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REPORT

Mesophotic coral ecosystems in the Hawaiian Archipelago

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Abstract Efforts to map coral reef ecosystems in the Hawaiian Archipelago using optical imagery have revealed the presence of numerous scleractinian, zoothanthellate coral reefs at depths of 30–130+ m, most of which were previously undiscovered. Such coral reefs and their associated communities have been recently defined as mesophotic coral ecosystems (MCEs). Several types of MCEs are found in Hawai‘i, each of which dominates a different depth range and is characterized by a unique pattern of coral community structure and colony morphology. Although MCEs are documented near both ends of the archipelago and on many of the islands in between, the maximum depth and prevalence of MCEs in Hawai‘i were found to decline with increasing latitude. The Main Hawaiian Islands (MHI) had significantly deeper and greater percentages of scleractinian coral, and peaks in cover of both scleractinian corals and macroalgae occurred within depth bins 20 m deeper than in the Northwestern Hawaiian Islands (NWHI). Across the archipelago, as depth increased the combined percentage of living cover of mega benthic taxa declined sharply with increasing depth below 70 m, despite the widespread availability of hard substrate.

Keywords Mesophotic coral ecosystem · Hawai‘i · Main Hawaiian Islands · Northwestern Hawaiian Islands · Coral morphology · Coral distribution

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Introduction

Scleractinian coral reefs have been the subject of formal scientific inquiry since at least 1842, when Darwin published his “Structure and Distribution of Coral Reefs”. However, the vast majority of research, monitoring, and resource management has been focused on reefs and corals within the depth range of traditional SCUBA diving. Little attention has been focused on scleractinian coral reefs and other associated benthic organisms below depths of ca. 30 m (Bak et al. 2005; Kahng and Maragos 2006; Kahng and Kelley 2007; Menza et al. 2007). The term “mesophotic coral ecosystem” (MCE) has been designated to describe light-dependant communities of corals and other organisms found at these depths (Hinderstein 2010).

The scarcity of studies of MCEs relative to those focused on shallow reefs is particularly acute in areas outside the Caribbean region, including the insular Pacific (Kahng et al. 2010). However, recent efforts to map coral reef ecosystems (PIFSC 2008) have revealed the presence of a number of scleractinian zoothanthellate coral reefs at depths of 30–130+ m. This study characterizes the distribution and community structure of these MCEs and compares and contrasts those found in the Main Hawaiian Islands (MHI) with those found in The Main Hawaiian Islands (MHI). The results are based on an analysis of more than 400 linear kilometers of seafloor video imagery collected at 19 islands, banks, and atolls within the Hawaiian Archipelago, supplemented by data collected during submersible and technical SCUBA dives.

Materials and methods

Data collection

Most of the data discussed here are seafloor videos, plus a limited number of still photographs, collected by several different underwater camera sleds (PIFSC 2008). Additional imagery and a limited number of coral samples were collected in the Au'au Channel between the islands of Maui and Lāna'i using *Pisces* submersibles and a *RCV-150* remotely operated vehicle (ROV) operated by the Hawai'i Undersea Research Laboratory (HURL). Direct observations in the Main Hawaiian Islands (MHI) were also made during HURL submersible dives and technical SCUBA dives. Coral samples were identified using published guides (Veron 2000; Fenner 2005), and identification was confirmed by invertebrate taxonomists at the Bishop Museum.

The camera sleds have all utilized a stainless steel frame approximately 1 × 0.6 × 0.6 m in size and have been deployed from small boats and NOAA ships to depths of approximately 150 m. They have been equipped with a color video camera including a Deep Sea Power and Light (DSP&L) Multi SeaCam 2050 or 2060, or a Remote Ocean Systems model MC055HR. These cameras had resolutions of 460 (H) × 400 (V) pixels for the Multi SeaCam 2050, and 768 (H) × 494 (V) pixels for the other two. The video feed from a sled was sent via an umbilical cable to a video monitor in the topside control unit, which an operator watched to adjust the altitude of the sled to keep it 1–3 m above the seafloor. The towing vessel drifted at speeds of approximately 0.8 m s^{-1} (1.6 knots) or less. Camera sleds were also equipped with two 500 W or 250 W DSP&L Multi-SeaLite underwater lights, a depth sensor, a sonar altimeter, and a set of parallel scaling lasers.

