Abstract

The mesophotic coral ecosystems (MCEs) of the Senyavin Islands (Pohnpei Island, and neighboring atolls Ant and Pakin) in the Federated States of Micronesia have received little research attention until recent years. These vibrant, environmentally dynamic ecosystems harbor a reservoir of biodiversity, with species and interactions new to science. Depths of $\geq 90$ m have up to 20 $^\circ$C annual variance. A strong El Niño event in 2016 resulted in a bloom-forming cyanobacteria smothering the upper MCEs of Pohnpei (25–65 m). Conditions persisted into 2017 with extensive coral bleaching and reef degradation with associated smothering by bloom-forming cyanobacteria and algae in the shallows. The initial bloom signature of 2016 at depth may, therefore, serve as a projected indicator of shallow reef health. Of the 160 reef-building scleractinian corals reported, 28 spanned the full depth range (0–45 m). Differences in irradiance due to geomorphology, as well as reef health, determined the depth transition between two primary benthic groups: photosynthetic scleractinians and filter-feeding azooxanthellate gorgonians, 60 m on low-relief atoll reefs and 45 m at high-relief walls and degraded reefs. Of the 109 gorgonian corals reported, 19 spanned the full depth range (0–140 m) with 70 morphospecies specific to lower mesophotic depths. Similarly, fish assemblages partitioned between shallow and mesophotic depths, characterized by herbivores and planktivores, respectively. Continuously growing marine resource exploitation and terrestrial runoff are heavily influencing reef health. The MCEs of Pohnpei are, thus, unique, yet vulnerable to the exacerbating stresses of man.

Keywords
Mesophotic coral ecosystems · Pohnpei · Micronesia · Thermally dynamic · Depth transition

17.1 Introduction

The Federated States of Micronesia (FSM) is one of five independent sovereign nations within Micronesia proper and consists of four states: Yap, Chuuk, Pohnpei, and Kosrae (collectively, the Caroline Islands). The FSM exclusive economic zone extends 3,000,000 km$^2$ with a total land area of 702 km$^2$ (Buden and Taboroši 2016). Thus the insular FSM landmass provides opportunities for evolutionary innovation and novelty through atoll and island isolation and also stepping-stones of connectivity for many taxa. Pohnpei Island (hereafter Pohnpei) is the largest of the FSM islands (Buden and Taboroši 2016), as well as the principle island of Pohnpei State. A further eight outer atolls Pingelap, Mwoakilloa (Mwokil*), Ant (Ahnd*), Pakin, Sapwuahfik (Ngetik*), Oroluk, Nukuoro (Madalama*), Kapingamarangi (Kirinidi*), and Minto Reef, a largely submerged atoll with only a 1.8 m high sand bar breaking the surface, constitute the state [*most commonly used names from Motteler (1986)]. Pohnpei and its neighboring atolls Ant and Pakin

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Y. Loya et al. (eds.), Mesophotic Coral Ecosystems, Coral Reefs of the World 12, https://doi.org/10.1007/978-3-319-92735-0_17
make up the Senyavin Islands (Fig. 17.1) and will herein be the primary focus of this chapter.

Mesophotic coral ecosystems (MCEs)—historically referred to as the “Twilight zone”—extend from ca. 30 to 150 m depth (Hinderstein et al. 2010) and are among the most diverse yet most unexplored realms on the planet (Pyle 1996). MCEs are primarily characterized by strong attenuation gradients in light, temperature, and wave action and, often, high-nutrient deepwater upwelling. Characterization of such ecosystems addresses questions of biodiversity, resilience, refugia, and priority conservation. In particular, the volcanic islands and atolls of the equatorial Pacific exhibit an increase in biodiversity and persistence of forms that would typically be selected against on the more diverse communities of continental regions and adjacent archipelagoes (Simberloff 1974).

### 17.1.1 Research History

Research on the MCEs of Pohnpei State is sparse, with the little conducted mostly confined to shallower depths (<30 m) (e.g., Rhodes et al. 2005, 2008, 2014a, b; Golbuu et al. 2008; Muir and Wallace 2016). Muir and Wallace (2016) reported low-light, “deepwater” scleractinian coral assemblages in the shallow (10–20 m depth) lagoon of southwest Pohnpei. In 1988, ichthyologists Randall Kosaki and Richard Pyle conducted an exploratory deep-reef expedition to Pohnpei and Ant Atoll. These preliminary dives to depths of up to 85 m yielded new fish geographic records (*Apolemichthys griffisi* Carlson and Taylor, 1981); *Chaetodon burgessi* Allen and Starck, 1973; *Centropyge multiclor* Randall and Wass 1974) and observations of unidentified new species (RL Pyle, pers. comm.). More recently, from 2014 to the present, the Association for Marine Exploration (AME) and collaborators have conducted research expeditions annually within the region (Rowley 2016). These expeditions have yielded new fish species at mesophotic depths (Copus et al. 2015; Anderson and Johnson 2017) along with ecological surveys of key MCE benthic components such as fishes (Bridge et al. 2016), scleractinian and gorgonian corals, as well as monitoring of environmental variables.

### 17.2 Environmental Setting

Pohnpei (6°52′ N, 158°13′ E) is an 8.7 million-year-old volcanic island (Rehman et al. 2013) with an area of 362 km². It is fringed by a discontinuous barrier reef that consists of 25 basaltic and coral islets enclosing an inner lagoon with an
area of ca. 69 m² and up to 90 m depth in places. A short
fringing reef surrounds the southeast portion of the island,
with the outer reef slope that surrounds the island dropping
to over 1000 m deep (Ashby 1993; OceanGrafix 2008).
Pohnpei is the tallest island in the FSM, with Mount Nanlaud
reaching 791 m above sea level and deep valleys bearing the
most extensive native tropical rainforest of Micronesia
(Balick 2009). Waterfalls and headwater streams feed the
2 km wide mangroves (ca. 17% of the island; Balick 2009)
and up to 6 km wide mostly low-light and high-sediment
lagoons, which border virtually the entire island (Buden and
Taboroši 2016). This combination of high island and high
vegetation density leads to a strong annual orographic
precipitation of >800 cm year⁻¹; Pohnpei, therefore, is one of
the wettest places on earth. It is also one of the most biodi-
verse in terms of botanical endemism (Balick 2009), how-
ever, comparatively less is known of its marine fauna and
flora. Moreover, the highland, rich vegetation, and marine
resources have, at least in part, resulted in Pohnpei having
the highest population density in the FSM (over 35,000
inhabitants). Pohnpei’s natural resource use continues to be
steeped in traditional cultural practices, yet the ongoing
pressures of upland disturbance and its associated runoff,
domestic and international fisheries (Rhodes et al. 2014a, b),
and climate change pose great threats to Pohnpei, its inhabit-
ants, and reef communities.

