



The Hawaiian Archipelago

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Abstract

The Hawaiian Archipelago is one of the largest and most isolated island chains in the world, and its marine ecosystems are well-studied. Research on Hawaiian mesophotic coral ecosystems (MCEs) began in the 1960s and has intensified during the past decade. In Hawai'i, rich communities of macroalgae, corals and other invertebrates, and fishes inhabit MCEs and are associated with increased

water clarity and decreasing average current strength with depth. Extensive calcified and fleshy macroalgal beds are found both in discrete patches, dense beds, and meadows over both hard and soft substrates. Several species of corals typical of shallow reefs extend to depths of ~60 m. The dominant corals below 60 m are in the genus *Leptoseris*, which can form extensive coral reefs spanning tens of km². Few octocoral species inhabit shallow reefs and upper MCEs (30–70 m) but are diverse at the deepest range of MCEs (>130 m). Sponges do not represent a major structural component of MCEs. Many species of fishes occur on both shallow reefs and MCEs, but MCEs harbor more endemic species (up to 100% endemism). Several new species of macroalgae, corals and other invertebrates, and fishes have recently been documented. Over 60% of the territorial waters surrounding the archipelago are protected as the Papahānaumokuākea Marine National Monument; however, no specific protections exist for MCEs. Generally, threats affecting Hawai'i's shallow reefs also affect MCEs to varying degrees. MCEs may be more insulated from some threats but more vulnerable than shallow reefs to others (e.g., water clarity).

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25.1 Introduction

The islands and reefs of the Hawaiian Archipelago stretch over 2500 km across the north-central tropical Pacific Ocean. This isolated archipelago consists of the eight Main Hawaiian Islands (MHI) in the southeast and a linear array of mostly uninhabited rocky islets, atolls, reefs, and seamounts comprising the Northwestern Hawaiian Islands (NWHI);

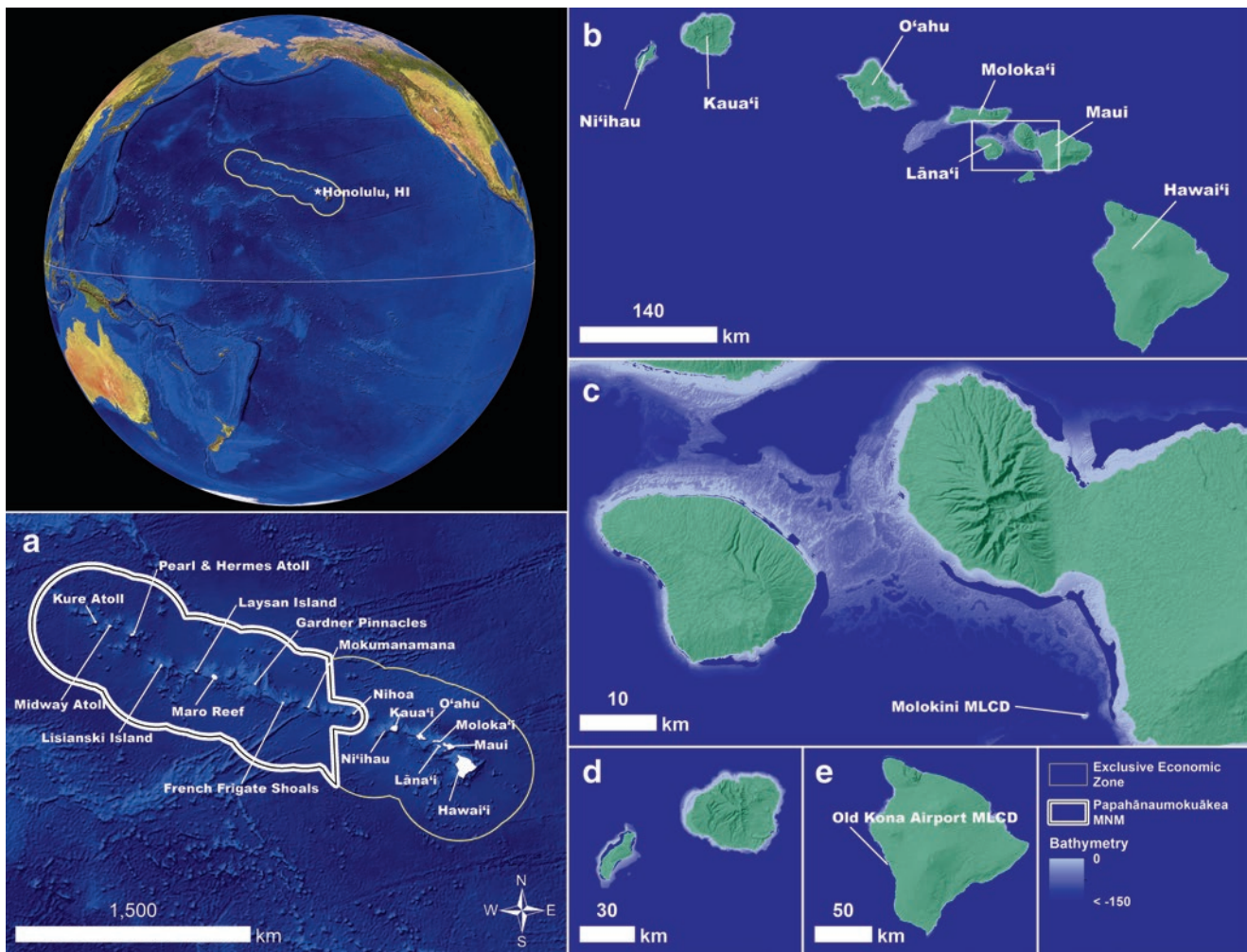


Fig. 25.1 The Hawaiian Archipelago is composed of the eight MHI and a series of islands, atolls, and banks to the northwest called the NWHI. The (a) NWHI are protected within the PMNM. (b) The eight MHI with the area of the 'Au'au Channel enclosed in white. (c) The 'Au'au Channel between the islands of Lana'i and Maui. MCEs within the 'Au'au Channel have been extensively studied due to its gently sloping substrate and calm waters. (d) Kaua'i and Ni'ihau. (e) Hawaii'i

Fig. 25.1). The Hawaiian Archipelago spans a broad latitudinal gradient, stretching from the southern tip of Hawaii'i Island (19° N) to Kure Atoll (28° N). Many Hawaiian reefs are protected by local, state, and federal laws, with a wide range of management and conservation efforts in place. The NWHI falls within the Papahānaumokuākea Marine National Monument (PMNM), a federally protected area larger than all US national parks combined ($>1,508,870$ km²). The PMNM is listed as a World Heritage site and includes about 10% of shallow (<30 m) coral reefs within US territorial waters (Rohmann et al. 2005). Coral reefs within the Hawaiian Archipelago have been extensively studied and documented (Maragos 1977; Chave and Malahoff 1998; Hoover 1998; Mundy 2005; Kahng and Kelley 2007; Randall 2007; Fletcher et al. 2008; Grigg et al. 2008; Jokiel 2008; Rooney et al. 2008; Toonen et al. 2011; Selkoe et al. 2016). Although Hawaii'i was among the first places where mesophotic coral ecosystems (MCEs), or communities of light-dependent corals and other organisms from 30–40 m to over

150 m depths (Hinderstein et al. 2010), were investigated, the most intensive research within this environment has occurred only within the past decade.

25.1.1 Research History

The first investigations of MCEs within the Hawaiian Archipelago were conducted in the 1960s with SCUBA (Grigg 1965) and manned submersibles (Brock and Chamberlain 1968; Strasburg et al. 1968). These early investigations found an unexpected abundance of reef-associated species (including hermatypic corals) at depths from 25 to 107 m. These studies also revealed that many species of fishes previously believed to be restricted to shallow coral reefs also inhabited much greater depths. In the decades that followed, several publications reported on MCEs within the Hawaiian Archipelago (Grigg 1976; Agegian and Abbott 1985; Maragos and Jokiel 1985; Moffitt et al. 1989; Chave and Mundy 1994;

Parrish and Polovina 1994; Pyle and Chave 1994), but most of these focused on either a few species or habitats or a broad depth range (with MCEs representing only a small portion of the study). Beginning in the late 1980s, the advent of technical, mixed-gas diving opened up new opportunities for the exploration of MCEs (Pyle 1996a, b, c, 1998, 2000, 2019; Grigg et al. 2002; Parrish and Pyle 2002; Pence and Pyle 2002; Parrish and Boland 2004; Boland and Parrish 2005; Grigg 2006). From 2004 to 2007, submersible and technical diving surveys funded by the National Oceanic and Atmospheric Administration (NOAA) Hawai'i Undersea Research Laboratory (HURL) discovered extensive mesophotic macroalgal assemblages around the MHI. In 2006, the discovery of extensive MCEs with near-100% coral cover off Maui at 40–130 m depths, coupled with interest in documenting MCEs in the NWHI and growing support for technical mixed-gas diving operations among Hawaiian research institutions, led to a surge of MCE research. A series of collaborative, multidisciplinary projects ensued including the 2007–2012 Deep Coral Reef Ecosystem Studies project supported by the NOAA National Centers for Coastal Ocean Science focused on the MCEs of the 'Au'au Channel (located on the submerged land bridge between the islands of Maui and Lana'i; Grigg et al. 2002), the 2010–2013 study contrasting MCEs between O'ahu and Maui funded by the NOAA Coral Reef Conservation Program, and annual NOAA research cruises to PMNM beginning in 2009 (Pyle et al. 2016a).