Primary cameras on the *Pisces* submersibles were Sony 3-chip PDX-10 digital video cameras with two 400 W DSP&L HMI lights. Submersible pilots also used an Olympus SP-550UZ camera with 7.1 megapixel resolution to shoot still images through the viewports. The *RCV-150* had a color analog video camera, two parallel lasers for scale, and six 250 W lamps.

Data processing

Video data from camera sleds and ROV dives were classified at 5 points spaced equidistantly in a horizontal line across the monitor screen, at 30 s intervals, with a mean distance between intervals of 10.3 m ±3.7 (mean ± SD). Substrate type, living cover (scleractinian coral, crustose coralline algae, macroalgae, non-scleractinian corals), and other benthic characteristics were recorded in the classification process. The non-scleractinian corals category includes black and soft corals, sea fans, sea whips, etc. A small percentage of living cover (2.8%) was labeled as unclassified when it was not possible to distinguish between different types of benthic organisms. Substrates types were classified as either hard (solid rock, boulders, rubble) or soft (sand, mud). All classification points fell into one of these categories, except for a small subset (0.96%), labeled as "unclassified," for which the substrate type could not be identified. Unclassified points were excluded from further analyses.

Methodological limitations

Video cameras on the camera sleds typically produce imagery that is not of sufficient resolution to identify corals or other organisms to species level. Frame grabs extracted from the videos yield a still image less than 0.4 megapixels in size. The image quality is further degraded by the video interlacing process, which gives them half the resolution of the source video. To minimize loss of resolution and enable video analysts to see objects at different angles as they move through the camera's field of view, analysis was done using the video itself rather than on frame grabs. The speed of the camera sled, especially when it was very close to the seafloor, was occasionally too fast to allow the camera to fully focus. Turbid water conditions, insufficient lighting, and excessively high camera altitudes also occasionally degraded image quality. Less visually obvious organisms were hard to distinguish and are probably under-represented.

Most often deployed from large research ships with limited maneuverability, the camera sleds have collected optical data with positional uncertainties that range between ca. ±15 to ±100 m. Data collection is often precluded on windward sides of islands, off coastlines with steep nearshore bathymetry, and other areas where it is unsafe for large vessels to operate. Imagery from the sleds is effective for identifying features such as mesophotic reefs at spatial scales from several tens of meters to a few kilometers, but rare organisms are under-represented, or missed altogether. These scales are adequate for identifying broad distribution patterns, for supporting some spatially based resource management actions, and for the identification of sites for more localized and detailed studies requiring other methods.

Results

A total of 334 seafloor videos and 3,733 still photographs collected by underwater camera sled and ROV dives, covering 407 linear km of seafloor, were analyzed and mapped (Table 1). Still and video imagery and direct observations from 18 submersible dives in the Au'au Channel and several dozen technical SCUBA dives at several of the MHI were used to collect samples and to help develop a better understanding of MCEs.

Imagery was collected around 6 of the 8 islands in the MHI, but 76% of the data are from the Au'au Channel. Likewise in the NWHI, a majority of the data came from a single location, French Frigate Shoals, with 56% of the imagery. Percentages of the seafloor composed of different substrates and colonized by different types of benthic organisms were recorded from seafloor imagery collected in the MHI (Fig. 1a) and NWHI (Fig. 1b) and binned by depth interval.

Discussion

Mesophotic corals have been found from near the southern end of the Hawaiian Archipelago off the southwestern corner of the island of Maui to the northern end, off Kure Atoll (Fig. 2). Thus, all Hawaiian Islands and atolls appear to have the potential to host MCEs. The level of survey effort at different islands has not been evenly distributed either geographically or vertically, and most islands need significantly more data collected before their distribution, and other characteristics of MCEs can be definitively described. However, the existing data suggest that several types of MCEs are found in the Hawaiian Archipelago. Each type dominates a different depth range, is characterized by a unique pattern of coral community structure and coral colony morphology (Fig. 3), and is hypothesized to be controlled by a suite of physical factors unique to that type.