The atolls Ant and Pakin have a steep bathymetry similar
to that of Pohnpei but are not exposed to the same freshwater
or agricultural runoff. Ant Atoll (6°45′ N, 158°00′ E) is 8
nautical miles southwest of Pohnpei and consists of 13 islets
with a land area of 1.16 km² and an open lagoon of 46 km²
(Ashby 1993). It is the largest of Pohnpei’s outlying atolls
with an open channel, Tauenai Passage, to the south into the
lagoon. Ant Atoll is privately owned and sparsely populated
(ca. 8–10 inhabitants), although has had a history of fluctuat-
ing residency primarily due to the production of copra from
the husk of coconuts until the 1970s. Pakin Atoll (7°02′ N,
157°47′ E) is situated 18 nautical miles west of Pohnpei and
has 16 islets, a land area of 0.68 km², and a largely closed
lagoon of 8.85 km² that can only be accessed by small boats
at high tide through a narrow opening on the southwestern
side. Pakin has a population of ca. 50–80 inhabitants primar-
ily on the islet Nikalap, which is on the northwestern side of
the lagoon.

In general, MCEs are characterized by strong attenuation
gradients in environmental variables such as water clarity
and wave surge. Light attenuation is due to the absorption,
reflection, and scattering of light by sediment, dissolved
organic matter, and phytoplankton. Therefore, the greater the
concentration of particulates in the water column results in
an increased attenuation in light availability for photosyn-
thesis. The euphotic zone is the depth range whereby photosyn-
thesis can take place, with the subsurface irradiance defined
as the percentage at which light has penetrated. Water clar-
ity¹ at the outer reefs of Pohnpei had a mean diffuse attenua-
tion coefficient of $K_0 = 0.043 ± 0.003$ m⁻¹ compared to the less
turbid atolls at $K_0 = 0.038 ± 0.002$ m⁻¹. Mean optical depths² at
the midpoint (10% subsurface irradiance) were at the upper
mesophotic at 42 m, 222 ± 17 SE μE m⁻² s⁻¹ for Pohnpei and
56 m, 212 ± 25 SE μE m⁻² s⁻¹ at the atolls. At 1% subsurface
irradiance (lower limit of the euphotic zone) was at 95 m, 29
± 3 SE μE m⁻² s⁻¹ for Pohnpei and ca. 110 m, 23 μE m⁻² s⁻¹
for the atolls, with a 1.4% subsurface irradiance at 100 m, 29
± 6 SE μE m⁻² s⁻¹ for the latter. Here the water clarity on the
outer reefs of Pohnpei and neighboring atolls is slightly
greater at the atolls, and comparable with other high water
quality regions (e.g., Hawai’i; Pyle et al. 2016; Spalding et al.
2019).

The MCEs of the Senyavin Islands are not benign environ-
ments, particularly in comparison to the shallow-water coral
reefs. In addition to irradiance, temperature variability across
bathymetry is likely a “first-order” determinant of MCE
health and distribution (see Kleypas et al. 1999). Pohnpei’s
MCEs are thermally dynamic environments (Figs. 17.2 and
17.3), a pattern that has also been shown at other Indo-Pacific
locations, e.g., Palau (Wolanski et al. 2004; Colin et al. 2017)
and Hawai’i (Pyle et al. 2016). Over a 3-year period, thermo-
graphs (Tidbit v2, Onset®) placed at 10 m increments from
10 to 140 m depth at Pohnpei, Ant, and Pakin revealed signifi-
cant diurnal and seasonal fluctuations. Diurnal temperature
variances were typically over 10 °C at depths greater than
60 m (Figs. 17.2 and 17.3b, c). In March 2016, temperatures
soared dramatically bringing the El Niño to a close (Oceanic
Niño Index [ONI]: Very Strong El Niño; Fig. 17.2). Shallow-
water communities from the Porites microatolls of the
lagoons to the scleractinian reefs began to bleach, and the
majority of reefs eventually became smothered in algae by
2017 (see Macroalgae). A succession of cyanobacteria and
invasive algae smothered communities to a depth of 68 m at
Pohnpei from 2016 to 2017. Temperatures at 130 m depth
ranged from a minimum of 10.5 °C to a maximum of 29.2 °C
yet continued to fluctuate ca.10 °C within any single day irre-
spective of the mean. Such thermally challenging environ-
ments have been suggested to be responsible for the
“biologically depauperate communities” observed at meso-
photic depths of Palau (Wolanski et al. 2004). A similar
reduction in biodiversity also characterizes depths of ≥130 m

¹In Pohnpei, water clarity (light penetration) was measured using a cali-
ibrated spherical (4π) quantum sensor (LI-1938A and logger LI-1500,
LI-COR, USA), which measures the photon flux of photosynthetically
active radiation (PAR: 400–700 nm) in μmol photons m⁻² s⁻¹. Light
profiles ($n = 17$, in 2017) were taken over a depth gradient of 0–100 m
and recorded every 1–5 m.

²Light attenuation values are independent of water depth and, therefore,
are defined as optical depth ($z$) to make them comparable with other
locations.
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at Pohnpei Island proper. However, rich octocoral communities (see Octocorallia) flourish at ≥130 m off Ant and Pakin Atolls, which are equally thermally challenged. Such observations suggest that temperature is not the primary variable that determines biological community structure at mesophotic depths, at least for the islands and atolls of Micronesia. Over 3 years, the diurnal, seasonal, and annual temperature variance ranged up to 20 °C in a single day at 90 m depth. These considerable thermal oscillations may likely be due to internal waves (e.g., Wolanski et al. 2004) coupled with a Rossby wave deepening the thermocline and a rapid increase in temperature as it passed through Micronesia in 2016 (Colin et al. 2017).

Oceanic islands and atolls are exposed to strong water currents and wave action, and the Senyavin Islands are no exception. Water flow has not been quantified in Pohnpei; however, temperature data thus far demonstrate high-energy hydrodynamic regimes with the influence of two different water bodies: oceanic and shallow reef. This can also be seen through the nonlinear relationship between water temperature and dissolved oxygen (Fig. 17.3). Shallow reef temperatures followed the diurnal influence of the sun’s irradiance. Tidal influence was exerted during spring tides similarly observed with dissolved oxygen: high values at high tide with correspondingly low values at low tide (days 4–7; Fig. 17.3a). With increased depth, values appeared progressively independent of the diurnal cycle (influence from the warmth of the sun), with isotherm vertical displacement likely due to internal waves (Wolanski et al. 2004). The reduction of dissolved oxygen (30 m, 4.5–7.1 mg L⁻¹; 90 m, 5.2–7.6 mg L⁻¹; 130 m, 3.4–9.4 mg L⁻¹; Fig. 17.3), with depth was likely due to an increase in bacterial respiration feeding on sinking organic matter (Talley 2011). Chlorophyll values peaked at depth (90 m, average 0.64 μg L⁻¹, max. 2098.5 μg L⁻¹) compared to shallow (30 m, average 0.87 μg L⁻¹, max. 127.5 μg L⁻¹; fast CTD profiler, Valeport) reefs. Ongoing monitoring across a depth gradient from <10 to 150 m or more of key environmental variables (including water flow, pH, nutrients, and carbonate saturation state) will be necessary to develop a better understanding of MCEs and enable elucidation of the biological success of MCE benthic communities in such dynamic environments.