25.2 Environmental Setting

The Hawaiian ridge spans the productivity gradient of the Central Pacific seascape. The northern atolls are located in the most productive waters, whereas the islands and banks in the central region experience the seasonal southern shift of productivity from the chlorophyll front (Polovina et al. 2001), and the larger MHI are removed to the south where ocean conditions are impoverished. It is unknown how the environment varies across the archipelago at mesophotic depths. Visual surveys exploring the archipelago show there is a wide range in the substrate composition and dominance of coral, algae (Pyle et al. 2016a), and the associated fish assemblage (Kane and Tissot 2017), but year-round environmental monitoring is lacking. Some fishery studies have opportunistically placed thermographs at mesophotic depths to characterize the seasonal range of temperatures (Parrish and Boland 2004; Parrish et al. 2015) but are too few to represent the wider realm. To understand the mesophotic environment, an important first step is to obtain measurements of light levels, temperature, salinity, oxygen, and currents at specific sites with benthic communities that are rich with mesophotic corals and algae. This focused study site approach would identify priority variables to form the basis for future comparative environmental studies across the archipelago.

25.2.1 'Au'au Channel

Most of the environmental data available on Hawaiian MCEs is from the 'Au'au Channel. The 'Au'au Channel has the most extensive MCEs and macroalgal beds and meadows in the MHI (Fig. 25.2) and was the site of an in-depth geophysical study (Pyle et al. 2016a). This area, in the lee of the island of Maui, is protected from dominant trade winds and seasonal swell (Fig. 25.1). This protection, coupled with clear water, thermal stability, and consistent water flow at 70–90 m, provides an environment conducive for thriving MCEs.

One of the most important geophysical characteristics of MCEs in Hawai'i is water clarity. Light profiles taken within one hour of high noon on calm, clear days over dense *Leptoseris* spp. reefs to a maximum depth of 94 m within the 'Au'au Channel and over macroalgal beds off O'ahu to 90 m depths revealed very clear water, with a mean diffuse attenuation coefficient (K_d) of $0.041 \pm 0.001 \text{ m}^{-1}$ (Spalding 2012; Pyle et al. 2016a). In comparison, nearby inshore areas of West Maui had a higher K_d (and more turbid water), ranging from 0.107 m^{-1} at 10 m depth to 0.073 m^{-1} at 30 m (Spalding 2012). The mean optical depths over MCEs, which correspond to the midpoint (10% subsurface irradiance) and the lower limit (1% subsurface irradiance) of the euphotic zone, are 56 and 112 m, respectively. In general, areas with the clearest water support the richest and most expansive MCEs in Hawai'i (Pyle et al. 2016a).

Depth profiles of salinity and dissolved oxygen are fairly constant across mesophotic depths, whereas temperature decreases variably with increasing depth (Pyle et al. 2016a). Bottom measurements showed salinity averaged 35.05 PSU (std 0.05) and remained constant across the habitats at different depths. Oxygen averaged 4.84 ml L^{-1} (std 0.09), increasing a tenth of a degree over the depth range sampled, while temperature declined from $24.9 \text{ }^\circ\text{C}$ to $21.2 \text{ }^\circ\text{C}$ with the mean $23.3 \text{ }^\circ\text{C}$ (std 1.0), matching the temperature of the 80 m depth where the richest community of *Leptoseris* spp. corals were found (Pyle et al. 2016a).

The variability in water temperature across mesophotic depths is most apparent when viewed seasonally. Water temperature collected between August 2008 and July 2009 on moorings at mesophotic depths, shallow (53 and 64 m), middle (73, 84, and 93 m), and deep (102, 112, and 123 m) in the 'Au'au Channel, ranged from $\sim 21 \text{ }^\circ\text{C}$ to $\sim 26.5 \text{ }^\circ\text{C}$ (Fig. 25.3). A seasonal cycle was apparent throughout the water column, with warmest temperatures from September to November and coolest temperatures from February to May (Fig. 25.3). The temperature was consistently 2–3 $^\circ\text{C}$ cooler at the deep end of the sampled depth range (102–123 m), with less short-term variability and seasonal fluctuation. Relatively large (1–2 $^\circ\text{C}$) short-term (1 day) temperature excursions occurred at 50–75 m but remained stable at the deepest site. The temperature at middle depths (70–90 m), where *Leptoseris* spp. corals were most abundant, was the most dynamic during the

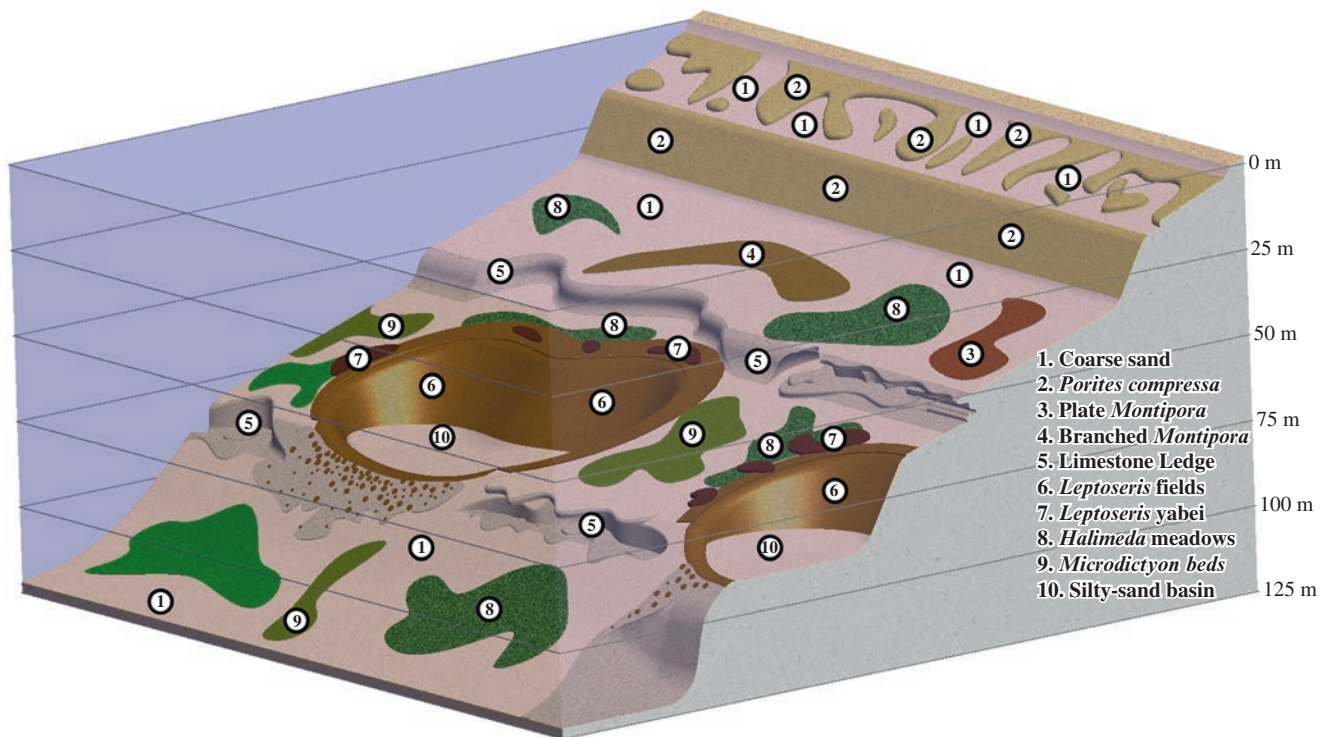


Fig. 25.2 Generalized diagram of the major components of MCEs in the 'Au'au Channel, MHI. (Reprinted from Pyle et al. 2016a)

warmest months and the most thermally stable during the coolest months. It is unclear whether MCEs are influenced by tidally correlated vertical thermocline shifts.

Acoustic profiler analysis indicates that the current magnitude at 70–90 m is $10\text{--}15\text{ cm s}^{-1}$ with sporadic, brief pulses $>25\text{ cm s}^{-1}$ (Pyle et al. 2016a). A clear pulsing (strengthening and weakening) corresponded with directional changes on a tidal frequency. At greater depths (90–110 m), the flow was almost stagnant with little tidal signal and variable direction. These results are in stark contrast to the higher magnitude currents ($>40\text{ cm s}^{-1}$) that occur in shallow waters subject to daily tidally forced flows. Although there are clear differences in flow rates within these MCEs, direction of flow is highly variable and difficult to attribute to tidal- or wind-driven processes.

25.3 Habitat Description

MCEs in the Hawaiian Archipelago are found mostly on gradual slopes with occasional rocky outcrops of both volcanic and carbonate materials. However, Kane and Tissot (2017) describe steep slopes in some areas on the island of Hawai'i. Discontinuities in the slope are common at 50–60, 80–90, and 110–120 m depths. Many of these features represent ancient shorelines of rocky undercut limestone ledges or steep sandy or limestone slopes parallel to shore (Fletcher and Sherman 1995; Grigg et al. 2002; Rooney et al. 2008). Gradually sloping, flat-bottom areas of carbonate are mostly

covered by sand, gravel, or rhodoliths with very little coral cover. Corals are more common on exposed rock surfaces along rock ledges and outcrops.

In the 'Au'au Channel, these discontinuities are the result of karstification and the formation of solution basins during a low sea-level stand (Fig. 25.2). Habitats in flat-bottom areas (i.e., between discontinuities) include macroalgal meadows (especially in the 40–90 m range) and expansive low-relief beds of interlocking branching colonies or laminar tiers of *Montipora* spp. (40–60 m). The 80–90 m discontinuity within the 'Au'au Channel includes a few exposed, steep rocky walls but is otherwise dominated by beds of *Leptoseris* spp. coral and mixed macroalgal beds over gently sloping substrate.