Table 1 Optical data collection statistics and coral reef ecosystem areas

	MHI	NWHI	Total
Seafloor transect total length (km)	154	253	407
Number of videos	108	226	334
Number of still photos	0	3,733	3,733
Shallow coral ecosystem area (km^2 < 30 m depths)	1,538	6,241	7,779
Mesophotic ecosystem area (km^2 30–100 m depths)	7,987	4,396	12,383

The size of the shallow coral reef ecosystem, calculated as the area of seafloor between the 0- and 30-m isobaths, shown for the different parts of the archipelago discussed in this study. Although they often extend deeper, the total size of MCE habitat in Hawai'i is conservatively calculated as the area of seafloor between the 30-m and 100-m isobaths

Upper mesophotic MCEs

Upper Mesophotic MCEs are found at depths from ca. 30–50 m. They are often found off coastlines exposed to winter season long period swell and appear to be sheltered by depth from the damage due to seasonal high wave events that preclude coral reef accretion at shallower depths (Dollar 1982; Dollar and Tribble 1993; Fletcher and Sherman 1995; Grigg 1998; Rooney et al. 2004). Conditions including relatively clear water in summer months and higher than average current velocities during the winter are hypothesized to provide optimal conditions for coral reefs in this zone. Upper Mesophotic MCEs are dominated by a few of the coral species found in shallow reefs including *Pocillopora meandrina*, *P. damicornis, Montipora capitata,* and *Porites lobata*. Other species including *Leptastrea purpurea, Leptoseris hawaiiensis, L. mycetoseroides, Pocillopora eydouxi*, and *Porites compressa* have also been occasionally observed. High densities of a species of *Pocillopora* (probably *P. meandrina*) are found in the Upper Mesophotic as far north as Kure Atoll. In the NWHI, large numbers of rare species of fish, such as the Hawaiian Morwong, *Cheilodactylus vittatus*, and the Masked Angelfish, *Genicanthus personatus*, are seen in abundance on Upper Mesophotic MCEs. Thick mats of the green alga *Microdictyon setchellienum* and a brown alga (*Dictyopteris* sp. or *Sargassum* sp.) are also common there (Parrish and Boland 2004).

Branching/plate coral MCEs

Branching/Plate Coral MCEs are typically found at depths between ca. 50–80 m. Some of these reefs were dominated by thick stands of low-relief branching corals that may stand as high as ca. 30 cm (Fig. 4a). A few samples of these corals have been tentatively identified as a species of *Montipora* or *Anacropora*. Work is on-going, including both skeletal structure and genetic analyses to positively identify this species (S. Coles, pers. comm.). Other reefs in this depth range were dominated by *Montipora capitata* with a plate-like morphology (Fig. 4b). Colonies of *Leptoseris* species including: *L. hawaiiensis, L. incrustans, L. mycetoseroides, L. papyracea,* and *L. tubulifera* were occasionally encountered, particularly near the deeper end