17.3 Habitat Description

The Senyavin islands all possess extensive MCE habitats. Pohnpei is a remnant of a shield volcano with shear drop-offs on the outer barrier reefs particularly on the western side of the island (Spengler 1990). The exposed windward/eastern outer reef also has steep drop-offs, as well as low-relief reefs with little coral cover in areas of very high wave and current exposure. The inner lagoon supports vast mangroves and thriving coral reefs loosely characterized as low-light, “platy assemblages” where the dominant coral form is platy yet can
include variable branching forms (Muir and Wallace 2016). Toward the outer lagoon outlets or passes, depths can reach over 60 m with strong currents transporting high-nutrient runoff from the mangrove areas. These deeper lagoonal habitats typically support gorgonian coral, algal, and sponge dominated hard substratum and sediment subject to significant bioturbation by benthic invertebrates. Research has primarily been conducted on the western outer reefs. These sites are characterized by shallow reef flats of low relief that typically extend to no more than 50 m out to a reef crest at 12–17 m depth. A steep wall or escarpment then extends to 70 m where the gradient reduces and then becomes a continuous and precipitous escarpment from 110 to 115 m depth. Buttresses are often present at ca. 70–90 m, attracting concentrated communities of invertebrates, mainly gorgonians and black corals, as well as fishes (Rowley, pers. obs.).

The atolls Ant and Pakin are characterized by near-vertical outer reef drop-offs on the western and southwestern sides. The eastern and northeastern sides have a sloping bathymetry from 3 to 30 m extending 80 m outward whereby the slope drops steeply with increasing depth to a distinct wave-cut ledge/notch at 100–110 m. Thereafter, is a steep wall with vertical fissures perpendicular to the ledge similarly observed in other tropical regions (Locker et al. 2010). These features are full of azooxanthellate invertebrates: mainly octocorals, antipatharians, sponges, bryozoans, ascidians, hydroids, crinoids, and the occasional benthic ctenophore (Rowley, pers. obs.).

**17.4 Biodiversity**

**17.4.1 Macroalgae**

The shallow-water flora from Pohnpei and Ant Atoll is diverse compared to other small similar-sized islands and atolls and consists of 133 Rhodophyta, 82 Chlorophyta, 26 Phaeophyta, and 3 Magnoliophyta, for a total of 244 species (Hodgson and McDermid 2000; McDermid et al. 2002). Biogeographic investigation of the shallow marine flora revealed that Ant Atoll and Pohnpei have a large number of widespread Indo-Pacific species, but very few probable regional endemics (McDermid et al. 2002). However, DNA-based species delineations of several macroalgal genera from island archipelagos in the Philippines (Payo et al. 2013), Hawaiian Islands (Spalding et al. 2016), and New Caledonia (Vieira et al. 2014) have shown extensive cryptic species diversity and fine-scale endemism. Although the use of molecular analyses would be needed to further refine and test these findings from Pohnpei and Ant Atoll, these collections provide a baseline for broad morphological comparisons with the mesophotic flora.
Macroalgae from 5 to 130 m depths were haphazardly recorded with photographs and video to document macroagal abundance at Pohnpei, Ant, and Pakin (Fig. 17.2) from 2014 to 2017. Species were identified to the lowest possible taxon based on images and preserved representative collections (n = 9). Although detailed molecular and morphological analyses are needed to properly assess the diversity of the MCE flora, general trends in comparison to the shallow flora and from year to year, particularly between 2016 (Very Strong El Niño) and 2017 (Weak La Niña), were possible for abundant macroalgae. From 2014 to 2016, macroalgae were generally in low to moderate abundance in comparison to corals. Small patches of a mat-forming *Cladophora* sp. were observed at 30 m. Occasionally, large individuals of *Avrainvillea* sp. (ca. 20–25 cm in height with clear concentric lines) would be observed only at Pakin Atoll growing on the surface of live colonies of *Porites* sp. colonies at 50–60 m depth (Fig. 17.4a). At this depth, non-geniculate (non-articulated) coralline algae and scattered clumps of an erect *Halimeda* sp. were observed growing at the base of plate corals (e.g., *Porites* sp. and *Acropora* sp.). By 130 m depth, non-geniculate corallines were abundant on vertical surfaces free of sedimentation and interspersed with a closely adhering green algal crust (Chlorophyta) resembling *Palmophyllum* sp. and a prostrate, irregularly branched green alga (Fig. 17.4b, c). Horizontal surfaces were covered in cascading sediment composed of dead *Halimeda* J.V. Lamouroux, 1812 segments, foraminifera, with occasional small patches of non-geniculate coralline algae (Fig. 17.4a).

In the summer of 2016, after the March Very Strong El Niño, the upper MCEs of Pohnpei experienced a cyanobacterial bloom smothering the reef to a depth range of 25–65 m (Fig. 17.5g), although not observed on the adjacent atolls. However, drastic changes were further observed in the MCE flora in 2017 at both Pohnpei and the atolls, with an increase in bloom-forming cyanobacteria, macroalgae, and non-geniculate corallines. In shallow water from 5 to 30 m depths, a shift from low-moderate abundance in previous years (Rowley, unpubl. data) to high abundance of *Caulerpa racemosa* (Forsskål) J. Agardh, 1873; *Microdictyon* Decaisne, 1841; *Dictyosphaeria cavernosa* (Forsskål) Børgeesen, 1932; a conspicuous orange cyanobacteria; brown-colored filamentous diatoms; and *Halimeda* spp. dominated the reefs, overgrowing corals, and other available substrate (Fig. 17.5a–f). White, bleached patches of *Halimeda* were observed inside *Halimeda* spp. beds and draperies, possibly due to sexual reproductive events, a disease outbreak, or other unknown causes (Fig. 17.5d). From 30 to 60 m depths, a dark-green mat of *Cladophora* cf. sp. (Fig. 17.5h–j) and *Halimeda* spp. covered at least 50% of available substrate, with non-geniculate coralline continuing to be abundant. By 120 m, macroalgal cover was low with no bloom-forming macroalgae observed and appeared similar to the reefs observed from 2016.