25.4 Biodiversity

25.4.1 Macroalgae

The low-light environment of MCEs requires obligate photosynthetic organisms, such as algae and zooxanthellate corals, to be highly efficient at light capture and photosynthesis. Surprisingly, mesophotic algae are often as productive as shallow-water algae despite the low-light environment (Jensen et al. 1985; Littler et al. 1985, 1986). Certain groups of algae are well adapted to growth in MCEs in general, and are conspicuous members of the deepwater algal assemblage, such as the green algal genera in the Bryopsidales

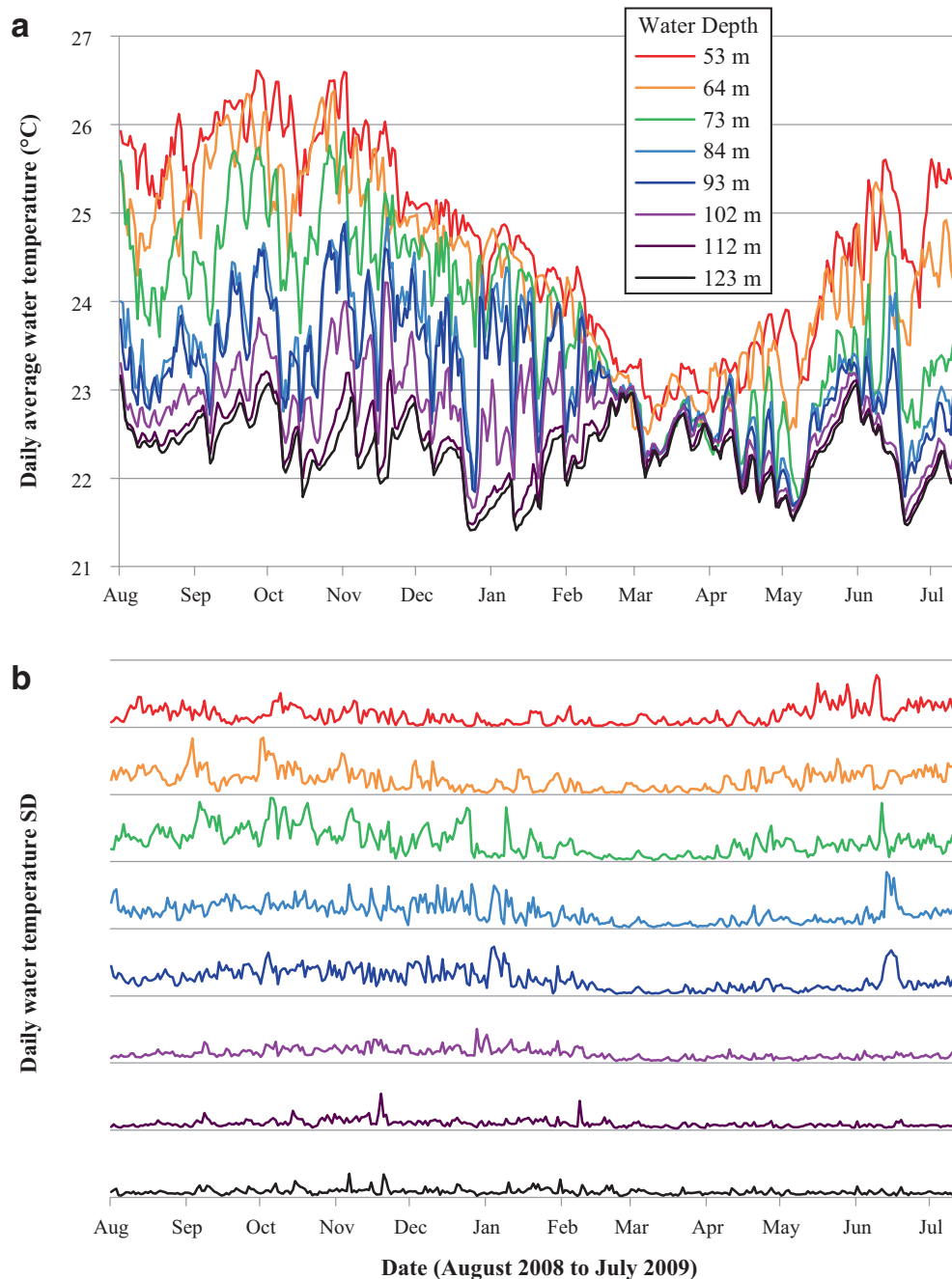


Fig. 25.3 Temperature data, comparing seasonal and daily fluctuations at eight different depths off the 'Au'au Channel from August 2008 to July 2009. Graphs represent the average daily temperature (**a**) and the daily standard deviation (SD) (**b**) at each depth. The thin black line below each depth trace in (**b**) represents SD = 0, and the thin black line above represents SD = 1; the greater the distance of the color line from the black line below (SD = 0), the more dynamic the daily temperature. SD is based on $n = 72$ temperature values per day for data recorded at 84 and 123 m, and $n = 36$ for other depths. (Reprinted from Pyle et al. 2016a)

(e.g., *Halimeda*, *Codium*, *Caulerpa*, *Udotea*, and *Avrainvillea*). These genera are all abundant within the Hawaiian Archipelago and form dense beds and meadows covering tens of km² over both hard and soft substrates.

Macroalgal communities are found in discrete patches (separated by sand or other benthic habitats) at all mesophotic depths in the MHI and are further described in Spalding et al. (2019). Examples include expansive meadows of *Halimeda*

kanaloana Vroom in sand; beds of *Halimeda distorta* (Yamada) Hillis-Colinvaux over hard substrates, as well as monospecific beds of *Distromium* spp., *Dictyopteris* spp., *Microdictyon* spp., *Caulerpa* spp.; and mixed assemblages of other macroalgal species (Fig. 25.4; Spalding 2012). Some species assemblages are restricted to specific islands, such as dense beds of the green alga *Udotea* sp. (currently undescribed) and the invasive species *Avrainvillea amadelpha*

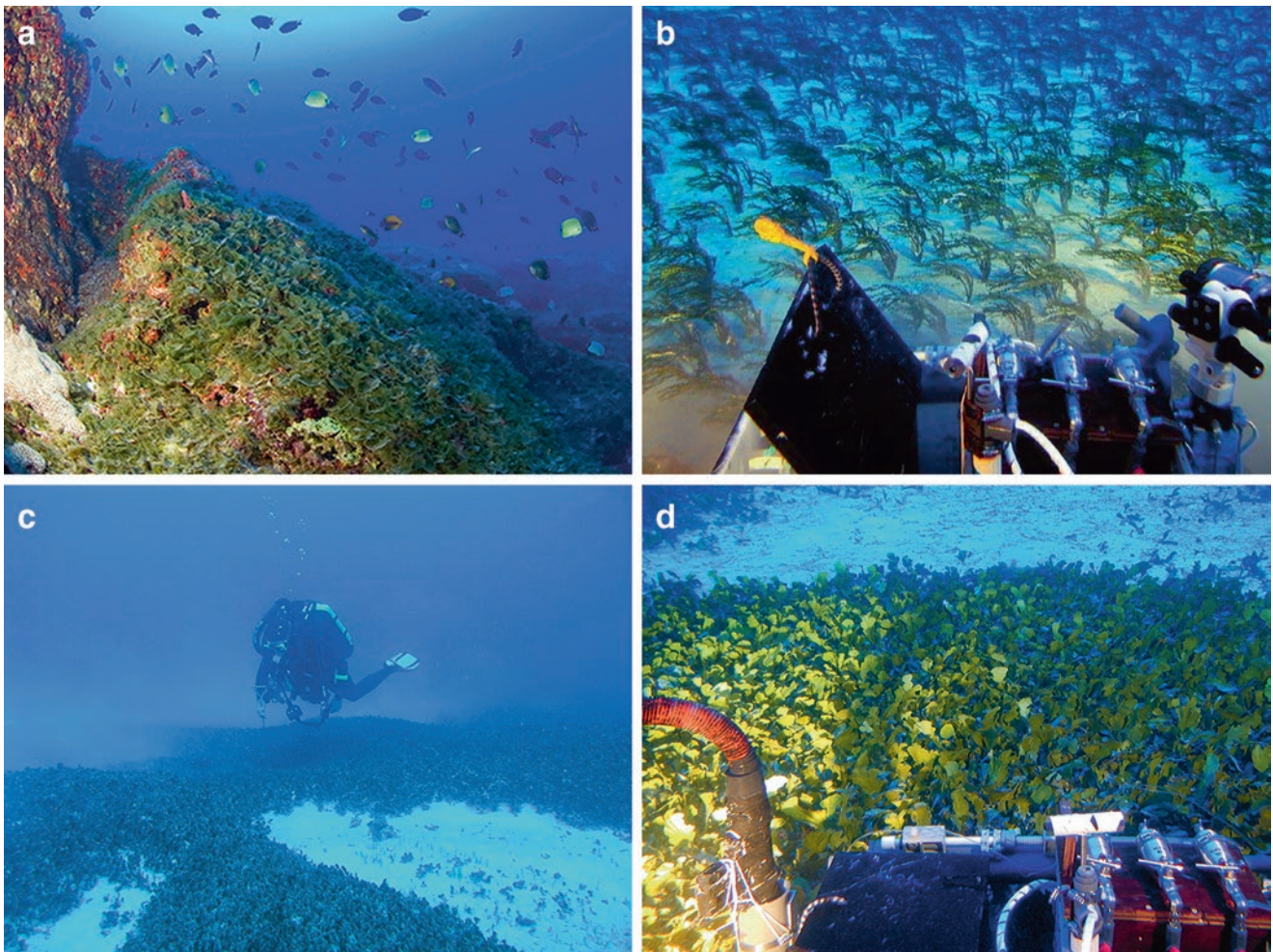


Fig. 25.4 Representative macroalgal communities in the Hawaiian Archipelago. (a) *Microdictyon* spp. bed at Pearl and Hermes Atoll, NWHI at 64 m. (b) *Halimeda kanaloana* bed at 90 m in the 'Au'au Channel, West Maui, MHI. (c) Dark mounds of invasive *Avrainvillea amadelpha* beds off O'ahu, MHI at 50 m depth. (d) Dense bed of *Udotea* sp. off south O'ahu at 50 m depth. (Photo credits: (a) PMNM (b, d) HURL, and (c) H.L. Spalding)

(Montagne) A. Gepp and E. S. Gepp to 90 m around the southern and western sides of O'ahu. In contrast, NWHI mesophotic macroalgal communities are dominated by beds of *Microdictyon* spp. The summits of eight banks from Lisianski to Mokumanamana Island (Necker) were also observed, using remotely operated vehicles (ROVs), to have dense beds of *Sargassum* or *Dictyopteris* species (Parrish and Boland 2004; collections needed for verification).

