th Indo-Pacific Fish Conference, Taipei, Taiwan, 16-20 May 2005. *Zenodo*, DOI: 10.5281/zenodo.16942.
- Pyle, R. and Myers, R. (2010). *Centropyge narcosis*. The IUCN Red List of Threatened Species. Version 2014.3. Available from www.iucnredlist.org/details/165903/0 [Accessed April 25, 2015].
- Pyle, R.L. and Randall, J.E. (1993). A new species of *Centropyge* from the Cook Islands, with a redescription of *Centropyge boylei*. *Revue Française d'Aquariologie*, vol. 19, No. 4, pp. 115-124.
- Pyle, R.L., Earle, J.L. and Greene, B.D. (2008). Five new species of the damselfish genus *Chromis* (Perciformes: Labroidae: Pomacentridae) from deep coral reefs in the tropical western Pacific. *Zootaxa*, vol. 1671, pp. 3-31.
- Pyle, R., Myers, R. and Craig, M.T. (2009). *Centropyge boylei*. The IUCN Red List of Threatened Species. Version 2014.3. Available from www.iucnredlist.org/details/165824/0 [Accessed April 25, 2015].
- Qureshi, A., Colin, P.L. and Faulkner, D.J. (2000). Microsclerodermins F-I, antitumor and antifungal cyclic peptides from the Lithistid sponge *Microscleroderma* sp. *Tetrahedron*, vol. 56, No. 23, pp. 3679-3685.
- Rabalais, N.N. (1990). Biological communities of the South Texas continental shelf. *American Zoologist*, vol. 30, pp. 77-87.
- Randall, J.E. (1968). *Caribbean Reef Fishes*. T.F.H. Publications, Neptune, New Jersey, 318 p.
- Randall, J.E. and Pyle, R.L. (2001a). Three new species of labrid fishes of the genus *Cirrhilabrus* from islands of the tropical Pacific. *Aqua*, vol. 4, No. 3, pp. 89-98.
- Randall, J.E. and Pyle, R.L. (2001b). Four new serranid fishes of the anthiine genus *Pseudanthias* from the South Pacific. *Raffles Bulletin of Zoology*, vol. 49, No. 1, pp. 19-34.
- Raymundo, L.J., Couch, C.S., and Harvell, C.D. (eds.). (2008). *Coral disease handbook: guidelines for assessment, monitoring and management*. GEF-CRTR-Currie Communications, Australia, 121 p.
- Reed, J.K. (1985). Deepest distribution of Atlantic hermatypic corals discovered in the Bahamas. In: Proceedings of the 5th International Coral Reef Congress, pp. 249-254.
- Reed, J.K. and Rogers, S. (2011). Final Cruise Report. Florida shelf-edge expedition (FLoSEE), *Deepwater Horizon* oil spill response: Survey of deepwater and mesophotic reef ecosystems in the eastern Gulf of Mexico and southeastern Florida. *R/V Seward Johnson, Johnson-Sea-Link II Submersible*, July 9-August 9, 2010. Report to NOAA Office of Ocean Exploration and Research and NOAA Deep Sea Coral Research and Technology Program. HBOI Technical Report Number 127, 82 p.
- Reed, J., Farrington, S., Harter, S., Moe, H., Hanisak, D. and David, A. (2015). Characterization of the mesophotic benthic habitat and fish assemblages from ROV dives on Pulley Ridge and Tortugas during 2014 *R/V Walton Smith* Cruise. NOAA Cooperative Institute for Ocean Exploration, Research and Technology. Report to NOAA-NOS-NCCOS. HBOI Technical Report Number 157, 133 p.
- Reed, J., Farrington, S., Moe, H., Harter, S., Hanisak, D. and David A. (2014). Characterization of the mesophotic benthic habitat and fish assemblages from ROV Dives on Pulley Ridge and Tortugas during 2012 and 2013 *R/V Walton Smith* Cruises. NOAA Cooperative Institute for Ocean Exploration, Research and Technology. Report to NOAA-NOS-NCCOS. HBOI Technical Report Number 147, 51 p.