As would be expected, genera that were described as dominant in the shallow flora, such as the brown algae *Dictyota* and *Padina* (Hodgson and McDermid 2000), were not observed at mesophotic depths. However, both the shallow and mesophotic flora contained similar species and genera, such as *Halimeda* spp., *Microdictyon* sp., *Dictyosphaeria cavernosa*, and *Avrainvillea* sp. (Hodgson and McDermid 2000). The majority of Rhodophyta described from shallow water included turf and diminutive algae, making comparisons with the MCE flora difficult without extensive collections. Additional samples analyzed with molecular and morphological analyses are needed to properly charac-

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Fig. 17.4 Mesophotic macroalgae from the northeastern side of Pakin Atoll in 2016. (a) A large *Avrainvillea* sp. with the coral *Porites* sp. at 50 m depth. (b) Benthic macroalgae at 130 m with the green algal crust resembling *Palmophyllum* sp., and (c) a prostrate, irregularly branched green alga. Intermittent sediment in both images largely consisted of dead *Halimeda* segments (white). Ca represents non-geniculate coralline algae overgrowing dead *Porites*, and Pa represents *Palmophyllum* sp. (Photo credits: S.J. Rowley, 2016, www.mesophotic.org, can be reused under CC BY license)
Fig. 17.5 Mesophotic macroalgae during 2017 from (a) southwest Pohnpei at 5 m depth; (b) filamentous diatom mats at 5 m, Ant Atoll; (c) start of Microdictyon beds at 5 m, Ant Atoll that extend to 50 m depth; (d) bleached Halimeda patches, 5 m; and (e) Caulerpa racemosa, 20 m depth at western Pohnpei. (f) Halimeda and non-geniculate coralline algae dominated reefs at 30 m depth, Pakin Atoll. (g) Bloom-forming cyanobacteria at 30 m, Pohnpei in July 2016, and (h) a shift to Cladophora cf. sp. at the same reef patch in August 2017. (i) Juvenile corals Seriatopora hystrix and Siphonogorgia cf. with other juvenile invertebrates and corallines at 60 m depth, Pohnpei in August 2016, and (j) the same reef and depth dominated by a Cladophora cf. sp. in August 2017. (Photo credits: S.J. Rowley, 2016–2017, www.mesophotic.org, can be reused under CC BY license)
terize the MCE macroalgal community in Pohnpei. Nevertheless, the current information suggests that this assemblage can experience dramatic and unexpected shifts in algal abundance, with a recent (2017) algal bloom event from shallow to MCE depths. The persistence and causes of this phase shift may likely, in part, be due to the very strong El Niño of 2016, with subsequent succession in dominant taxa. Moreover, eutrophication at Pohnpei and increased fishing pressure further encourage algal overgrowth. Future research directions should focus on extensive collections for molecular analyses of the MCE flora, including non-geniculate and turf algae. Even though ecological benthic transect imagery data has been collected (Rowley, unpubl. data), the lack of funds and personnel render conclusions wanting. Nonetheless, continued monitoring of sites through time would determine temporal changes in community structure and abundance. This coupled with ecophysiological studies including top-down and bottom-up processes is required to elucidate the drivers of algal blooms from the shallow reefs to MCE depths.

17.4.2 Anthozoans

Coral is essentially a polyphyletic term, defined by Cairns (2007): “as those Cnidaria having continuous or discontinuous carbonate or horn-like skeletal elements.” It is estimated that over 5080 coral species are currently described, 66% of which are found at depths below 50 m (Cairns 2007). Of this 66%, azooxanthellate (corals without the photosynthetic dinoflagellate symbiont Symbiodinium) octocorals constitute 75% of the species found at depth with a rate of species discovery unlikely to reach an asymptote in the near future. Nearly 42% of the scleractinians currently described occur at depth (below 30 m), with new coral species being discovered at mesophotic depths (e.g., Randall 2015).

It is important to note that other coral groups are well represented on the MCEs of Pohnpei, most notably the Antipatharia and Zoanthidea. However, no research has been conducted on these taxa within the region.

17.4.2.1 Scleractinia

Pohnpei and the surrounding atolls of Ant and Pakin support a variety of benthic habitats and a corresponding diversity of coral communities. In particular, the outer edges grade steeply to deep depths, in clear oligotrophic waters, which are well suited to the development and maintenance of photosynthetic MCEs, with high levels of light penetration into deeper waters. Additionally, the lagoonal patch reefs provide low-light habitats in shallower waters, creating a “shallow mesophotic-like” community in some locations (Muir and Wallace 2016).

Surveys of the reef-building zooxanthellate coral species over depth (0–45 m) were conducted in August 2017, using upslope point count transects (sensu Roberts et al. 2016). Of the 160 species reported, 56 were present at depths below 30 m (Fig. 17.6a). Half of these species (28) were also represented in the shallowest 15 m of the water column, although this number represented ca. one-quarter of the 117 species recorded in the top 15 m. Only 15 species were solely recorded from the mid-depths (15–30 m). These results suggest that the deeper water MCE communities are a partially nested subset of the shallow communities. This has significant implications for the vertical connectivity of these communities, and the potential for MCE communities to act as refugia for the shallow-water communities (Bongaerts et al. 2010; Bongaerts and Smith 2019).

To assess the changes in species richness over depth, species accumulation curves were generated for each depth bin (n = 9), with 1000 repetitions completed at each depth. The resulting values were used to demonstrate the species richness trend over depth (Fig. 17.6b) and fitted with a Huisman-Olff-Fresco model (Jansen and Oksanen 2013; Jansen et al. 2017), which fits one of seven ecologically relevant shapes to the data. The most commonly chosen model fit after 100 permutations of the model was a gradual monotonic decline with depth (Fig. 17.6b), although the trend showed no continued decline beyond ca. 20 m depth.

Severe bleaching episodes in 2016 and 2017 impacted the shallow regions of the reefs, and the effects were visible up to and beyond 30 m in some cases. Despite this, some regions showed little effect of the bleaching, in particular one site populated heavily by plating Acropora hyacinthus (Dana, 1846) colonies, which all appeared to be the result of a single recruitment pulse. The extent of the variability in the damage caused by the repeat bleaching events was greatest in the shallow depths (15 m), which is likely responsible for the retention of a surprisingly large species pool at these depths. The variety of habitats provided around the island of Pohnpei and the associated atolls has maintained a source pool of colonies in spite of the bleaching damage, which could allow for a rapid recovery. Clear, oligotrophic water conditions on the atolls mean that the shallow coral communities were entombed in crustose coralline algae (CCA) on their death, without the colonization of filamentous algae, cyanobacteria, or other benthic megafauna likely to inhibit coral recruitment. This phenomenon has created a substratum that is

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3 Transects were run from 45 m to the surface, with count stations located in nine depth bins monitored at 5 m depth increments. In total, 1236 individual colonies were recorded from a depth range of 0 to 45 m, representing 160 nominal species. Where species could not be confidently identified in the field, they were photographed, and temporary working names given to unclear taxonomic units. A proportion of these species with working names are likely to result in novel species descriptions, or new geographic records.
Fig. 17.6 (a) Depth ranges of scleractinian coral species. Each bar represents the depth range of a species, arranged by the mid-depth of the range. The x-axis represents depth (m), and y-axis is each species. (b) Species richness of scleractinian corals over depth. Species richness accumulation estimates at each of nine, 5 m wide depth bins. The red line represents the projected trend of species richness over depth by fitting a Huisman-Olff-Fresco model (Jansen and Oksanen 2013; Jansen et al. 2017). Gray dots represent 999 permutations of species accumulation estimates at a common sample size of 72 individuals. Red line represents trend of richness over depth. (Graphs are by T.E. Roberts, www.mesophotic.org, can be reused under CC BY license)
extremely well suited to coral recruitment, as corals are known to recruit onto CCA (Harrington et al. 2004) and more complex substrates (Hata et al. 2017). When combined with the retention of the regional species pool, and the extensive MCE habitats, the recovery potential of these reefs is highly encouraging and worth continuing to monitor.