In the MHI, 72 species of frondose macroalgae have been identified based on morphological characteristics from MCEs, including 29 Chlorophyta, 31 Rhodophyta, and 12 Phaeophyceae (Spalding 2012; Pyle et al. 2016a). Estimates of macroalgal diversity are likely conservative because of the taxonomic limitations inherent in some morphological identifications of algae. For instance, large-bladed green algae ("sea lettuce") from MCEs were all identified morphologically as the shallow-water species "*Ulva lactuca*." However, recent molecular analyses revealed that these specimens rep-

resent four undescribed species belonging to the genera *Ulva* and *Umbraulva*, which cannot be identified using morphological characters alone; three of these species are probably endemic to Hawaiian MCEs (Spalding et al. 2016). Nevertheless, the methods used to identify the 72 species were similar to current taxonomic treatments in Hawai'i (Abbott 1999; Abbott and Huisman 2003; Huisman et al. 2007) allowing for comparisons with the better-known shallow-water flora across depths. Overall, the biodiversity of macroalgae changes with increasing depth, with more species found at 70–100 m than at 40–60 m. The most distinctive changes in diversity (i.e., the most substantial changes in total number of species at each depth interval) occurred at 80–90 m and 110–120 m (Pyle et al. 2016a). Although molecular methods are needed for further comparison between macroalgal communities on MCEs and shallower reefs, ~45% of the species recorded thus far are unique to MCE environments, based on morphology.

25.4.2 Anthozoans

The diversity of shallow anthozoan corals is well documented in Hawai'i. There are approximately 66 species of shallow scleractinian coral species (Fenner 2005), 8 species of antipatharians (< 150 m; Wagner 2015), and approximately 5 shallow species of octocorals (Fenner 2005) recorded from Hawai'i. Of these species, approximately 20 scleractinian species, all 8 antipatharian species, and 14 octocoral species are found within Hawai'i's MCEs (Table 25.1). Despite these species being documented from MCEs, there has been no comprehensive systematic taxonomic analysis of the anthozoan species across all mesophotic depths, and hence the complete anthozoan diversity is unknown. Further exploration and molecular genetic studies will likely uncover more biodiversity in MCEs.

Across the Hawaiian Archipelago, there is higher coral cover and well-developed reef habitats at deeper depths in the MHI than NWHI (Rooney et al. 2010). In addition to

scleractinian corals, the eight antipatharian black coral species representing six genera are found widely distributed throughout the Hawaiian Archipelago but appear to be less abundant in the NWHI (Wagner 2015; Table 25.1). Gorgonians and soft corals are equally as sparse, with increasing abundance and diversity at deeper depths. However, the majority of MCEs of the NWHI have yet to be explored, and additional diversity unique to the NWHI is likely to be discovered.

MCEs in Hawai'i are often dominated by a few scleractinian species occurring in distinct depth ranges (Table 25.1; Fig. 25.5). At depths of 30–60 m, the dominant corals are also commonly found on shallow reefs, including *Montipora capitata*, *Pocillopora meandrina*, *P. damicornis*, *P. eydouxi*, *Pavona varians*, *Leptastrea purpurea*, *Porites compressa*, and *Porites lobata* (Rooney et al. 2010; Pyle et al. 2016a). Below 60 m, *Leptoseris* spp. form extensive reefs (Table 25.1; Fig. 25.5) with ~100% coral cover and high 3-D complexity in some locations (Rooney et al. 2010; Pyle et al. 2016a). Other

Table 25.1 Scleractinian and antipatharian coral species in MCEs in Hawai'i

Species	30–60 m	60–100 m	100–150 m
Scleractinia			
<i>Leptastrea purpurea</i> (Dana, 1846)	3		
<i>Leptoseris hawaiiensis</i> Vaughan, 1907		3,6	6,7
<i>Leptoseris incrustans</i> (Quelch, 1886)		3	
<i>Leptoseris mycetoseroides</i> Wells, 1954	3,6,12	3	
<i>Leptoseris papyracea</i> (Dana, 1846)	12	3,6,7	
<i>Leptoseris scabra</i> (Vaughan, 1907)	12	6,7	6
<i>Leptoseris</i> sp. 1		6,7	7
<i>Leptoseris tubulifera</i> Vaughan, 1907	6	3,6,7	
<i>Leptoseris yabei</i> (Pillai & Scheer, 1976)		3,6,10	
<i>Montipora capitata</i> (Dana, 1846)	3,10		
<i>Pavona</i> sp. 1		6	
<i>Pavona varians</i> Verrill, 1864	12	6	
<i>Pocillopora damicornis</i> (Linnaeus, 1758)	3,10		
<i>Pocillopora grandis</i> (=eydouxi) Dana, 1846	3		
<i>Pocillopora meandrina</i> Dana 1846	3,10		
<i>Pocillopora molokensis</i> Vaughan, 1907	12		
<i>Porites compressa</i> Dana, 1846	3,12		
<i>Porites hawaiiensis</i> Vaughan, 1907	2		
<i>Porites lobata</i> Dana, 1846	3,10		
<i>Porites rus</i> (Forskål, 1775)		12	
<i>Porties</i> cf. <i>studer</i> Vaughan, 1907	3,12		
Antipatharia			
<i>Acanthopathes undulata</i> (van Pesch, 1914)	8,9,11	11	8,9,11
<i>Antipathes grandis</i> (Verrill, 1928)	4,8,9,11	4,8,9,11	8,9,11
<i>Antipathes griggsi</i> Opresko, 2009	8,9,11	8,9,11	9,11
<i>Aphanipathes verticillata mauiensis</i> Opresko et al., 2012		5,8,9,11	5,8,9,11
<i>Cirrhopathes</i> cf. <i>anguina</i> (Dana, 1846)	8,9,11	8,9,11	9
<i>Myriopathes</i> cf. <i>ulex</i> (Ellis and Solander, 1786)	8,9,11	8,9,11	8,9,11
<i>Stichopathes echinulata</i> Brook, 1889		8,9	8,9,11
<i>Stichopathes?</i> sp.	8,9,11	8,11	

References: ¹Fenner (2005), ²Forsman et al. (2010), ³Rooney et al. (2010), ⁴Wagner et al. (2010), ⁵Opresko et al. (2012), ⁶Luck et al. (2013), ⁷Pochon et al. (2015), ⁸Wagner (2015a), ⁹Wagner (2015b), ¹⁰Pyle et al. (2016a, b), ¹¹Bo et al. (2019), ¹²A.D. Montgomery, unpublished data