- Reed, J.K., Koenig, C.C. and Shepard, A.N. (2007). Impacts of bottom trawling on a deep-water *Oculina* coral ecosystem off Florida. *Bulletin of Marine Science*, vol. 81, pp.481-496.
- Reid, R. and Macintyre, I. (1988). Foraminiferal-algal nodules from the eastern Caribbean: growth history and implications on the value of nodules as paleoenvironmental indicators. *Palaeos*, vol. 3, pp. 424-35.
- Reyes, J., Santodomingo, N. and Flórez, P. (2010). Corales escleractinios de Colombia. Santa Marta, Instituto de investigaciones Marinas y Costeras "Jose Benito Vives de Andrés" (INVERMAR), Columbia, 246 p.
- Rezak, R., Gittings, S.R. and Bright, T.J. (1990). Biotic assemblages and ecological controls on reefs and banks of the Northwest Gulf of Mexico. *American Zoologist*, vol. 30, pp. 23-35.
- Rhodes, K.L. (2012). Chapter 12.5: Camouflage Grouper — *Epinephelus polyphedion*. In: Sadovy de Mitcheson, Y. and Colin, P.L. (eds.). *Reef fish spawning aggregations: biology, research and management*. Springer, New York, pp. 422-428.
- Rhodes, K.L. and Sadovy de Mitcheson, Y. (2012). Chapter 12.8: Squaretail Coral grouper — *Plectropomus areolatus*. In: Sadovy de Mitcheson, Y. and Colin, P.L. (eds.). *Reef fish spawning aggregations: biology, research and management*. Springer, New York, pp. 445-449.
- Rhynne, A.L., Thlusty, M.F., Schofield, P.J., Kaufman, L.E.S., Morris, J.A. and Bruckner, A.W. (2012). Revealing the appetite of the marine aquarium fish trade: the volume and biodiversity of fish imported into the United States. *PLoS ONE*, vol. 7, No. 5, e35808.
- Richards, Z.T., van Oppen, M.J.H., Wallace, C.C., Willis, B.L. and Miller, D.J. (2008). Some rare Indo-Pacific coral species are probable hybrids. *PLoS ONE*, vol. 3, No. 9, e3240.
- Richmond, R.H. (1987). Energetic relationships and biogeographical differences among fecundity, growth and reproduction in the reef coral *Pocillopora damicornis*. *Bulletin of Marine Science*, vol. 41, pp. 594-604.
- Riegl, B. and Branch, G.M. (1995). Effects of sediment on the energy budgets of four scleractinian (Bourne 1900) and five alcyonacean (Lamouroux 1816) corals. *Journal of Experimental Marine Biology and Ecology*, vol. 186, pp. 259-275.
- Riegl, B. and Piller, W.E. (2003). Possible refugia for reefs in times of environmental stress. *International Journal of Earth Sciences*, vol. 92, pp. 520-531.
- Rinkevich, B. and Loya, Y. (1987). Variability in the pattern of sexual reproduction of the coral *Stylophora pistillata* at Eilat, Red Sea: a long-term study. *The Biological Bulletin*, vol. 173, pp. 335-344.
- Rivero-Calle, S., Armstrong, R.A. and Soto-Santiago, F.J. (2009). Biological and physical characteristics of a mesophotic coral reef: Black Jack reef, Vieques, Puerto Rico. In: Proceedings of the 11th International Coral Reef Symposium, Ft. Lauderdale, Florida, 7-11 July 2008, pp. 574-578.
- Roark, E., Guilderson, T., Dunbar, R. and Ingram, B. (2006). Radiocarbon-based ages and growth rates of Hawaiian deep-sea corals. *Marine Ecology Progress Series*, vol. 327, pp. 1-14.
- Roberts, C.M. (1996). Settlement and beyond: population regulation and community structure in reef fishes. In: Polunin, N.V.C. and Roberts, C.M. (eds.). *Reef Fisheries*. Springer Netherlands. Chapman & Hall Fish and Fisheries Series, vol. 20, pp. 85-112.