Among the coral habitats found around Pohnpei, the “shallow mesophotic-like” communities found in the lagoon of Pohnpei at 15–30 m depth are particularly intriguing. These habitats have been described in the literature (Muir and Wallace 2016; Fig. 17.7a, b), and the species composition of these communities is in keeping with those found at upper mesophotic depths (i.e., 30–40 m) in other Indo-Pacific locations, for example, Kimbe Bay in Papua New Guinea (Fig. 17.7c). Notably, the species found at both Kimbe Bay and the shallow lagoon of Pohnpei [such as Acropora pichoni Wallace, 1999 (Fig. 17.7a), and Acropora tenella (Brook 1892); Fig. 17.7b] were not found in the upper 45 m on the outer barrier habitats, suggesting that they either exist further down the slope or have extensive dispersal ranges and particular environmental requirements. Pursuing a quantitative analysis of the deeper (depths greater than 45 m) regions of these habitats will provide answers to some of these questions.

17.4.2.2 Octocorallia

The subclass Octocorallia comprises the orders Alcyonacea (soft corals and gorgonians), Helioporacea (blue coral), and Pennatulacea (sea pens). The zooxanthellate blue coral Heliopora coerulea Pallas, 1766 is the only extant octocoral that produces a massive aragonite exoskeleton. Branching forms of this species are particularly abundant on the south to northwestern side of the atolls Ant and Pakin, extending into the upper mesophotic (≤ 45 m depth). Laminar colonies were only present in the shallow waters (≤ 5 m depth), which may suggest the presence of two (cryptic) species partitioned by depth: branching forms at depth and laminar forms in the shallows. Distinct lineages reflected by growth form have been shown in H. coerulea yet are not segregated by depth (Yasuda et al. 2014). Whatever the case, neither morphotype present in the Pohnpei region was affected by the temperature anomalies or algal overgrowth described in this chapter.

Sea pens, such as those within the genus Virgularia Lamarck, 1816 were also observed at mesophotic depths; however, no known research has been conducted on this group throughout the region. It is the gorgonian corals within the Alcyonacea that has received the most research attention and thus will be the primary focus of this section.

MCEs within the Indo-Pacific are typically dominated by a diverse array of gorgonian (sea fan) octocorals (Pyle 1996; Rowley 2014). Of the 65 genera and 15 families currently recorded at mesophotic depths throughout the Indo-Pacific (see Sánchez et al. 2019), 35 genera and 11 families were present within the Senyavin Islands and comprised all higher-order groups (total of 897 specimens collected during four expeditions 2014–2017; see also Rowley 2016). The majority of taxa are found at depths below 70 m, consisting of 32 genera within 11 families. This is in contrast to gorgonians on the shallow reefs (<30 m), where there are 16 genera within 8 families. However, 12 genera

Fig. 17.7 Mesophotic coral communities at Pohnpei lagoon and Kimbe Bay, PNG, showing a similar composition of species. (a) Acropora cf. pichoni and (b) A. tenella, both at a depth of 18 m in Pohnpei lagoon. (c) Kimbe Bay coral communities at a depth of 35 m. (Photo credits: T.C.L. Bridge, 2016–2017, www.mesophotic.org, can be reused under CC BY license)
within 7 families occur throughout the full bathymetric range (1–157 m; Rowley 2016).

In August and September 2017, quantitative surveys were conducted as described by Roberts et al. (2016); see Sect. 17.4.2.1 Anthozoans: Scleractinia. Within the narrow band of the upper mesophotic (30–60 m), 38 morphospecies of gorgonians and 18 genera within 9 families were present. At this “transitional” depth, the majority of taxa were those spanning the full bathymetric range such as *Viminella* Gray, 1870 (Fig. 17.8a). In the shallows (<30 m) dense communities of a sciophilous (shade tolerant) *Subergorgia* Gray, 1857 populated the caves and under overhangs (Fig. 17.8b). However, only two morphospecies were specific to the shallows. Both morphospecies were within the azooxanthellate genus *Melithaea* Milne Edwards, 1857, and also appeared sciophilous, being found exclusively under overhangs and crevices (Fig. 17.8c, d). Only two zooxanthellate gorgonians were present at mesophotic depths at Pakin Atoll, *Rumphella* Bayer, 1955 (up to 61 m; Fig. 17.9f), and *Briareum* Blainville, 1834 (up to 75 m; Fig. 17.8g), most likely due to the water clarity at this site. Whether such colonies are reproductively viable is unknown. These were single observations of each taxon, both typically at depths shallower than 40 m (Rowley, pers. obs.).

Specific to the lower depths were morphospecies mostly within the Plexauridae (n = 27; genera = 8), particularly within the genus *Paracis* Kükenthal, 1919 (Fig. 17.8i), as well as *Ellisellidae* (n = 14; genera = 5; Fig. 17.8k) and *Acanthogorgiidae* (n = 12; genera = 3; see Fig. 17.8j). Less diverse yet characteristic taxa that generally increase in diversity and abundance with increased depth are those within the Keroeididae (n = 3; genus = 1), *Primnoidae* (n = 2; genera = 2), and *Parisididae* (n = 2; genus = 1; see Fig. 17.8l). In total, 19 morphospecies occurred throughout the bathymetric range, most notably *Annella* spp. (Fig. 17.8e), *Acanthogorgia* spp., and *Astrographia* spp. (e.g., Fig. 17.8h). Nevertheless, all such “depth generalists” were typically more abundant with depth.

Changes in species richness across depth between Pohnpei and the atolls were assessed. Notably, gorgonian diversity increased with depth a pattern that has been reported previously (Rowley 2018). Their high overall diversity may well be a consequence of a continuously dynamic environment (Connell 1978) at depth, particularly with regard to temperature. Conversely, the hermatypic scleractinian corals, the primary benthic space competitors throughout the shallow reefs, follow a depth trajectory consistent with light availability. The transition between these two benthic groups, gorgonians and scleractinians, within the Senyavin Islands occurs at ca. 60 m depth (Fig. 17.9a). However, at Pohnpei the depth transition is at ca. 45 m (Fig. 17.9b). This shallower transition depth at Pohnpei, compared to the atolls, may be due to a combination of high-relief walls and the effects of overfishing at many sites (Fig. 17.9c). Therefore, characterizing the transition from a photosynthetic community to a non-photosynthetic filter-feeding community (i.e., scleractinians to gorgonians with increased depth) may assist with reef health assessments and resilience to anthropogenically induced environmental change (Knights et al. 2017).