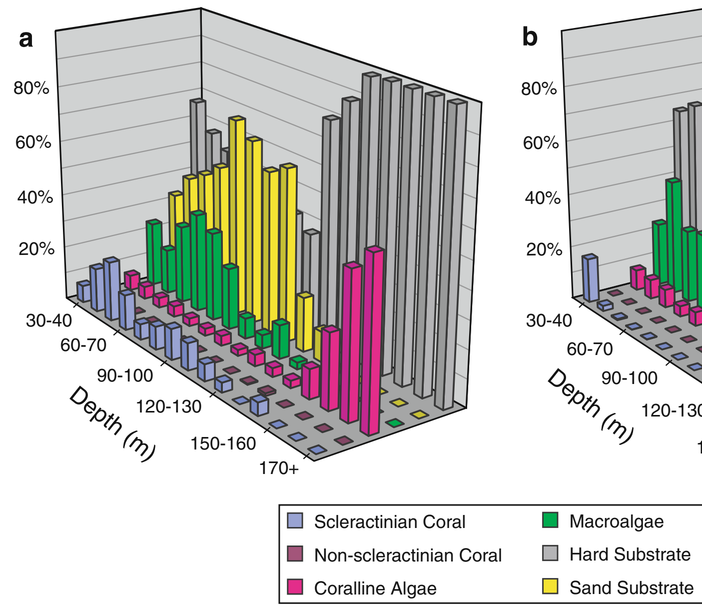
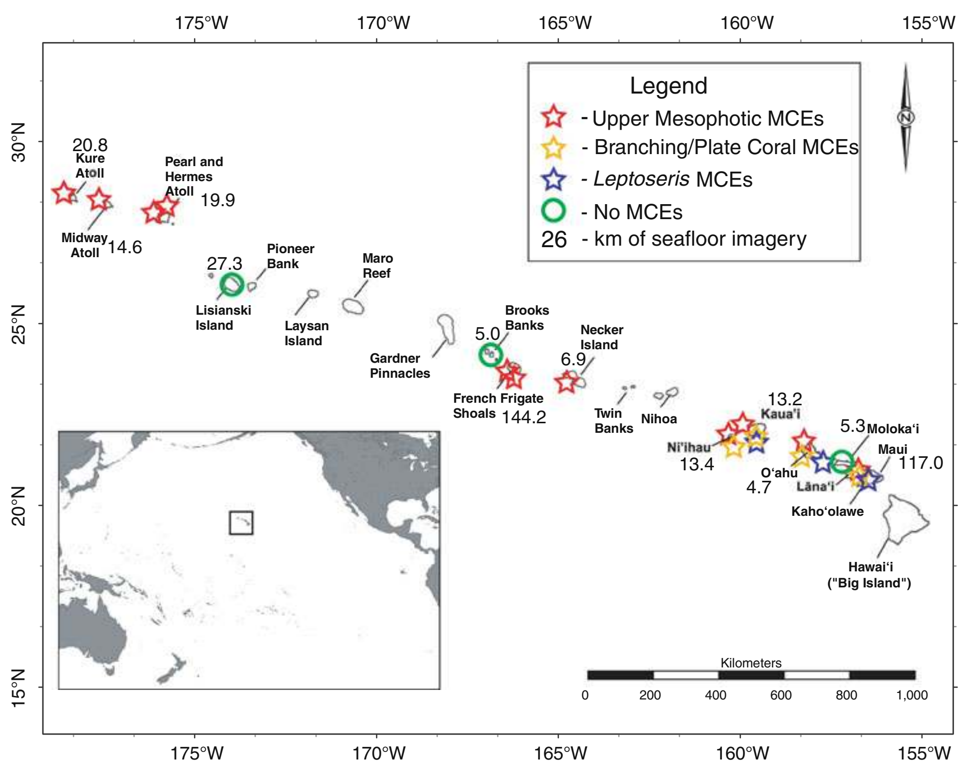


Fig. 1 The percent cover (shown on the *vertical axis*) of substrate type, scleractinian corals, and other megabenthic taxa from mesophotic depths binned into 10-m depth intervals, for: **a** Main Hawaiian Islands, **b** Northwestern Hawaiian Islands

Fig. 2 Known mesophotic coral ecosystems (MCEs) in the Hawaiian Islands. Locations of different types of MCEs are shown with color coded stars. Areas where imagery from multiple camera sled deployments has been collected and no MCEs have been found are shown within the green circles



of this depth range and were often interspersed with branching corals. It has been demonstrated that *Montipora capitata* is able to meet all of its metabolic energy requirements through heterotrotropic feeding (Grottoli et al. 2006), and optimal conditions for these reefs are hypothesized to include direct exposure to strong currents with high concentrations of zooplankton.