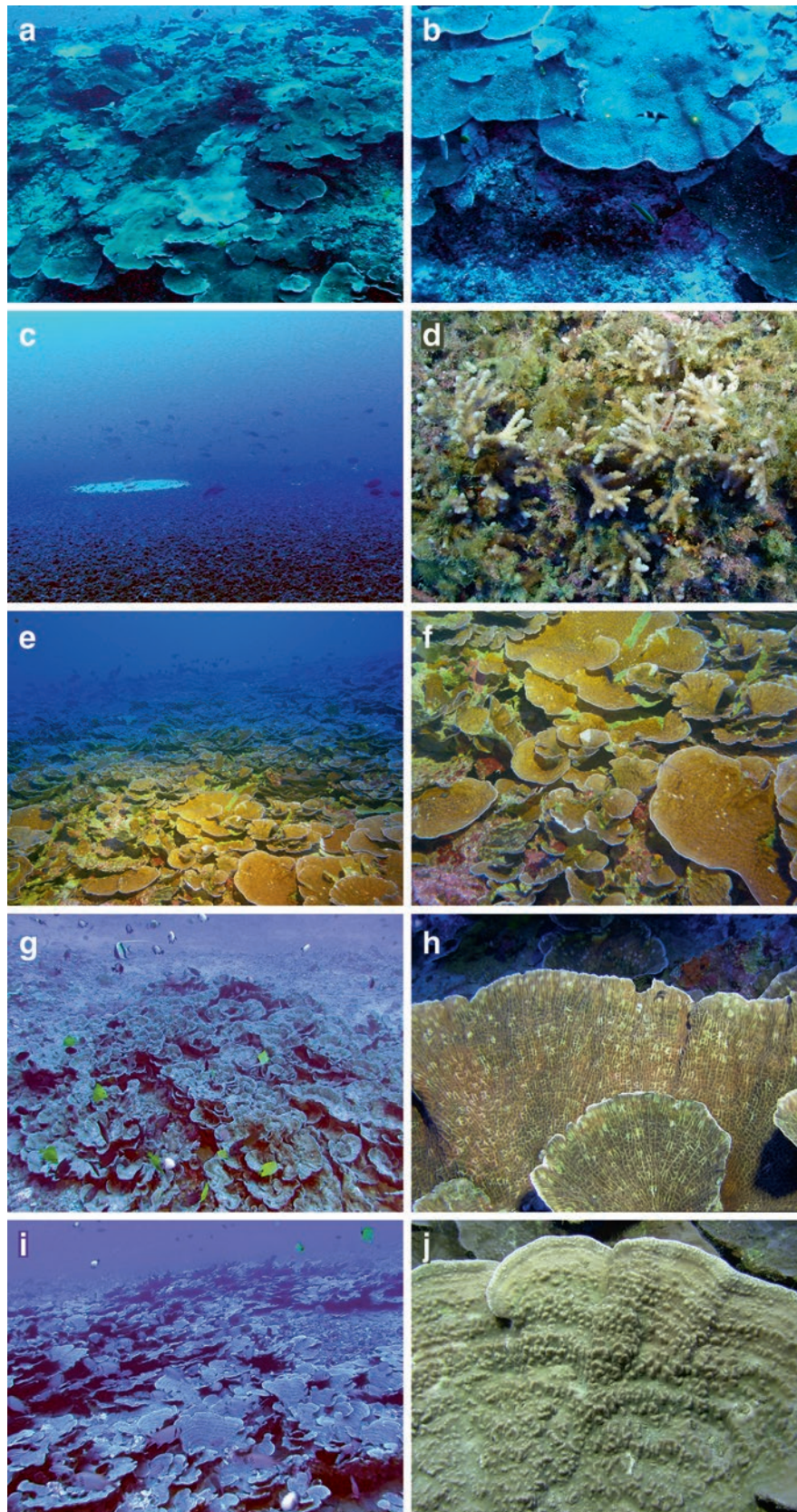


Fig. 25.5 Examples of MCE coral communities. (a) Upper MCE plating/encrusting *Montipora* assemblage at 50 m. (b) Close-up of a plating *M. capitata*. (c) Upper MCE branching *Montipora* assemblage at 57 m (note the low rugosity habitat). (d) Close-up of a branching *M. capitata*. (e) Lower MCE of monospecific aggregation of *Leptoseris* sp. at 75 m. (f) Close-up of *Leptoseris* sp. (g) Lower MCE of monospecific aggregation of *L. yabei* at 70 m. (h) Close-up of *L. yabei*. (i) Transitional MCE of monospecific aggregation of *Porites rus* at 65 m. (j) Close-up of *P. rus*. (Photo credits: (a–d; g–j) A.D. Montgomery and (e, f) HURL)

Table 25.2 A list of gorgonian and other notable octocoral taxa recorded throughout the Hawaiian Archipelago at mesophotic depths

Family	Species	Depth range (m)	Location
Nidaliidae	<i>Siphonogorgia collaris</i> Nutting, 1908	108–145	NWHI
Chrysogorgiidae	<i>Chrysogorgia</i> sp. Duchassaing & Michelotti, 1864	85–1050	HI
Isididae	<i>Lepidisis olapa</i> Muzik, 1978	175–665	MHI
Primnoidae	<i>Callogorgia gilberti</i> (Nutting, 1908)	106–960	HI
Primnoidae	<i>Callogorgia formosa</i> Kükenthal, 1907	146–750	HI
Primnoidae	<i>Candidella helminthophora</i> (Nutting, 1908)	85–1801	MHI
Primnoidae	<i>Thouarella biserialis</i> (Nutting, 1908)	73–426	HI
Acanthogorgiidae	<i>Acanthogorgia</i> sp. Gray, 1857	110	MHI
Acanthogorgiidae	<i>Cyclomuricea flabellata</i> Nutting, 1908	71–335	MHI
Keroeidae	<i>Keroeides mosaica</i> Bayer, 1956	103–388	MHI
Plexauridae	<i>Bebryce brunnea</i> (Nutting, 1908)	71–388	HI
Plexauridae	<i>Muriceides alba</i> (Nutting, 1908)	56	MHI
Plexauridae	<i>Psammogorgia arbuscula</i> (Verrill, 1866)	72	MHI
Coralliidae	<i>Pleurocorallium secundum</i> (Dana, 1846)	116–463	MHI
Melithaeidae	<i>Melithaea (Acabaria) bicolor</i> (Nutting, 1908)	6–429	HI
Clavariidae	<i>Carijoa riisei</i> (Duchassaing & Michelotti, 1860)	1–120	MHI
Indeterminate	<i>n</i> = 29 specimens	77–201	HI

For location, *MHI* Main Hawaiian Islands, *NWHI* Northwestern Hawaiian Islands, and *HI* Hawaiian Archipelago (both MHI and NWHI). Data sources: see Sánchez et al. (2019) and references therein

species are present that are less common or absent in shallow water (< 30 m), such as *Leptoseris mycetoseroides*, *L. papyracea*, *L. tubulifera*, *L. scabra*, and *Porites* cf. *studerii*. Recent molecular work from 65 to 150 m has unveiled six species of *Leptoseris*, including an undescribed *Leptoseris* sp. 1 (Luck et al. 2013; Pochon et al. 2015). *Symbiodinium* diversity in these corals also shows depth zonation indicating niche specialization for host-*Symbiodinium* relationships, limiting potential connectivity between depths (Pochon et al. 2015).

The antipatharian species have fairly broad depth ranges (*Antipathes griggi*, *A. grandis*, and *Myriopathes* cf. *ulex*) with some depth specialists (*Stichopathes echinulata* and *Acanthopathes undulata*) (Wagner 2015). Typically, tropical MCEs are dominated by gorgonian octocorals (Colin et al. 1986; Rowley 2014a, b; Sánchez et al. 2019). However, Hawaiian MCEs are an exception possessing few or no gorgonians. The paucity of octocoral taxa on the shallow reefs of Hawai‘i compared to other regions has been well documented (Nutting 1908; Bayer 1952, 1956; Grigg and Bayer 1976; Cairns and Bayer 2008; Rowley 2014b). Yet, historic expeditions, such as the US Fish Commission Steamer *Albatross* (Nutting 1908; Bayer 1952, 1956), the “Sango expedition” series (Grigg and Bayer 1976), and the submersible *Asherah* (Brock and Chamberlain 1968; Strasburg et al. 1968), and recent submersible research with the HURL submersibles *Pisces IV* and *V* revealed the presence of gorgonian taxa at lower MCEs throughout the Hawaiian Archipelago (Table 25.2). In particular, the Pleistocene terraces off west O‘ahu (at depths of 137 and 183 m) are characterized by gorgonians within the family Coralliidae, as well as stylasterids (*Stylaster* spp.) and antipatharians (Strasburg et al. 1968). Thus in Hawai‘i, the typical

gorgonian-dominated reefs of other tropical locations begin to emerge at greater depths.

25.4.3 Sponges

Marine sponges are often dominant in MCEs, with both benthic cover and diversity increasing with depth (up to tenfold) in MCEs relative to shallow reefs in Palau and Chuuk (Slattery and Lesser 2012), the Bahamas (Liddell et al. 1997; Reed and Pomponi 1997), and the Caribbean (Slattery and Lesser 2012). Despite being important components of the MCE community, sponges throughout the Hawaiian Archipelago are not well-studied. For example, surveys throughout the ‘Au‘au Channel either showed that sponges exist in low densities growing cryptically under rocks (Kahng and Kelley 2007) or did not occur in more than 407 linear km of seafloor habitat (Rooney et al. 2010). However, the latter survey denoted that the cameras used were unable to provide high-resolution images of cryptic organisms. Evaluating marine sponge diversity in Hawai‘i’s MCEs is compounded by taxonomic difficulties. For example, surveys of Kāne‘ohe Bay, one of the best-studied coral reef ecosystems in the world (Hunter and Evans 1995; Bahr et al. 2015), have historically reported on the order of 25 species of sponges (De Laubenfels 1950), but a recent survey combining morphological and molecular approaches suggests that number is grossly underestimated (J. Vicente, unpubl. data). Thus, future efforts to characterize the sponge communities must involve not only quantitative observations but also sample collections for further molecular and taxonomic evaluation.

25.4.4 Fishes

The fish fauna of the Hawaiian Archipelago is perhaps the most thoroughly documented in the tropical Pacific, with relatively comprehensive inventories spanning more than a century (Jordan and Evermann 1905; Mundy 2005; Randall 2007). Pyle et al. (2016a, b) provide the most recent summary of Hawaiian MCE fishes. They are not ubiquitous, but occur in a broad array of MCE habitats, including black coral beds (Boland and Parrish 2005), *Leptoseris* beds within the 'Au'au Channel (Pyle et al. 2016a), macroalgal meadows (Langston and Spalding 2017), and limestone ledges associated with ancient sea-level stands (Brock and Chamberlain 1968). Species diversity varies among and within habitats. For example, observations by both divers and submersibles in the 'Au'au Channel noted that some areas were almost devoid of fishes, whereas others harbored high levels of both diversity and abundance (Pyle et al. 2016a).

Modern documentation of the mesophotic fish fauna of the NWHI began in 1902, when the Steamer *Albatross* conducted a series of dredge hauls and trawls (Gilbert 1903; Snyder 1904). Between 1976 and 1981, exploratory fishery surveys were conducted on the NOAA Ship *Townsend Cromwell*. These surveys recorded 263 species of fish, including many from depths beyond the range of conventional SCUBA (>30 m; Uchida and Uchiyama 1986). Diver-based surveys of NWHI MCEs began in 2004, with surveys of fish assemblages on bank tops (Parrish and Boland 2004).