### 17.4.3 Sponges

Sponges (Phylum: Porifera) are a highly complex, diverse group and the oldest living metazoans on earth (Van Soest et al. 2012). Nevertheless, sponges are notoriously difficult to identify due to intra- and interspecific variability in response to environmental factors such as hydrodynamics, light, and turbidity (Van Soest et al. 2012). Initial observations and surveys of the diversity and distribution of sponges on shallow and mesophotic outer reefs throughout the Senyavin Islands reveal an increase in diversity and abundance with increasing depth. The shallow portions of the reef (5–10 m) are low in sponge diversity and abundance. Nonetheless, sponge diversity increased with increasing depth, particularly on the topographically complex outer steep reefs with undercut walls and overhangs, where the more delicate species could be found. Encrusting taxa such as *Siphonodictyon* Bergquist, 1965; *Clathria* Schmidt, 1862; and *Hyrtios erectus* (Keller, 1889) were prevalent in the shallows within the shadows of the *Acropora* spp.-dominated portions of reef. Other notable shallow reef taxa include those within the Demospongiae genera *Cinachyrella* Wilson, 1925; *Coscinoderma* Carter, 1883; and *Hymeniacidon* Bowerbank, 1858. As the topography shifts at the reef crest to the high-relief walls particularly characteristic of the western reefs, sponges become larger with a branching morphology. For example, species within the genera *Cymbastela* Hooper and Bergquist, 1992, and *Cribrochalina* Schmidt, 1870, were increasingly observed between the depths of 50 and 100 m. Furthermore, at depths ≥90 m *Niphates* Duchassaing and Michelotti, 1864, as well as lithistid sponges were also present, the
Fig. 17.8  Gorgonian corals across bathymetry. (a) *Viminella* sp., at Ant Atoll, 65 m depth; (b) *Subergorgia* sp., populating the underside of overhangs and small caves at Ant and Pakin Atoll, 12 m depth; (c) and inset (d) *Melithaea* sp., in crevices and under the overhangs, 10 m depth at Pohnpei. (e) *Anella reticulata* at 90 m depth, Pohnpei. This species typically spans the full depth range (5 to >150 m). The zooxanthellate gorgonians (f) *Rumphella* sp., at 20 m, and (g) *Briareum* sp., at 38 m depth at Pakin Atoll. Both taxa span the shallow to upper mesophotic depth range. (h) The depth-generalist genus *Astrogorgia*, which spans the full bathymetric range, 75 m, Pakin Atoll. (i) *Paracis* sp., at 110 m, Pohnpei, and (j) *Acanthogorgia* sp., 125 m at Pakin Atoll. Both morphospecies are specific to the lower mesophotic, although species within the genera can be found across the full depth range. Deep-reef specialists (k) *Helania* sp., at 106 m, and (l) *Parisis* at 95 m at Pohnpei. Both genera increase in abundance and diversity with increased depth. (Photo credits: S.J. Rowley, 2014–2017, www.mesophotic.org, can be reused under CC BY license)
latter previously noted in Palau (Colin 2009). A variety of morphospecies were observed from shallower depths past the reef crest in the low-light environments of the over hangs and small caves. Taxa spanning the shallow and mesophotic depths included those within *Dactylospongia* Bergquist, 1965; *Spongia* Linnaeus, 1759; and *Luffariella* Thiele, 1899, as well as the previously noted *Clathria*, *Cribrochalina*, and *Cymbastela*.

These preliminary observations on the Porifera assemblages of the Senyavin Islands across bathymetry suggest two patterns: firstly, that they appear to correspond with that of the azooxanthellate gorgonians of the region, reflecting a
reduction of irradiance (also observed in Palau: Colin 2009; Kelly and Bell 2016), and, secondly, that there may be little difference in sponge assemblages between the outer reefs of Pohnpei and the atolls, Ant and Pakin.

17.4.4 Fishes

From 2014 to 2016, a total of 473 fishes have been collected from the waters of the Senyavin Islands for taxonomic, biogeographic, and population genetic research (by Brian D. Greene, RL Pyle, Joshua Copus, and Richard R. Coleman; see Rowley 2016). The majority of these fishes are from mesophotic depths with at least 11, collected below 90 m depth that are new species to science. These include the recently described *Luzonichthys seaver* Copus, Ka’apu-Lyons, and Pyle, 2015, *Grammatonotus xanthostigma* Anderson and Johnson, 2017, and *Grammatonotus pelipel* Anderson and Johnson, 2017 (Fig. 17.10).

Recent research on the island of Pohnpei (and neighboring Ant Atoll) investigated fish assemblages across depths and found patterns related to trophic position and highlighted patterns that are specific to the Central Pacific region. Pohnpei supports over 650 species of reef fishes (Allen 2005;
Goldberg et al. 2008). To document the shift from a shallow to mesophotic reef fish community, we conducted visual and roving-video surveys of reef fishes along a gradient (0–130 m) using closed-circuit rebreathers.

Trophic position has previously been found to be a distinguishing feature between shallow and mesophotic-associated fishes (Bejarano et al. 2014; Kane and Tissot 2017), with few herbivores at mesophotic depths, a trend that remained consistent in Pohnpei (Coleman et al. 2018). At 30 m trophic assemblages were indistinguishable from other depths; however, shallow (<30 m) and deep (>30 m) assemblages were found to be significantly different from each other (PERMANOVA, *Pseudo*-*F* = 4.43, *p* < 0.001; Coleman et al. 2018). These observations corroborate 30 m as the depth at which shallow assemblages begin to shift to mesophotic assemblages, which has also been observed in the Caribbean (García-Sais 2010), the South Atlantic (Rosa et al. 2016), Hawai‘i (Kane and Tissot 2017), and the Red Sea (Brokovich et al. 2008). Concordance of a 30 m transitional depth across different ocean basins provides further support that this is a global phenomenon.

Trophic position was also found to be associated with a species ability to specialize in shallow or mesophotic depths. Our results indicated that the probability of a deep specialist being a planktivore ranged from 33% to 61% and the probability of a shallow specialist being an herbivore was high ranging from 91% to 99% (Coleman et al. 2018). Food availability of herbivores is directly related to light intensity, which decreases with depth. Algal communities are known to thrive as deep as 268 m allowing for the potential for food availability for herbivores in MCEs (Littler et al. 1985). However, as depth increases the algal community, composition changes considerably (Littler et al. 1985) leading to a decline in grazing pressure (Brokovich et al. 2010). Furthermore, no macroalgae were observed deeper than 30 m at the time of study (2014; Coleman and Rowley, pers. obs.) in contrast to subsequent years. Alternatively, planktivores can potentially thrive at any depth, and it has been suggested that upwelling increases food availability in MCEs via primary production for planktivores (Leichter and Genovese 2006; Leichter et al. 2013).