Leptoseris coral MCEs

Leptoseris coral MCEs were the dominant reef type found at depths from ca. 80 m to at least 130 m (Fig. 4c). In the Hawaiian Archipelago, *Leptoseris* MCEs are dominated by large thin-walled colonies with plate-like to foliaceous morphologies. Believed to be a compromise between

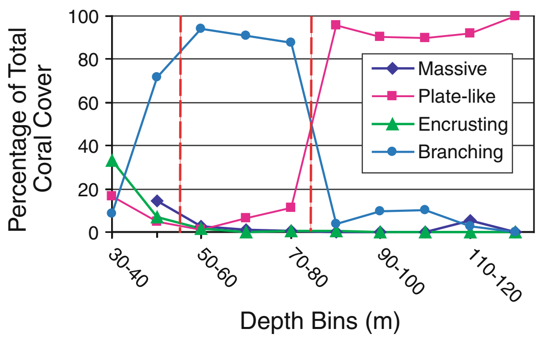


Fig. 3 Mean percentages of coral colony morphologies versus depth. Vertical red-dashed lines indicate divisions between different types of MCEs, based on morphological considerations

optimal light interception and reduced skeletal carbonate deposition (Fricke et al. 1987), they create a myriad of small crevices and holes on the seafloor. Species richness of some fishes has been found to correlate strongly with live coral cover, while the abundance of other fish species is thought to be enhanced by habitat with crevices and escarpments (Colin 1974). Thus, it is hypothesized that *Leptoseris* MCEs, in particular, provide desirable habitat for some fish species. The most common coral species observed was *Leptoseris hawaiiensis*, but colonies of *L. papyracea, L. scabra, L. tubulifera,* and *L. yabei* have also been found. No shallow water coral species were observed on *Leptoseris* coral MCEs and, consistent with other studies (Goreau and Goreau 1973; Reaka et al. 2010), they appear to have the lowest species diversity of the different types of MCEs discussed in this study.

Vertical zonation

Scleractinian coral cover at mesophotic depths in the MHI (Fig. 1a) peaked between depths of 50–60 m with a value of 22% and gradually declined with increasing depth. Macroalgal cover peaked deeper (60–70 m) at a value of 36% before declining to near zero below 130 m. Non-scleractinian coral remained at low levels at all mesophotic depths in both the MHI and NWHI. Data density is quite low below 140 m in the MHI and covers less than 200 m of seafloor. Thus, the high percentages of coralline algae recorded below 140 m (Fig. 1a) must be considered to be more representative of the limited areas where data were collected than of the entire MHI at those depths.

Vertical distribution patterns for benthic communities in the NWHI (Fig. 1b) were markedly different than those from the MHI. Mean scleractinian coral cover peaked at 17% in the 30–40 m depth bin and declined to near zero below 50 m. Peak abundance of macroalgae was found at