- Roberts, T.E., Moloney, J.M., Sweatman, H.P.A. and Bridge, T.C.L. (2015).

- Benthic composition on submerged reefs in the central Great Barrier Reef. *Coral Reefs*, vol. 34, No. 2, pp. 569-580.
- Rooney, J., Donham, E., Montgomery, A., Spalding, H., Parrish, F., Boland, R., Fenner, D., Gove, J. and Vetter, O. (2010). Mesophotic coral ecosystems of the Hawaiian Archipelago. *Coral Reefs*, vol. 29, pp. 361-367.
- Rooney, J., Wessel, P., Hoeke, R., Weiss, J., Baker, J., Parrish, F., Fletcher, C., Chojnacki, J., Garcia, M. and Brainard, R. (2008). Geology and geomorphology of coral reefs in the Northwestern Hawaiian Islands. In: Riegl, B.M. and Dodge, R.E. (eds.). *Coral Reefs of the USA*. Springer, pp. 519-571.
- Rosenberg, E. and Ben-Haim, Y. (2002). Microbial diseases of corals and global warming. *Environmental microbiology*, vol. 4, No. 6, pp. 318-326.
- Sadd, J.L. (1984). Sediment transport and CaCO₃ budget on a fringing reef, Cane Bay, St. Croix, U.S. Virgin Islands. *Bulletin of Marine Science*, vol. 35, pp. 221-238.
- Sade, A.R., Hall, J.K., Tibor, G., Niemi, T., Ben-Avraham, Z. and Al-Zoubi, A.S. (2008). Multibeam bathymetry of the northern Gulf of Aqaba/Elat. GSI Report GSI/03/2008, IOLR Report IOLR/08/2008.
- Sadovy de Mitcheson, Y. and Colin, P.L., (eds.). (2012). Reef fish spawning aggregations: biology, research and management. Springer, New York, 584 p.
- Salih, A., Larkum, A., Cox, G., Kühl, M. and Hoegh-Guldberg, O. (2000). Fluorescent pigments in corals are photoprotective. *Nature*, vol. 408, No. 6814, pp. 850-853.
- Sandler, J.S., Colin, P.L., Kelly, M. and Fenical, W. (2006). Cytotoxic macrolides from a new species of the deep-water marine sponge *Leiodermatium*. *The Journal of Organic Chemistry*, vol. 71, No. 19, pp. 7245-7251.
- Sattar, S.A. and Adam, M.S. (2005). Review of Grouper Fishery of the Maldives with additional notes on the Faafu Atoll Fishery. Marine Research Centre, Malé, Maldives, 54 p.
- Saunders, W.B. (1984). The role and status of *Nautilus* in its natural habitat: Evidence from deep-water remote camera photosequences. *Paleobiology*, vol. 19, No. 4, pp. 469-486.
- Schärer, M.T., Nemeth, M.I., Mann, D., Locascio, J., Appeldoorn, R.S. and Rowell, T.J. (2012). Sound production and reproductive behavior of yellowfin grouper, *Mycteroperca venenosa* (Serranidae) at a spawning aggregation. *Copeia*, vol. 2012, pp. 135-144.
- Schärer, M.T., Nemeth, M.I., Rowell, T.J. and Appeldoorn, R.S. (2014). Sounds associated with the reproductive behavior of the black grouper (*Mycteroperca bonaci*). *Marine Biology*, vol. 161, pp. 141-147.
- Schärer-Umpierre, M., Mateos-Molina, D., Appeldoorn, R., Bejarano, I., Hernández-Delgado, E., Nemeth, R., Nemeth, M., Valdés-Pizzini, M. and Smith, T. (2014). Marine managed areas in the U.S. Caribbean marine ecosystems. In: Johnson, M. L. and Sandell, J. (eds.). *Advances in Marine Biology: Marine Managed Areas and Fisheries*, vol. 69, pp. 129-152.
- Schofield, P.J. (2009). Geographic extent and chronology of the invasion of non-native lionfish (*Pterois volitans* [Linnaeus 1758] and *P. miles* [Bennett 1828]) in the Western North Atlantic and Caribbean Sea. *Aquatic Invasions*, vol. 4, No. 3, pp. 473-479.