Most recently, mixed-gas diving using closed-circuit rebreathers has produced quantitative documentation of NWHI fish assemblages on MCEs (Kane et al. 2014; Papastamatiou et al. 2015; Fukunaga et al. 2016, 2017a, b; Kosaki et al. 2016) and a number of new species (Pyle and Kosaki 2016; Pyle et al. 2016b). Visual diver surveys have been supplemented with video bait stations to assess predator abundances along mesophotic depth gradients (Asher et al. 2017a).

The remoteness of the Hawaiian Archipelago coupled with its high volcanic islands and low carbonate atolls provides a variety of environments and opportunities for life to settle and evolve. Endemism, therefore, is high within many taxonomic groups including location, regional, and depth specificity (e.g., Kosaki et al. 2016). Randall (2007) reported 612 total species of reef and shore fishes occurring within the Hawaiian Archipelago to depths of 200 m. A quarter of these species are endemic to Hawai'i (including Johnston Atoll), representing one of the highest rates of reef and shore fish endemism in the world. Pyle et al. (2016a, b) recorded 259 species on MCEs, representing 42% of all Hawaiian reef and shore fish species. The proportion of endemic species on MCEs is much greater than for shallow reefs, particularly in the NWHI (Kane et al. 2014; Kosaki et al. 2016; Fig. 25.6). Only 17% of reef fish species found exclusively shallower than 30 m are Hawaiian endemics, whereas the rate of endemism among reef fishes found exclusively deeper than 30 m is 43%. The rate of endemism increases with depth, with

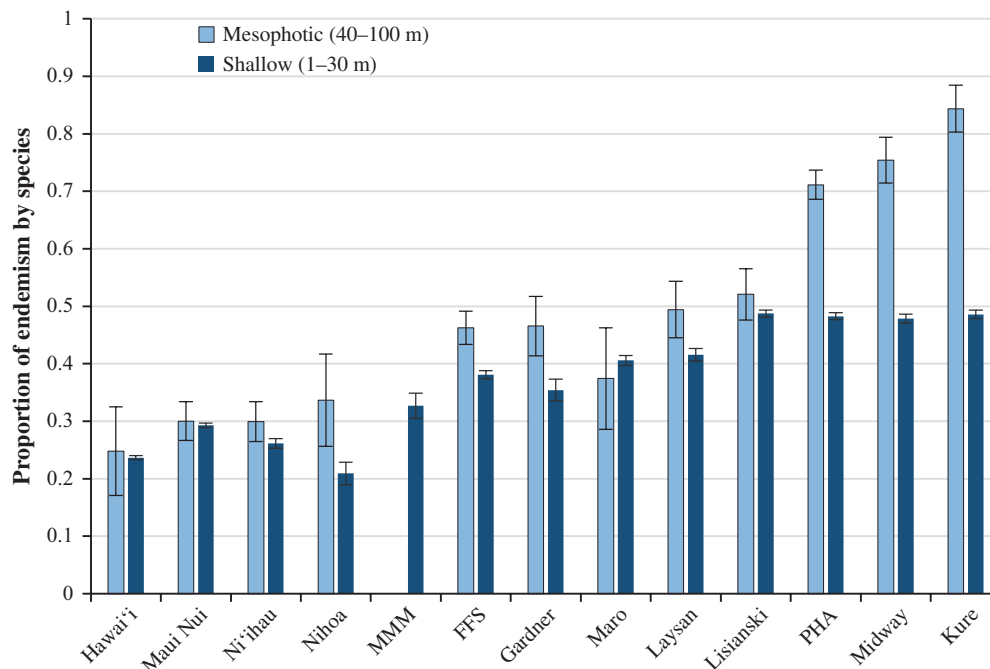


Fig. 25.6 Increase in fish endemism on MCEs across the Hawaiian Archipelago. MMM is Mokumanamana (Necker), FFS is French Frigate Shoals, and PHA is Pearl and Hermes Atoll

44% endemism among fishes restricted to depths greater than 40 m, 41% below 50 m, 50% below 60 m, and 51% for fishes found only deeper than 70 m. This trend is limited to fishes inhabiting MCEs, as the rate of endemism among fishes deeper than 150 m is only 14% (Mundy 2005).

The general pattern of depth stratification for fishes in Hawai'i reveals a broad overlap between shallow and mesophotic reef habitats. Most (87%) of the fish species recorded at depths greater than 30 m also occur at shallower depths; only 12% of fishes recorded from MCEs are restricted to MCEs. The most substantial faunal transitions in fishes occur in the ranges of 10–30 m and 110–140 m, with less substantial transitions at 40–60 m and 70–100 m.

Despite the extensive documentation of fishes in Hawai'i, new species continue to be discovered, including a highly conspicuous butterflyfish (*Prognathodes basabei* Pyle and Kosaki 2016), two less-conspicuous species belonging to the genera *Scorpaenopsis* Heckel 1839 and *Suezichthys* Smith 1958, and the basslet *Tosanoides obama* Pyle, Greene, and Kosaki 2016 (Pyle et al. 2016b).

Near the center of the Hawaiian Archipelago, Mokumanamana Island (23°34' N) lies almost directly on the Tropic of Cancer. The eight remaining reefs of the NWHI lying north of Mokumanamana are thus technically subtropical. The composition of shallow-reef fish assemblages changes along this gradient (Friedlander et al. 2009), with levels of endemism increasing with latitude (Fig. 25.6). Recent research has focused on determining whether this pattern also exists for Hawaiian mesophotic fish assemblages.

When compared with shallow Hawaiian reef fish assemblages, mesophotic fish assemblages are characterized by lower abundances of herbivores and are numerically dominated by omnivorous invertivores and planktivores (Fukunaga et al. 2016; Kane and Tissot 2017). In the NWHI, MCE fish assemblages exhibit greater numerical dominance by Hawaiian endemics (Fig. 25.6; Kane et al. 2014; Fukunaga et al. 2017a, b). Up to 100% endemism has been recorded in fish assemblages at 90–100 m at Kure Atoll (Kane et al. 2014; Kosaki et al. 2016).

Tropical submergence (sensu Lowe-McConnell 1987), whereby subtropical or temperate species are found at greater depths at warmer tropical latitudes, may be one of the primary factors shaping the differences between mesophotic fish assemblages of the MHI and NWHI. Many species of fishes that are found deep in the MHI are found at shallower depths in the NWHI. For example, the butterflyfish *Prognathodes basabei* was originally observed from a submersible at depths up to 187 m in the MHI (Pyle and Chave 1994) but was not described until specimens were regularly encountered and collected at 55–60 m in the NWHI (Pyle and Kosaki 2016). Similarly, the angelfish *Genicanthus personatus* Randall, 1975 is found in the MHI at depths as great as 175 m (Randall 2007) but is routinely observed at 20 m or less in the NWHI. Several other fishes in the MHI, including

the damselfish *Chromis struhsakeri* Randall and Swerdloff, 1973 and the wrasse *Bodianus bathycapros* Gomon 2006, have been observed from submersibles at depths of up to 219 m or collected via hook and line at 302 m (Randall 2007), but had never been recorded in the NWHI until diver surveys were conducted at 90–100 m at the northernmost atolls, Midway and Kure Atolls (Kosaki et al. 2016). The seranids *Caprodon unicolor* Katayama 1975 and *Epinephelus quernus* Seale 1901 are rarely observed at less than 100 m in the MHI but are frequently encountered at shallower depths in the NWHI (Kosaki et al. 2016).

The MCEs of northwestern atolls in the NWHI (Pearl and Hermes, Midway, and Kure Atolls) harbor several species of fishes that are not found in the MHI and which exhibit close affinities to southern Japan. The Japanese pygmy angelfish, *Centropyge interrupta* (Tanaka, 1918), is known only from these northern atolls and southern Japan (Ralston 1981; Mundy 2005). A recently described basslet, *Tosanoides obama*, collected from 90 m at Pearl and Hermes and Kure Atolls, is most similar to two congeners found in southern Japan (Pyle et al. 2016a).

The extent to which fish populations among geographically separated MCEs are connected, and the degree to which subpopulations on MCEs are connected to adjacent shallow coral reefs, is largely unknown. Increasing evidence suggests that upper MCEs are largely an extension of shallow coral reef habitat; many of the organisms that occur on Hawaiian MCEs are abundant on shallow reefs (Pyle et al. 2016a; Kahng et al. 2017). The Hawaiian endemic threespot *Chromis verater* Jordan and Metz 1912 has a single continuous population across shallow reefs and adjacent MCEs in the Hawaiian Archipelago (Tenggardjaja et al. 2014). Toonen et al. (2011) summarized population genetic data from 27 taxa (including fishes and invertebrates) across the archipelago and concluded that the marine fauna shares at least four significant barriers to dispersal (Fig. 25.7). Although specimens were collected on shallow reefs, at least half of the taxa have distributions extending into MCEs. These findings reinforce the conclusion that population processes within MCEs (such as fluctuations in recruitment or population size) are similar or identical to the processes on shallow reefs. Analyses of three deep-dwelling species of snapper (genera *Etelis* Cuvier in Cuvier & Valenciennes 1828 and *Pristipomoides* Bleeker 1852), which occur within MCEs and at greater depths, revealed high connectivity across the archipelago (Gaither et al. 2011; Andrews et al. 2014). All of these species show patterns of genetic diversity that are typical of shallow-reef fishes, indicating that fishes on MCEs are not fundamentally different in terms of population history.