Although trophic position can influence the depth distribution of fish species, an assessment of Hawaiian fish assemblages found that it accounted for only 33% of the variation, with additional factors explaining distribution across depth (Kane and Tissot 2017). Morphological characteristics (Bridge et al. 2016), habitat availability (Brokovich et al. 2008), and the physical and geological environment (Kahng et al. 2010) have been identified as other potential drivers influencing the depth distribution of fish assemblages. Taxonomic grouping has also previously been used to predict species distribution. However, highly variable patterns among distant regions suggest taxonomic grouping is not a sufficient predictor of inhabiting MCEs. Snappers (Lutjanidae) were associated with mesophotic depths in both Pohnpei and the Red Sea. Additionally, surgeonfish (Acanthuridae) were found to be the dominant family at shallow depths in both regions, as well as the South Atlantic (Rosa et al. 2016). However, we also observed conflicting patterns in damselfish (Pomacentridae) and wrasse (Labridae) distributions between regions. Red Sea damselfish were associated with shallow habitat due to the presence of branching coral, which served as shelter from predation (Brokovich et al. 2008). Conversely, in Pohnpei, damselfish were associated with deeper depths, an environment where branching corals are rare. Red Sea wrasses were associated with deeper depths and thought to be outcompeting planktivorous damselfish for space, whereas in Pohnpei, we found that wrasses were more associated with shallow depths. It is not immediately clear what the drivers are that are facilitating the disparity between these regions. Nonetheless, identifying these inconsistencies will help to illuminate and explain unknown drivers that influence species vertical distributions.

The upper boundary of mesophotic communities is likely to shift in response to a changing climate. Although the impacts to shallow and MCEs remain unknown, identifying the mechanisms that drive species depth distributions will help us to understand how species will respond to these events. At the family and trophic level, we found that there is little overlap between shallow and MCE fish assemblages in Pohnpei, and this pattern limits the utility of MCEs to act as a refuge from disturbances from which shallow reefs can be replenished. Management strategies must take into account the distinction between shallow and mesophotic ecosystems in the development of future protective measures.

17.4.4.1 Elasmobranchs

The subclass Elasmobranchii Bonaparte, 1838, within the class Chondrichthyes Huxley, 1880 (cartilaginous fish), comprises sharks, rays, skates, and sawfish. The oceanic islands and atolls of the Pacific attract migratory taxa and provide ideal habitat for species migrating locally between the atolls and islands, as well as vertically. Relatively little is known about the sharks and rays of the Senyavin Islands. What has been documented is primarily associated with bycatch from the industrial tuna fisheries (Hutchinson et al. 2015), with young silky sharks, *Carcharhinus falciformis* (Bibron, 1839), constituting 95% of the entire elasmobranch bycatch (Lawson 2011; Rice 2013). From 2014 to 2017, the abundance of sharks on the reefs of Pohnpei has dramatically declined (Rowley, pers. obs.). Nevertheless, at both Ant and particularly Pakin Atolls, large numbers of juvenile black tip reef sharks and white tip reef sharks populate the shallow reefs. At mesophotic depths of >50 m depth, sharks are frequently present. Numerous white tip reef sharks, *Triakis ansel*
obidents, can be observed resting on the sandy bottoms of the passes between the lagoons and the open ocean (40–60 m depth). Solitary grey reef sharks, *Carcharhinus amblyrhynchos* (Bleeker, 1856), are territorial and are often observed at upper mesophotic depths. Yet, shark aggregations in general are becoming increasingly rare. In 2015, an aggregation of 50 or more, silky sharks, *C. falciformis*, were recorded at Pakin Atoll. However, such numbers have not been recorded since, likely due to population decimation as bycatch by the international purse seine tuna industry (Lawson 2011; Rice 2013). With greater depths, an increase for aggressive offshore taxa can be observed, such as black tip [*Carcharhinus limbatis* (Müller and Henle, 1841)] and silver tip sharks [*Carcharhinus albisquamatus* (Rüppell, 1837)]. These patterns are curious, but the latter species are territorial in twos or fours, often displaying aggressive behavior and posture (Rowley pers. obs.).

The rays of Pohnpei, Ant, and Pakin are typically seen on shallow reefs. Nonetheless, some species of rays, such as the blotched fantail ray [*Taeniuraus meyeni* (Müller and Henle, 1841)], have been observed resting at 90 m depth in Pohnpei. The majority of ray taxa are sensitive to temperature, which may limit their bathymetric distribution (Jawad 2011). Rays are also targets for local fishing (Yamauchi and Ota 2012).

### 17.4.5 Other Biotic Components

The invertebrate taxa at mesophotic depths, other than those within the Hexacorallia (i.e., Antipatharia and Scleractinia) and Octocorallia (i.e., gorgonians and soft corals), are poorly known. The MCEs of the Senyavin Islands harbor a remarkable biodiversity of invertebrates; however, no research on other than those taxonomic groups discussed herein has been conducted. Moreover, the upper mesophotic zone is not immune to the invertebrate predators of the shallows. The voracious coral predator *Acanthaster planci* (Linnaeus, 1758) (commonly known as the Crown-of-Thorns starfish) is present on the MCEs of Pohnpei, although little is known about them. Numbers of *A. planci* are observed to decline at depths of ca. 40 m likely due to the lack of prey and the concomitant increase in macroalgae.

Observations suggest an overall increase in biodiversity with increased depth, particularly on the atolls (Rowley, pers. obs.). Notable taxa include numerous vagile (mobile, not stalked) crinoids, benthic ctenophores (*Lycoteis* Komai, 1941), black corals (e.g., *Antipathes* Pallas, 1766; *Cirrhipathes* de Blainville, 1830; *Stichopathes* Brook, 1889), bryozoans (particularly taxa within the genus *Reticoporellina* Harmer, 1933, and family Crisinidae d’Orbigny, 1853), and a variety of ascidians, flatworms, crustaceans, mollusks, and hydroids (including the Stylasteridae Gray, 1847, and the family Aglaopheniidae Marktanner-Turneretscher, 1890). Few holothurians or echinoids were found. Large oysters similar to those seen in Palau (see Colin 2009) were present at under overhangs and deep ledges from ≥90 m depth. Azoanthellate scleractinians within the families Dendrophylliidae and Caryophylliidae Dana, 1846, were common throughout the deeper depths, a pattern also noted at other Indo-Pacific locations (e.g., Marshall Islands, reviewed in Kahng et al. 2010; Hawai‘i, Wagner et al. 2016).

Many taxa are in association with other invertebrates, as well as fishes, demonstrating that this environment most likely reflects fascinating coevolutionary interactions between taxa over geological time. For example, numerous individuals of the decapod shrimp *Plesionika cf. flavicauda* invariably occur with the deep-reef specialist grouper *Cephalopholis igarashiensis* Katayama, 1957 (Greene and Pyle, pers. comm.). Gorgonians, soft corals, and sponges host an extraordinary array of associate taxa. Gorgonians, in particular, provide a protective “nursery” for juvenile fish species, as well as the pygmy seahorse (*Hippocampus* Rafinesque, 1810), brittle stars (e.g., *Ophiothela* Verrill, 1867), caprellid shrimps, host color-specific cowries, as well as occasional high numbers of *Ophiothrix* Müller and Troschel, 1840, populating the fringes of sea fans with no obvious detrimental effects. Motile crinoids also utilize the elevated positioning of sea fans to capture high nutrients in the water column and possibly avoid predation from benthic predators (e.g., echinoids; Gorzelak et al. 2012; Donovan and Renema 2016). With the exception of Pakin Atoll, few large fish can be found at depth, other than the small, yet diverse, taxa of interest to ichthyologists and the aquarium trade (Fig. 17.10). Therefore, with a paucity of predators, filter feeders such as crinoids are likely to be successful in the MCEs of the Senyavin Islands.