- Schofield, P.J. (2010). Update on geographic spread of invasive lionfishes (*Pterois volitans* [Linnaeus, 1758] and *P. miles* [Bennett, 1828]) in the Western North Atlantic Ocean, Caribbean Sea and Gulf of Mexico. *Aquatic Invasions*, vol. 5, pp. S117-S122.
- Searles, R.B. and Schneider, C.W. (1987). Observations on the deep-water flora of Bermuda. *Hydrobiologia*, vol. 151-152, pp. 261-266.
- Serrano, X.M. (2013). Horizontal vs. vertical connectivity in Caribbean reef corals: identifying potential sources of recruitment following disturbance [dissertation]. University of Miami, Miami, 171 p.
- Serrano, X., Baums, I.B., O'Reilly, K., Smith, T.B., Jones, R.J., Shearer, T.L., Nunes, F.L.D. and Baker, A.C. (2014). Geographic differences in vertical connectivity in the Caribbean coral *Montastraea cavernosa* despite high levels of horizontal connectivity at shallow depths. *Molecular Ecology*, vol. 23, No. 17, pp. 4226-4240.
- Sherman, C., Nemeth, M., Ruiz, H., Bejarano, I., Appeldoorn, R., Pagán, F., Schärer, M. and Weil, E. (2010). Geomorphology and benthic cover of mesophotic coral ecosystems of the upper insular slope of southwest Puerto Rico. *Coral Reefs*, vol. 29, No. 2, pp. 347-360.
- Sinniger, F., Morita, M. and Harii, S. (2013). "Locally extinct" coral species *Seriatopora hystrix* found at upper mesophotic depths in Okinawa. *Coral Reefs*, vol. 32, p. 153.
- Slattery, M. and Lesser, M.P. (2012). Mesophotic coral reefs: a global model of community structure and function. In: Proceedings of the 12th International Coral Reef Symposium, 2012 July 9-13, Cairns, Australia. James Cook University, Queensland, 5 p.
- Slattery, M. and Lesser, M.P. (2014). Allelopathy in the tropical alga *Lobophora variegata* (Phaeophyceae): mechanistic basis for a phase shift on mesophotic coral reefs? *Journal of Phycology*, vol. 50, No. 3, pp. 493-505.
- Slattery, M. and Lesser, M.P. (2015). Tropic ecology of sponges from shallow to mesophotic depths (3 to 150 m): comment on Pawlik et al. (2015). *Marine Ecology Progress Series*, vol. 527, pp. 275-279.
- Slattery, M., Gochfeld, D.J., Diaz, M.C., Thacker, R.W. and Lesser, M.P. (2016). Variability in chemical defense across a shallow to mesophotic depth gradient in the Caribbean sponge *Plakortis angulospiculatus*. *Coral Reefs*, vol. 35, In Press, DOI 10.1007/s00338-015-1324-9.
- Slattery, M., Lesser, M.P., Brazeau, D., Stokes, M.D. and Leichter, J.J. (2011). Connectivity and stability of mesophotic coral reefs. *Journal of Experimental Marine Biology and Ecology*, vol. 408, No. 1, pp. 32-41.
- Smith, J., Hunter, C. and Smith, C. (2002). Distribution and reproductive characteristics of non-indigenous and invasive marine algae in the Hawaiian Islands. *Pacific Science*, vol. 56, pp. 299-315.
- Smith, T.B. (2013). United States Virgin Island's Response to the proposed listing or change in status of seven Caribbean coral species under the U.S. Endangered Species Act. University of the Virgin Islands, 43 p.
- Smith, T.B., Blondeau, J., Nemeth, R.S., Pittman, S.J., Calnan, J.M., Kadison, E. and Gass, J. (2010). Benthic structure and cryptic mortality in a Caribbean mesophotic coral reef bank system, the Hind Bank Marine Conservation District, U.S. Virgin Islands. *Coral Reefs*, vol. 29, pp. 289-308.