The preliminary conclusion from these studies is that mesophotic fishes show high connectivity with adjacent shallow-reef cohorts, with geographic population structure (in at least some cases) typical of shallow-reef species. Fishes that occur both within MCEs and deeper habitats

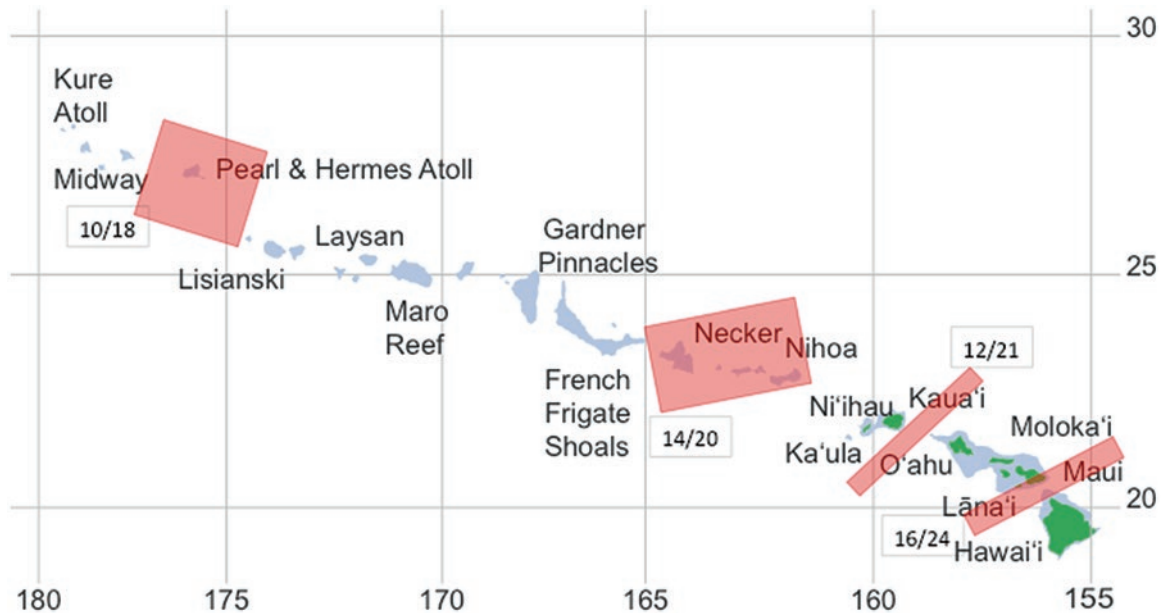


Fig. 25.7 Map of the Hawaiian Archipelago with significant genetic breaks among 27 taxa represented as red bars between islands. For each bar, the number of species exhibiting evidence of restricted gene flow is listed in the numerator, and the number of species with data across that geographic area is listed in the denominator. At least half of these taxa have ranges that extend into MCEs. The broad red bars at Pearl and Hermes Atoll, and at Necker/Nihoa, indicate uncertainty about the precise location of the barrier. (Modified from Toonen et al. 2011)

are highly dispersive. However, the study of connectivity within and among MCEs is in its infancy. Due to the difficulties of acquiring sufficient sample sizes at mesophotic depths, it may be years before robust patterns start to emerge.

25.4.5 Other Biotic Components

Over 8000 currently described invertebrate species inhabit the reefs of Hawai'i, but knowledge of species diversity decreases with both body size and depth (Fautin et al. 2010). Endemism among the shallow-water Hawaiian biota is the highest of any tropical marine ecosystem on earth (Fautin et al. 2010), but systematic surveys of MCE invertebrates (other than corals) are lacking. The most detailed comparison of invertebrate fauna between shallow-water reefs and MCEs in the archipelago used Autonomous Reef Monitoring Structures (ARMS; Zimmerman and Martin 2004; Leray and Knowlton 2015) to sample brachyuran crab communities across a depth gradient (12, 30, 60, and 90 m) off O'ahu. Based on 69 morphospecies (16 families) of brachyurans sampled via ARMS, species were highly stratified with 4–27 unique species per depth, and only ~4% of species occurring across the entire depth range (Hurley et al. 2016). Brachyuran communities at 30 and 60 m were least dissimilar from one another, and mesophotic depths were found to host significantly different communities at much lower total abundance than shallow-reef communities (Hurley et al. 2016). This

stratification provides a marked contrast to the high connectivity in reef fishes.

25.5 Ecology

25.5.1 Macroalgae

Mesophotic macroalgal assemblages across the archipelago are abundant, diverse, and spatially heterogeneous with complex distributional patterns (Kahng and Kelley 2007; Rooney et al. 2010; Spalding 2012). Understanding the specific ecological roles of macroalgal meadows and beds in Hawai'i is of importance to resource managers interested in the population dynamics of keystone species and related organisms inhabiting coral reefs. Although macroalgal communities generally do not comprise major habitats for large-bodied fishes in the MHI (either on MCEs or shallow reefs), endemic reef-associated fishes were found in macroalgal (*Microdictyon* spp.) beds at mesophotic depths in the NWHI (Kane et al. 2014). Cryptic fishes also inhabit mesophotic algal beds (Langston and Spalding 2017), and larger, predatory fish such as jacks (Carangidae) have been observed foraging in these algal beds in the MHI (Spalding 2012). Additional studies are needed on MCEs in adjacent areas with and without dense macroalgal beds or meadows to further refine the potential role of macroalgae as mesophotic habitat for reef fishes in both the MHI and NWHI. Special attention should be given to the morphology and species of the alga involved;

morphological complexity (i.e., prostrate blades [e.g., *Udotea* sp.] versus upright branches [e.g., *Halimeda kanaloana*] versus net-like flattened fronds [e.g., *Microdictyon* spp.]) likely influences the quality of fish habitat. Holdfast morphology, depth of holdfast penetration, and density should also be considered in terms of their influence on sediment geochemistry (Sansone et al. 2017) and the resulting infaunal community (Fukunaga 2008).

Less is known about the role of macroalgal communities in relation to other taxa in Hawai'i, such as competitive interactions with coral or as habitat for other invertebrates. Studies in deep subtidal *Halimeda kanaloana* meadows (to 30 m depth) indicate that a variety of epibenthic and epifaunal invertebrates use these meadows for habitat (Fukunaga 2008). Infaunal polychaete abundances, species richness, and diversity were higher inside the meadows than in adjacent unvegetated areas. The abundance of epibenthic organisms were greater at deeper stations with higher densities of plants (Fukunaga 2008), indicating that dense macroalgal populations associated with MCEs may also host a diverse and abundant community of invertebrates relative to unvegetated habitats. Macroalgae in MCEs also contain a rich community of fungi, with 27% species overlap with Hawaiian terrestrial ecosystems (Wainwright et al. 2017). Based on the four genera of mesophotic algae studied, the host species had significantly different fungal community composition, suggesting a much higher diversity of fungi may be present in MCEs as additional host species are considered (Wainwright et al. 2017). However, the exact nature of the algal/fungal interactions on MCEs remains unknown.

25.5.2 Anthozoans

The distribution of coral assemblages on MCEs within the archipelago is patchy and often consists of monospecific coral aggregations with a few cryptic species. Little is known about the ecology of corals on MCEs in the NWHI given their infrequent occurrence in that region. Species assemblages in the MHI have vertical zonation (Kahng and Kelley 2007; Rooney et al. 2010), as well as horizontally dispersed patchy distributions (Rooney et al. 2010). Rooney et al. (2010) and Pyle et al. (2016a, b) reported three significant types of MCE communities: upper MCEs, branching/plate coral MCEs, and *Leptoseris* MCEs (Table 25.1); Kahng and Kelley (2007) described four distinct vertical communities. Using a 40–150 m range for MCE habitat (Hinderstein et al. 2010), the upper MCE is generally accepted to be 40 to 60–70 m, whereas the lower MCE habitat is >60–70 m with a lower limit for scleractinians between 130 and 150 m (Kahng et al. 2010), although there can be variability in the depth of transition from upper to lower MCEs.

Within the upper mesophotic zone are four distinct MCE coral communities (refining Rooney et al. 2010): (1) plating/encrusting *Montipora capitata*, (2) mixed *Porites* species, (3) branching *M. capitata*, and (4) shallow black corals (Fig. 25.5). The plating/encrusting *M. capitata* assemblage is similar in species composition to shallow reefs but dominated by plating or encrusting forms of *M. capitata* and is common near the top of remnant paleo-shorelines. Mixed *Porites* spp. assemblages are common near paleo-shorelines or hard-bottom mounds and are very similar to shallow reefs dominated by *Porites* spp. Branching *Montipora* assemblages are a mixture of a unique finely branched form of *M. capitata* and macroalgae (e.g., *Distromium* spp., *Microdictyon* spp., and *Caulerpa filicoides*), often found on flat, unconsolidated sediment, where reef systems are generally not expected. There is also a unique shallow black coral community dominated by *Antipathes griggi* between 30 and 60 m.

The lower mesophotic zone also has some distinct coral assemblages and includes monospecific aggregations of *Leptoseris hawaiiensis*, *L. yabei*, *L. papyracea*, or *Porites rus*. These monospecific aggregations may also contain cryptic species, but the community structure is clearly dominated by a single species. The foliose, three-dimensional colony structure of *L. yabei* is inhabited by fish communities. The *P. rus* assemblage is a plate-forming coral community similar to *L. hawaiiensis*, but *P. rus* is also a common shallow coral species. Additionally, there is a deep black coral community dominated by *A. grandis* from 70 to >100 m.