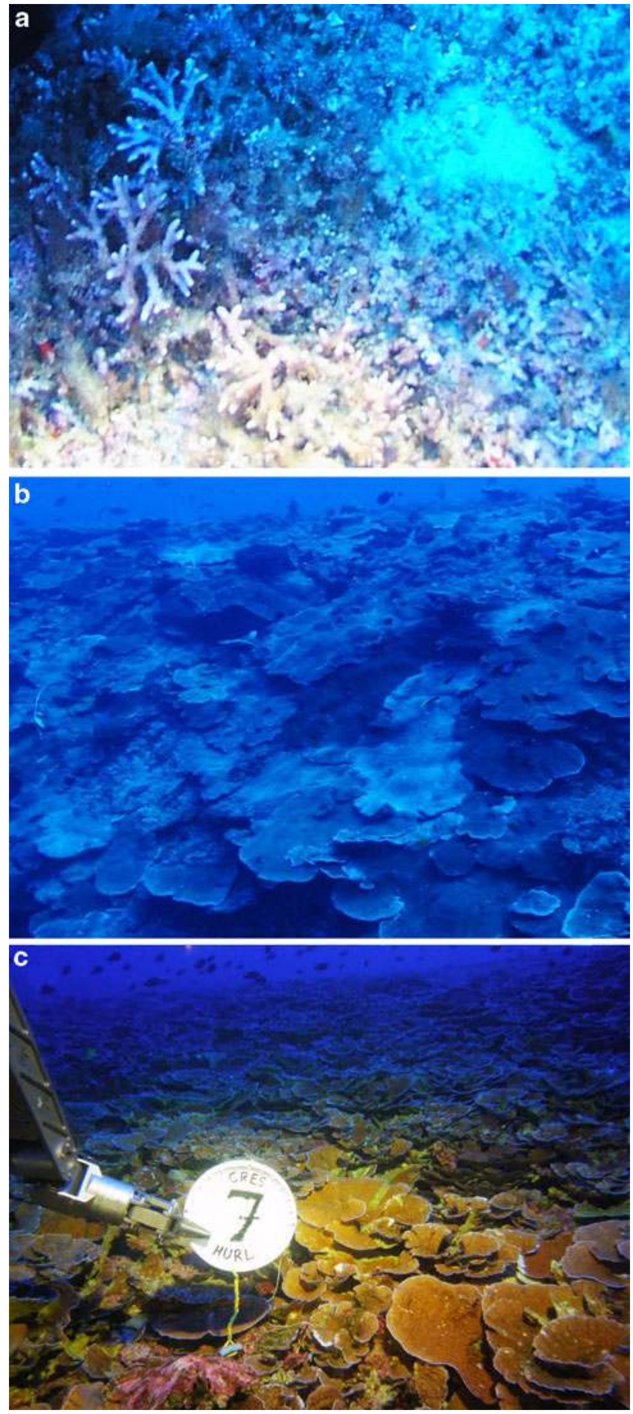


Fig. 4 Types of mesophotic coral ecosystems found in the Hawaiian Archipelago, including: **a** Branching coral MCE found off Kauai, at a depth of 56 m. The coral colonies on the left-hand side of the image are approximately 10 cm in diameter. Photograph credit: Jason Leonard. **b** Plate coral MCE, dominated by colonies of *Montipora capitata*, at a depth of 55 m off Oahu. Photo credit: Tony Montgomery. **c** *Leptoseris* MCE, dominated by colonies of *Leptoseris hawaiiensis*, at a depth of 90 m in the Au'au Channel off Maui. Note the cluster of fish in the background. Photo credit: Hawai'i Undersea Research Laboratory

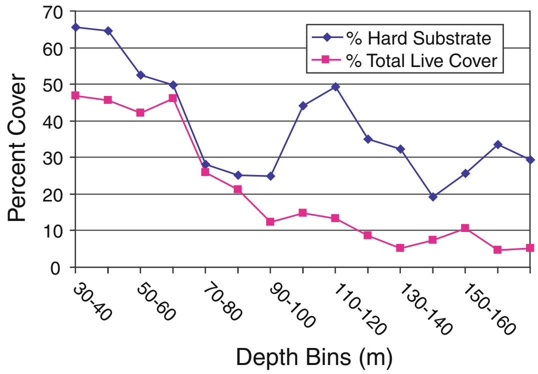


Fig. 5 Total percentages of living cover of megabenthic taxa (scleractinian and non-scleractinian corals, macroalgae, and crustose coralline algae), and hard substrate, plotted against depth, for the Hawaiian Archipelago

43% in the 40–50 m depth range and then declined more rapidly than in the MHI. Coralline algae peaked at 8% in the 30–40 m depths and declined gradually.