- Smith, T.B., Gyory, J., Brandt, M.E., Miller, W.J., Jossart, J. and Nemeth, R.S. (2015). Caribbean mesophotic coral ecosystems are unlikely climate change refugia. *Global Change Biology*.
- Smith, T.B., Kadison, E., Ennis, R., Gyory, J., Brandt, M.E., Wright, V., Nemeth, R.S. and Henderson, L. (2014). The United States Virgin Islands Territorial Coral Reef Monitoring Program. 2014 Annual Report. University of the Virgin Islands, United States Virgin Islands, 273 p.
- Smith, T.B., Nemeth, R.S., Blondeau, J., Calnan, J.M., Kadison, E. and Herzlieb, S. (2008). Assessing coral reef health across onshore to offshore stress gradients in the US Virgin Islands. *Marine Pollution Bulletin*, vol. 56, pp. 1983-1991.
- Spalding, H. (2012). Ecology of mesophotic macroalgae and *Halimeda kanaloana* meadows in the Main Hawaiian Islands [dissertation]. University of Hawai'i at Mānoa, Honolulu, 199 p.
- Spalding, M., Ravilious, C. and Green, E.P. (2001). World atlas of coral reefs. University of California Press, Berkeley, USA.
- Stachowicz, J.J. and Tilman, D. (2005). Species invasions and the relationships between species diversity, community saturation, and ecosystem functioning. In: Sax, D.F., Stachowicz, J.J. and Gaines, S.D. (eds.). *Species invasions: insights into ecology, evolution, and biogeography*. Sinauer Associates, Inc., Sunderland, MA, pp. 41-64.
- Stambler, N. and Dubinsky, Z. (2007). Marine phototrophs in the twilight zone. In: *Algae and cyanobacteria in extreme environments*. Springer Netherlands, pp. 79-97.
- Starck, W.A. II. (1969). Deep-diving scuba. *Oceans*, vol. 1, pp. 45-48.
- Starck, W.A. II and Starck J.D. (1972). Probing the deep reefs' hidden realm. *National Geographic Magazine*, vol. 142, No. 6, pp. 867-886.
- Starr, R.M., Sala, E., Ballesteros, E. and Zabala, M. (2007). Spatial dynamics of the Nassau grouper *Epinephelus striatus* in a Caribbean atoll. *Marine Ecology Progress Series*, vol. 343, No. 2002, pp. 239-249.
- Stat, M., Baker, A.C., Bourne, D.G., Correa, A.M., Forsman, Z., Huggett, M.J., Pochon, X., Skillings, D., Toonen, R.J., van Oppen, M.J. and Gates, R.D. (2012). Molecular delineation of species in the coral holobiont. *Advances in Marine Biology*, vol. 63, pp. 1-65.
- Stat, M., Carter, D. and Hoegh-Guldberg, O. (2006). The evolutionary history of *Symbiodinium* and scleractinian hosts — symbiosis, diversity, and the effect of climate change. *Perspectives in Plant Ecology Evolution and Systematics*, vol. 8, pp. 23-43.
- Stella, J., Pratchett, M.S., Hutchings, P.A. and Jones, G.P. (2011). Coral-associated invertebrates: diversity, ecological importance and vulnerability to disturbance. *Oceanography and Marine Biology: an Annual Review*, vol. 49, pp. 43-116.
- Stokes, M.D., Leichter, J.J. and Genovese, S.J. (2010). Long-term declines in coral cover at Bonaire, Netherlands Antilles. *Atoll Research Bulletin*, No. 582, 21 p.
- Strasburg, D.W., Jones, E.C. and Iversen, R.T. (1968). Use of a small submarine for biological and oceanographic research. *Journal du Conseil*, vol. 31, No. 3, pp. 410-426.
- Tameler, J., Sattar, S., Campbell, S., Hoon, V., Arthur, R., Patterson E.J.K., Satapoomin, U., Chandhi, M., Rajasuriya, A. and Samoilys, M. (2008). Reef fish spawning aggregations in the Bay of Bengal: Awareness and occurrence. In: Proceedings of the 11th International Coral Reef Symposium, Ft. Lauderdale, Florida, 7-11 July 2008, pp. 1043-1047.