The physiological adaptations and mechanisms that allow resident species to live in these low-light MCE environments in Hawai'i remain largely unknown. Corals in the genus *Leptoseris*, the most dominant group at 60–150 m depth, are photosynthetic, grow up to 1 cm year⁻¹ in situ (Pyle et al. 2016a), exhibit flatter morphologies with increasing depth, and possess skeletal structures that maximize light scatter through the coral tissue (Kahng et al. 2012, 2014). How host-*Symbiodinium* spp. associations influence *Leptoseris* spp. photophysiology is an important area for future investigations. The majority (~70%) of *Leptoseris* spp. colonies fluoresce (Roth et al. 2015). Cyan fluorescent proteins (CFP) are dominant in shallower mesophotic corals (65–85 m), green fluorescent protein (GFP) are dominant in deeper corals (96–125 m), and CFP and GFP are present in corals from middle depths (86–95 m). *Symbiodinium* spp. from corals with and without fluorescence emission have similar genotypes, abundances, chlorophyll excitation spectra, and photosynthetic pigments, efficiencies, and rates (Roth et al. 2015). Approximately 85% of the colonies have endolithic algae; yet, their role remains unclear. Gametes in *Leptoseris* spp. have not been observed, but sampling has been restricted to a few months.

Sexual reproduction has been examined in Hawaiian antipatharians (Wagner et al. 2011, 2012); all colonies have

the characteristics of one sex only (gonochoric), and there is no evidence of internal fertilization.

In the Hawaiian Archipelago, the diversity and abundance of gorgonian corals (Table 25.2) increase as temperature stabilizes with increased depth (Brock and Chamberlain 1968; Muzik 1979). Growing evidence reveals that the greatest temperature variance and often higher nutrient levels occur at mid-mesophotic depths (~90 m) on oceanic islands and atolls (Hawai'i: Brock and Chamberlain 1968; Palau: Wolanski et al. 2004; Colin 2001; Colin et al. 2017; Papua New Guinea: Longenecker et al. 2019; Pohnpei: Rowley et al. 2019). Such variance has been attributed to internal waves exacerbated by decadal shifts (Colin et al. 2017). The extent and source of such variance and the effects on MCE benthic communities in the archipelago are unclear.

25.5.3 Fishes

The depth-related community structure of reef fishes from the archipelago generally conform to patterns observed worldwide. Overall, fish abundance and herbivores decrease with depth (Fukunaga et al. 2016; Asher et al. 2017a, b; Kane and Tissot 2017), despite the presence of large macroalgal meadows in MCEs (Pyle et al. 2016a; Langston and Spalding 2017). The most-abundant fishes in Hawaiian MCEs are planktivores and benthic-feeding invertivores (Fig. 25.8; Brock and Chamberlain 1968; Parrish and Boland 2004; Pyle et al. 2016a; Asher et al. 2017a, b; Fukunaga et al. 2017a, b; Kane and Tissot 2017).

Stable isotope analyses of the two dominant trophic groups indicate higher trophic position for benthic-feeding



Fig. 25.8 Representative coral reef fish at 76 m depth in a *Leptoseris* sp. reef in the 'Au'au Channel, West Maui. (Photo credit: HURL)

Table 25.3 Traits of mesophotic fish populations relative to shallow populations in the MHI

Species	K	L_{∞}	Mean L	Density	φL_{50}	Annual biomass production	Egg production per m ²	Migration rate
<i>Parupeneus multifasciatus</i> (Quoy and Gaimard 1825) ¹	↑	↓	↓	↓	↓	↓	↓	–
<i>Centropyge potteri</i> (Jordan and Metz 1912) ¹	↑	↓	↑	↓	↑	↓	↓	–
<i>Chromis verater</i> Jordan and Metz 1912	↑ ²	↓ ²	–	–	–	–	–	↓ ³
<i>Ctenochaetus strigosus</i> (Bennett 1828) ¹	↓	↓	↓	↓	↓	↓	↓	–

K growth coefficient, L length, L_{∞} mean asymptotic length, φL_{50} the length class in which 50% of females are expected to be mature
References: ¹Pyle et al. (2016a, b), ²Winston et al. (2017), ³Tenggardjaja et al. (2014)

invertivores in MCEs relative to their shallow-water counterparts, whereas planktivores use similar nutrient resources and occupy similar trophic positions regardless of depth (Bradley et al. 2016). These results suggest that plankton are the base of the MCE food web (rather than primary production by algae and phytoplankton as in shallow waters) and that upwelling provides a source of nitrogen (Bradley et al. 2016). In the NWHI, acoustic tagging and stable isotope studies found that large apex predators such as Galapagos sharks (*Carcharhinus galapagensis*) and giant trevally (*Caranx ignobilis*) move regularly between shallow reefs and MCEs, but isotopic profiles indicate that a majority of their foraging is on shallow reefs (Papastamatiou et al. 2015). Thus, these predators may be significant transporters of nutrients and energy from shallow reefs to MCEs.

Several fishes occurring in both shallow reefs and MCEs in the Hawaiian Islands have been the subjects of detailed life history and size-structure analyses. Although individual life history traits vary by species (Table 25.3), biomass and egg production were lower on MCEs typically by an order of magnitude (Pyle et al. 2016a). The single genetic analysis of *Chromis verater* available indicated high levels of connectivity between shallow reefs and MCEs, but the mean number of migrants per generation was estimated to be higher from shallow to deep reefs than in the reverse direction (Tenggardjaja et al. 2014).

The introduced, invasive blue-lined snapper (*Lutjanus kasmira*) is abundant on shallow reefs throughout the archipelago (Gaither et al. 2010). It has not been detected between 50 and 100 m in the northern half of the Hawaiian Islands up to French Frigate Shoals (Fukunaga et al. 2017a, b). Thus, the northernmost MCEs of the archipelago may represent an ecosystem where native species can thrive in the absence of invasive species.

25.5.4 Other Biotic Components

High densities of the spiny lobster *Panulirus marginata* Quoy and Gaimard, 1825, were found at over 140 m depth, as well as large beds (extending up to 1500 m in diameter) of the Pinnidae bivalves *Pinna muricata* (Fig. 25.9; Linnaeus 1758), perhaps due to elevated nutrients (Brock and Chamberlain 1968). Even though such *P. muricata* beds were believed to have been decimated during hurricanes Iwa (1982) and Iniki (1992) at shallow depths, recent observations reveal extensive beds below 60 m depth off south Kaua‘i (Fig. 25.9) and near Penguin Banks offshore Moloka‘i at similar depths. Furthermore, beds of what appears to be the invasive hydrozoan *Pennaria* populate hard substratum up to 107 m. Increased exploration and research would further substantiate such observations and biological interactions at depths below 100 m throughout the Hawaiian Archipelago.



Fig. 25.9 *Pinna muricata* Linnaeus, 1758 beds at 60–65 m on the south coast of Kaua‘i. (Photo credit: S.J. Rowley)

25.6 Threats and Conservation Issues

A thorough understanding of the human-mediated impacts on MCEs is urgently needed, and biodiversity studies are a necessary prerequisite. Cryptic species continue to emerge in Hawai'i, even in well-studied groups, and this trend has accelerated with genetic surveys (Bowen 2016; Spalding et al. 2016). The protection status of MCEs in the archipelago is geographically limited except for MCEs within the PMNM. Within the MHI, the only MCE habitat fully protected is the Molokini Marine Life Conservation District (MLCD) (Fig. 25.1d) and the Old Kona Airport MLCD (Fig. 25.1b).

The State of Hawai'i's coral reef management priorities (2010–2020) for the MHI (State of Hawai'i 2010) identifies threats to coral reefs including fishing pressure, recreational overuse, land-based sources of pollution, invasive species, climate change, and lack of awareness. Another more acute threat is from ocean development projects such as alternative energy infrastructure and associated cables. The gap between scientific understanding and conservation planning has spurred investigations for impact avoidance including predictive modeling of MCE distributions (Costa et al. 2015; Bauer et al. 2016; Veazey et al. 2016).

While all of these threats apply to MCEs, they may affect MCEs differently than shallow coral reefs. Fishing pressure has not been considered a major threat to MCEs in Hawai'i; however, some MCE species such as black coral, aquarium fishes, and bottomfishes are targeted at mesophotic depths. Ancillary effects of fishing activities (anchoring, derelict gear, or line entanglement) may pose a risk to MCEs, but this has not been documented. Recreational activities have begun to move deeper with advances in diving technology (Parrish and Pyle 2002), but the scale of these activities is significantly smaller compared to shallow coral reefs.

Land-based sources of pollution, such as sedimentation, may represent one of the most significant threats to the MCEs in the MHI. Given that MCEs are characterized by low-light levels, any decrease in water clarity may have severe impacts to these communities (Pyle et al. 2016a). Although there are no documented or observed impacts from land-based sources of pollution in Hawai'i, this may largely be a result of the distance from shore for most of Hawai'i's MCEs, which are generally far from shore.

Invasive species impacts on coral reefs are well documented in Hawai'i with the majority of these impacts focusing on introduced, invasive macroalgae in shallow water. Two introduced species have been documented on MCEs, the macroalga *Avrainvillea amadelpha* (Fig. 25.4c; Peyton 2009; Spalding 2012), and the octocoral, *Carijoa* sp. (Grigg 2004). However, the significance or long-term impact of these two species remains uncertain.

Climate change-related effects such as increased temperature are poorly understood on Hawaiian MCEs. While MCEs are often thought to be insulated from increased temperature anomalies in shallow water due to their lower temperatures, deep (>90 m) MCEs may potentially be more susceptible to increased temperatures due to their lack of exposure to high temperature fluctuations (Pyle et al. 2016a). The resiliency of MCEs is a significant research gap in understanding the role MCEs play in Hawai'i's broader coral reef ecosystem. Alternatively, MCEs have widely been suggested to serve as refugia for shallow reefs. Pyle et al. (2016a, b) provided an in-depth review of the potential for MCEs as refugia in Hawai'i but concluded that the role of any potential refugia should be assessed on a case-by-case basis and cautioned that MCEs could be more at risk than shallower reefs.

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