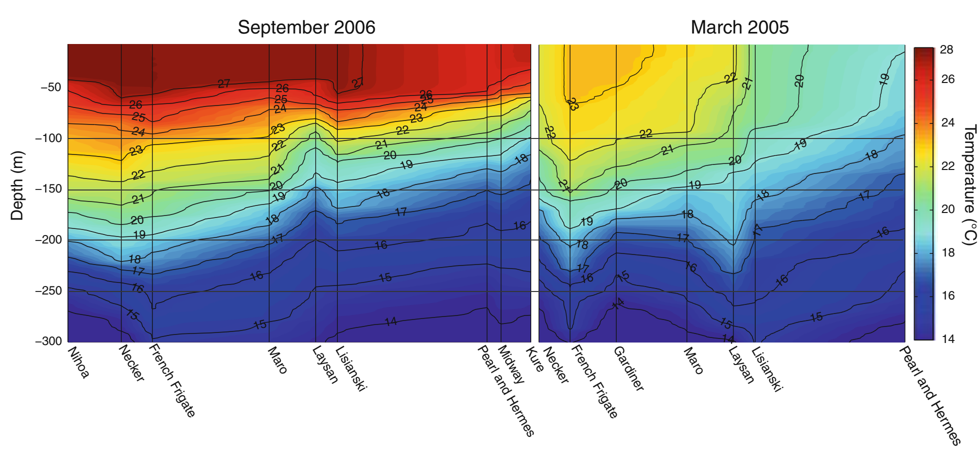
Peaks in cover of both scleractinian corals and macroalgae occurred within depth bins 20 m shallower in the NWHI than in the MHI. Overall, the MHI had markedly deeper and greater percentages of scleractinian coral. Within the archipelago as a whole, the total mean percentage of all types of living cover hovered between 40 and 50% between depths of 30–70 m and then abruptly declined to levels slightly above 10% at depths of 90 m (Fig. 5). The percentage of hard substrate uncolonized by megabenthic taxa hovered between 0 and 20% between depths of 30–100 m. Consistent with other studies (Lang 1974; Avery and Liddell 1997; Kahng and Kelley 2007), the uncolonized percentage then jumped to an average of 25% below 100 m, suggesting that competitive exclusion has less influence on community structure and diversity at deeper depths throughout the archipelago.

Archipelago-wide observations

Growth rates of shallow water corals in fore reef zones across the Hawaiian Archipelago decrease linearly with increasing latitude due to reduced sea surface temperatures and light (Grigg 1981; Siciliano 2005). Likewise, MCEs were found to be generally better developed and found at deeper depths closer to the southern end of the archipelago. Isotherms become shallower moving to the northwest along the Hawaiian Ridge (Fig. 6), particularly during the winter season, and are likely to limit reef growth at deeper depths (Grigg 1981). The annual range in seawater temperature at mesophotic depths becomes larger toward the northern end of the NWHI and is hypothesized to be another factor inhibiting reef growth.

This study documents the presence of MCEs on many islands and near both ends of the Hawaiian Archipelago, suggesting that the potential exists for many, if not most, islands to host them. Although individual MCEs have been found to have high densities and cover of scleractinian corals, mean cover at island or archipelago scales is generally low, reflecting the patchy distribution of MCEs. Moreover, the potential habitat for MCEs in the Hawaiian Islands, conservatively estimated as the area of seafloor between the 30- and 100-m isobaths, is quite large. Encompassing 13,180 km^2, it is 62% larger than the potential habitat of shallow reefs, or the area of seafloor between the shoreline and the 30-m isobath (Table 1). These factors and the challenges of working at mesophotic depths (e.g., Menza et al. 2007) have prevented the discovery of many of the MCEs analyzed here until recently and suggest that additional surveying is likely to discover new MCEs. In addition, information regarding the species composition of MCEs, their ecological roles in wider coral reef ecosystems, how these change along gradients of depth and latitude, and many other questions remain unanswered.

Fig. 6 Typical thermal structure of the upper water column of the Northwestern Hawaiian Islands during near peak winter and summer seasonal conditions



Effective ecosystem-based management requires that all of the significant components of the ecosystem be explicitly considered and included in management efforts. Programs that ignore the mesophotic realm are systematically neglecting a major component, at least in Hawai'i, of the overall coral reef ecosystem. Given the collective magnitude of threats facing coral reefs today (e.g., Jackson et al. 2001; Hughes et al. 2003; Pandolfi et al. 2005; Hoegh-Guldberg et al. 2007; Stone 2007), it is important to improve our understanding of MCEs and to explicitly include them in studies, monitoring programs, and management strategies.

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