- Tenggardjaja, K.A., Bowen, B.W. and Bernardi, G. (2014). Vertical and

- horizontal genetic connectivity in *Chromis verater*, an endemic damselfish found on shallow and mesophotic reefs in the Hawaiian archipelago and adjacent Johnston Atoll. *PLoS ONE*, vol. 9, No. 12, e115493.
- Thresher, R.E. and Colin, P.L. (1986). Trophic structure, diversity and abundance of fishes of the deep reef (30–300m) at Eniwetok, Marshall Islands. *Bulletin of Marine Science*, vol. 38, No. 1, pp. 253-272.
- Todd, P.A. (2008). Morphological plasticity in scleractinian corals. *Biological Reviews*, vol. 83, No. 3, pp. 315-337.
- Trench, R.K. (1993). Microalgal-invertebrate symbiosis: a review. *Endocytobiosis and Cell Research*, vol. 9, Nos. 2-3, pp. 135-175.
- Tsounis, G., Rossi, S., Grigg, R., Santangelo, G., Bramanti, L. and Gili, J.M. (2010). The exploitation and conservation of precious corals. *Oceanography and Marine Biology*, vol. 48, pp. 161.
- Tuohy, E., Nemeth, M.I., Bejarano, I., Schärer, M.T. and Appeldoorn, R.S. (2015). *In situ* tagging of Nassau grouper *Epinephelus striatus* using closed-circuit rebreathers at a spawning aggregation in Puerto Rico. *Marine Technology Society Journal*, vol. 49, pp. 115-122.
- U.S. Congress Office of Technology Assessment [U.S. Congress OTA]. (1993). Harmful non-indigenous species in the United States, OTA-F-565. U.S. Government Printing Office, Washington, DC, 397 p.
- Valdés-Pizzini, M. and Schärer-Umpierre, M.T. (2014). People, habitats, species, and governance: An assessment of the social-ecological system of La Parguera, Puerto Rico. Interdisciplinary Center for Coastal Studies, University of Puerto Rico, Mayagüez, Puerto Rico, 111 p.
- van Hooijdonk, R., Maynard, J.A. and Planes, S. (2013). Temporary refugia for coral reefs in a warming world. *Nature Climate Change*, vol. 3, pp. 508-511.
- van Oppen, M.J., Bongaerts, P., Underwood, J.N., Peplow, L.M. and Cooper, T.F. (2011). The role of deep reefs in shallow reef recovery: an assessment of vertical connectivity in a brooding coral from west and east Australia. *Molecular Ecology*, vol. 20, No. 8, pp. 1647-1660.
- Vega-Thurber, R.L., Burkepille, D.E., Fuchs, C., Shantz, A.A., McMinds, R. and Zaneveld J.R. (2013). Chronic nutrient enrichment increases prevalence and severity of coral disease and bleaching. *Global Change Biology*, vol. 20, No. 2, pp. 544-554.
- Veron, J. (1990). New scleractinia from Japan and other Indo-West Pacific countries. *Galaxea*, vol. 9, pp. 95-173.
- Veron, J.E.N. (1993). A biogeographic database of hermatypic corals: species of the central Indo-Pacific, genera of the world. Australian Institute of Marine Science Monograph Series, vol. 10, Townsville, Australia.
- Veron, J.E.N. (1995). Corals in space and time: the biogeography and evolution of the Scleractinia. Cornell University Press, 321 p.
- Veron, J.E.N. (2000). Coral of the World, 3 vols., Australia Institute of Marine Sciences, Townsville, Australia.
- Vroom, P. and Smith, C. (2001). The challenge of siphonous green algae. *American Scientist*, vol. 89, No. 6, pp. 524-31.
- Wabnitz, C., Taylor, M., Green, E. and Razak, T. (2003). From Ocean to Aquarium. UNEP-WCMC, Cambridge, UK.
- Wagner, D. (2015). The spatial distribution of shallow-water (< 150 m) black corals (Cnidaria: Antipatharia) in the Hawaiian Archipelago. *Marine Biodiversity Records*, vol. 8, e54.