The bathymetric distribution of the Foraminifera d’Orbigny, 1826 (hereafter forams) relates to irradiance, substratum type, nutrient, and hydrodynamic regime (Renema 2018). Notably, large benthic foramin taxa with flat calcareous tests (shell) are found at deeper depths (Song et al. 1994; Hohenegger et al. 2000). In the Senyavin Islands, forams and *Halimeda* segments are the major sediment components, the latter dominating in the shallows. With increased depth, a shift toward the deep-reef specialist foramin *Cycloclypeus carpenteri* Brady, 1881, occurs (Fig. 17.11a). This species is the largest living foramin (>100 mm in diameter) and has a typical depth range of 50–120 m throughout its geographic distribution (Koba 1978; Song et al. 1994; Iryu et al. 1995; Webster et al. 2009; Bridge et al. 2011). *C. carpenteri* is a free living benthic foramin that is slightly convex, planar, and discoid in shape (Song et al. 1994; Fig. 17.11b). This flattened discoid morphology optimizes the surface area for photosynthesis by the endosymbionts within its calcareous test. However, this
morphology has been shown to reduce mechanical stability in high water energy environments, particularly in the shallows (Song et al. 1994). On the MCEs of Pohnpei, fields of *C. carpenteri* have been discovered at 80–100 m depth (Rowley, pers. obs.). Such high abundances may be due, in part, to the clear waters and likely low-energy hydrodynamic regime at some of the sites on Pohnpei. Irradiance and hydrodynamic regime have been shown to determine the depth distribution of this species, with less mechanical stability in the high water energy environments of shallow reefs (Song et al. 1994).

### 17.5 Threats and Conservation Issues

The health of the shallow-water coral reefs of the Senyavin Islands is being severely compromised, the signature of which can be seen at deeper depths with increased algal dominance in the upper mesophotic zone and with a reduction of reef and food fish. The 2016 bloom signature at depth may act as a predictor of reef health in months to come, particularly for reefs excessively exposed to multiple stressors. Ocean temperatures have fluctuated over the millennia, a single stressor that reefs may well have the capacity to recover from in our current climate, but the addition of multiple stressors such as eutrophication and international fishing exploitation compromise coral reef resilience. The potential thermal tolerance of MCE taxa may provide insights into the mechanisms of biological success of MCE communities over geological time. This, in turn, may then assist in predictions of which taxa and communities are likely to persist and perhaps even act as refugia in the advent of global climate change.

Ant and Pakin Atolls have the greatest abundance and diversity of fishes and invertebrates of the Senyavin Islands, particularly at depth. The marine environments of these atolls are considered the most valuable for protection (Allen 2005; Conservation Society of Pohnpei 2006). Yet, between 2016 and 2017, the coral reefs of Ant and Pakin underwent a shift from vibrant coral reefs to CCA-dominated reefs. An increase in scleractinian corals in the upper mesophotic zone (Fig. 17.10b) plus a large abundance of fish taxa at greater depths may, if protected, reseed the shallow populations of the atolls. Sharing research findings, footage, and imagery with local communities has enhanced their understanding of these valued environments and has led to the desire to protect such rich biodiverse resources. Bottom fishing is considered the most skilled and sustainable practice, targeting fishes from 40 to 140 m depth (Joseph pers. obs.). Therefore, the opportunity to bridge science and policy through adaptive management strategies, making use of MCEs, may assist local community members and chiefs, who are keen to protect their resources. It is unclear if and how the MCEs of the Senyavin Islands will be either affected by and/or effective for mitigating the detrimental effects of anthropogenic disturbance. It is also unclear if and how the reefs of Pohnpei and its sister atolls will recover and persist, but the most powerful tool for change has been to help communities become aware of the importance of their marine resources (Joseph pers. obs.).

### 17.6 Conclusion

The research presented here on the mesophotic reefs of the Senyavin Islands is a summary of what has been conducted by the Association for Marine Exploration (AME) and col-
laborators since 2014. Annual expeditions have revealed that MCEs are biodiverse, dynamic environments that provide refuge for certain megafauna, have species-specific bathymetric distributions, and display remarkable resilience to diurnal fluctuations in temperature. Depth transitions between functional groups of fish and benthic taxa such as the photosynthetic corals and filter-feeding azooxanthellate gorgonians are predominantly a function of irradiance. Taxonomic groups such as Porifera and Foraminifera are highlighted as fruitful areas for future research. However, the rapid declines in reef health and marine resources have been apparent, particularly on the shallows reefs. The lush reefs and huge abundances of fishes of previous times (Turak and DeVantier 2005) are successively being replaced by barren reefs, smothered by invasive algae, filamentous cyanobacteria, or crustose coralline algae of the atolls. The surrounding oceanic islands and atolls of Micronesia may act as refugia, representing stepping-stones of dispersal within and between the regions and bathymetry. Yet, resource management strategies developed by Pacific Island cultures over hundreds of generations face significant challenges in the modern world. Nevertheless, exploration and research of MCEs of oceanic islands and atolls not only reveal species and ecological patterns new to science but must also shape priority conservation management decisions. Taken together, the MCEs of the Senyavin Islands provide a natural laboratory to test adaptive capacity and resilience to environmental change and address questions relating to biodiversity, resilience, refugia, and priorities for conservation.

Acknowledgments  Sincere gratitude is extended to Walter Wilbur and family at the Nihco Marine Park, Pohnpei, the Conservation Society of Pohnpei (CSP), to all at the Office of Fisheries and Aquaculture (OFA), the late Souminrek Pakin and his community, and the Hawley family at the Pohnpei LP Gas Distributing Company, FSM. Special thanks also go to S.M. Stanley, D. Bushis, F. Butschek, B.D. Greene, R.L. Pyle, A. Baird, L. Briones, D. Johnson, J. Hartup, A. Malfitani, K. Longenecker, R. Langston, S. Lindfield, and many more. SJR was generously supported by the Association for Marine Exploration (AME), the Systematic Research Fund (SRF) as supported by the Linnean Society of London and the Systematics Association, Ocean First Education (formerly Ocean Classrooms), and the Edmondson Foundation of the Bishop Museum. Poseidon/Cis-Lunar Technology and Valeport Ltd., UK, generously provided technical equipment support. RRC would like to thank the Seaver Foundation for their generous support in 2014. MKD would like to thank the Our World Underwater Scholarship Society, the society’s sponsors, and Rolex for her funding and support during Pohnpei 2017.

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