- Walker, D.I. and Ormond, R.F.G. (2003). Coral death from sewage and phosphate pollution at Aqaba, Red-Sea. *Marine Pollution Bulletin*, vol. 13, No. 1, pp. 21-25.
- Ward, P., Carlson, B., Weekly, M. and Brumbaugh, B. (1984). Remote telemetry of daily vertical and horizontal movement of *Nautilus* in Palau. *Nature*, vol. 309, No. 5965, pp. 248-250.
- Webster, J.M., Clague, D.A., Braga, J.C., Spalding, H., Renema, W., Kelley, C., Applegate, B., Smith, J.R., Paull, C.K., Moore, J.G. and Potts, D. (2006). Drowned coralline algal dominated deposits off Lanai, Hawaii: carbonate accretion and vertical tectonics over the last 30 ka. *Marine Geology*, vol. 225, pp. 223-246.
- Weil, E. (2004). Coral reef diseases in the Wider Caribbean. In: Rosenberg, E. and Loya, Y. (eds.). Coral reef health and diseases. Springer-Verlag, pp. 35-68.
- Weil, E. (2006). Coral, octocoral and sponge diversity in the reefs of the Jaragua National Park Dominican Republic. *Revista de Biología Tropical*, vol. 54, No. 2, pp. 423-443.
- Weil, E. and Hooten, A.J. (2008). Underwater cards for assessing coral health on Caribbean coral reefs. GEF-CRTR-Currie Communications, Australia, 30 p.
- Weil, E. and Rogers, C. (2011). Coral reef diseases in the Atlantic-Caribbean. Part 5. In: Dubinsky, Z and Stambler, N. (eds.). Coral reefs: an ecosystem in transition, pp. 465-491.
- Weil, E., Cróquer, A. and Urreiztieta, I. (2009a). Temporal variability and consequences of coral diseases and bleaching in La Parguera, Puerto Rico from 2003-2007. *Caribbean Journal of Science*, vol. 45, Nos. 2-3, pp. 221-246.
- Weil, E., Cróquer, A. and Urreiztieta, I. (2009b). Yellow band disease compromises the reproductive output of the reef-building coral *Montastraea faveolata* (Anthozoa, Scleractinia). *Diseases of Aquatic Organisms*, vol. 87, pp. 45-55.
- Weinstein, D.K., Smith, T.B. and Klaus, J.S. (2014). Mesophotic bioerosion: variability and structural impact on US Virgin Island deep reefs. *Geomorphology*, vol. 222, pp. 14-24.
- Wells, J.W. (1954). Recent corals of the Marshall Islands, Bikini and nearby atolls. U.S. Geological Survey Professional Paper 260, pp. 385-486.
- Wells, J.W. (1973). New and old scleractinian from Jamaica. *Bulletin of Marine Science*, vol. 2, pp. 16-58.
- White, K.N., Ohara, T., Fujii, T., Kawamura, I., Mizuyama, M., Montenegro, J., Shikiba, H., Naruse, T., McClelland, T., Denis, V. and Reimer J.D. (2013). Typhoon damage on a shallow mesophotic reef in Okinawa, Japan. *PeerJ*, vol. 1, e151.
- Whitfield, P.E., Gardner, T., Vives, S.P., Gilligan, M.R., Courtenay, W.R., Ray, G.C. and Hare, J.A. (2002). Biological invasion of the Indo-Pacific lionfish *Pterois volitans* along the Atlantic coast of North America. *Marine Ecology Progress Series*, vol. 235, pp. 289-297.
- Wilkinson, C. (ed.). (2008). Status of coral reefs of the world: 2008. Global Coral Reef Monitoring Network and Reef and Rainforest Research Centre, Townsville, Australia, 296 p.
- Williams, B. and Grottole, A.G. (2010). Recent shoaling of the nutricline and thermocline in the western tropical Pacific. *Geophysical Research Letters*, vol. 37, L22601.
- Williams, G.C. (2003). Capitate taxa of the soft coral genus *Eleutherobia* (Octocorallia: Alcyoniidae) from Palau and South Africa; a new species and a new combination. *Zoologische Verhandlungen*, vol. 345, pp. 419-436.
- Williams, I.D., Baum, J.K., Heenan, A., Hanson, K.M., Nadon, M.O. and Brainard, R.E. (2015). Human oceanographic and habitat drivers of central and western Pacific coral reef fish assemblages. *PLoS ONE*, vol. 10, No. 4, e0120516.
- Williams, S.B., Pizarro, O., Webster, J.M., Beaman, R.J., Mahon, I., Johnson-Roberson, M. and Bridge, T.C.L. (2010). Autonomous underwater vehicle-assisted surveying of drowned reefs on the shelf edge of the Great Barrier Reef, Australia. *Journal of Field Robotics*, vol. 27, pp. 675-697.
- Winters, G., Beer, S., Zvi, B.B., Brickner, I. and Loya, Y. (2009). Spatial and temporal photoacclimation of *Stylophora pistillata*: zooxanthella size, pigmentation, location and clade. *Marine Ecology Progress Series*, vol. 384, pp. 107-119.
- Wolanski, E., Colin, P.L., Naithani, J., Deleersnijder, E. and Golbuu, Y. (2004). Large amplitude, leaky, island-generated, internal waves around Palau, Micronesia. *Estuarine, Coastal and Shelf Science*, vol. 60, pp. 705-716.
- Wood, E. (2001). Global advances in conservation and management of marine ornamental resources. *Aquarium Sciences and Conservation*, vol. 3, No. 1, pp. 65-77.
- Wood, E., Suliansa, M.S. and Mustapa, I. (2006). Fishing practices, status of coral reef resources and tactics for reversing unsustainable use on the Semporna Island reefs (Sabah, Malaysia). Proceedings of 10th International Coral Reef Symposium, pp. 1211-1217.
- Woodley, J.D., Chornesky, E.A., Clifford, P.A., Jackson, J.B.C., Kaufmann, L.S., Lang, J.C., Pearson, M.P., Porter, J.W., Rooney, M.C., Rylaarsdam, K.W., Tunnicliffe, V.J., Wahle, C.M., Wulff, J.L., Curtis, A.S.G., Dallmeyer, M.D., Jupp, B.P., Koehl, M.A.R., Neigel, J. and Sides, E.M. (1981). Hurricane Allen's impact on Jamaican coral reefs. *Science*, vol. 214, No. 4522, pp. 749-755.
- Woodroffe, C.D. and Webster, J.M. (2014). Coral reefs and sea-level change. *Marine Geology*, vol. 352, pp. 248-267.
- Yamazato, K. (1972). Bathymetric distribution of corals in the Ryukyu Islands. In: Mukundan, C. and Pillai, C.S.G. (eds.). Proceedings of the First International Symposium on Corals and Coral Reefs. Marine Biological Association of India, Mandapam Camp, India, pp. 121-133.
- Yokohama, Y. (1981). Distribution of the green light-absorbing pigments siphonaxanthin and siphonoin in marine green algae. *Botanica Marina*, vol. 24, pp. 637-40.
- Yokohama, Y., Kageyama, A., Ikawa, T. and Shimura, S. (1977). A carotenoid characteristic of chlorophycean seaweeds living in deep coastal waters. *Botanica Marina*, vol. 20, pp. 433-36.

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Picture a coral reef — most people will probably imagine brightly coloured corals, fish and other animals swimming in well-lit shallow waters. In fact, the coral reefs that live close to the surface of the sea — the ones that we can swim, snorkel, or dive near and see from space — are only a small portion of the complete coral reef ecosystem. Light-dependent corals can live in much deeper water (up to a depth of 150 m in clear waters). The shallow coral reefs from the surface of the sea to 30–40 m below are more like the tip of an iceberg; they are the more visible part of an extensive coral ecosystem that reaches into depths far beyond where most people visit. These intermediate depth reefs, known as Mesophotic Coral Ecosystems (MCEs), are the subject of this report.