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REPORT

Mesophotic communities of the insular shelf at Tutuila, American Samoa

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Abstract An investigation into the insular shelf and submerged banks surrounding Tutuila, American Samoa, was conducted using a towed camera system. Surveys confirmed the presence of zooxanthellate scleractinian coral communities at mesophotic depths (30–110 m). Quantification of video data, separated into 10-m-depth intervals, yielded a vertical, landward-to-seaward and horizontal distribution of benthic assemblages. Hard substrata composed a majority of bottom cover in shallow water, whereas unconsolidated sediments dominated the deep insular shelf and outer reef slopes. Scleractinian coral cover was highest atop mid-shelf patch reefs and on the submerged bank tops in depths of 30–50 m. Macroalgal cover was highest near shore and on reef slopes approaching the bank tops at 50–60 m. Percent cover of scleractinian coral colony morphology revealed a number of trends. Encrusting corals belonging to the genus *Montipora* were most abundant at shallow depths with cover gradually decreasing as depth increased. Massive corals, such as *Porites* spp., displayed a similar trend. Percent cover values of plate-like corals formed a normal distribution, with the highest cover observed in the 60–70 m depth range. Shallow plate-like corals belonged mostly to the genus *Acropora* and appeared to be significantly prevalent on the northeastern and eastern banks. Deeper plate-like corals on the reef slopes were dominated by *Leptoseris*, *Pachyseris*, or *Montipora* genera. Branching coral cover was high in the 80–110 m depth range. Columnar and free-living corals were also occasionally observed from 40–70 m.

Keywords Mesophotic coral ecosystem · Insular shelf · Submerged banks · Coral reefs · Tutuila · American Samoa

Introduction

Deep, zooxanthellate, scleractinian coral reefs have been documented in both the Pacific and Atlantic Oceans and often occur around islands in clear tropical oceanic waters (Lang 1974; Fricke and Meischner 1985; Reed 1985; Kahng and Maragos 2006). Recently being defined as mesophotic coral ecosystems (MCEs), these reefs are found at depths starting at 30–40 m, extending to over 150 m, and occasionally feature well-developed coral communities that cover greater percentages of the seafloor than their shallow-water (<30 m deep) counterparts (Bak et al. 2005; Jarrett et al. 2005; Armstrong et al. 2006; Menza et al. 2007; Menza et al. 2008; Hinderstein et al. 2010).

MCEs are some of the most understudied components of entire coral reef ecosystems. The majority of coral reef research focuses on reefs within traditional scuba limits, shallower than depths of 30 m (Bak et al. 2005; Kahng and Maragos 2006; Kahng and Kelley 2007; Menza et al.

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2007). Until recently, obtaining equipment and methods for conducting research in depths greater than 30 m was expensive and difficult (Menza et al. 2007). Early studies of MCEs relied on methods such as trawls and dredges to obtain bottom samples but had limitations with often imprecise location and depth information (Reed 1985; Kahng and Maragos 2006). With the recent increased availability of equipment such as drop cameras, remotely operated vehicles, autonomous underwater vehicles, submersibles, and advancements in technical scuba diving practices, some focus has shifted to examine these deeper zooxanthellate reefs (Menza et al. 2007).

Formed by hotspot shield volcanoes during the Pliocene to Holocene epochs, Tutuila is the largest island of American Samoa, with a land area of 145 km^2 and approximately 315 km^2 of coral reef habitat area (Brainard et al. 2008; Birkeland et al. 2008). The geologically young (~1.5 million years) island has possibly subsided faster than reefs could grow upward, leaving former barrier reefs as submerged offshore banks along the seaward edges of the insular shelf (Birkeland et al. 2008). Little was previously known about the ecosystems that exist on these banks (Wright et al. 2002).

The first surveys on MCEs in Tutuila were concentrated within Fagatele Bay National Marine Sanctuary (FBNMS). The surveys conducted were brief, focusing on algal reconnaissance in 1996 and an assessment of fish and coral species in 1998 (Green et al. 1999; Wright et al. 2002). In 2001, one 3.5-h closed-circuit rebreather dive was conducted in FBNMS (Pyle 2001; Wright 2002). Other research included three *Pisces V* submersible dives at Fagatele Bay and Taema Bank (Wright 2005). In addition, Towed Optical Assessment Device (TOAD) camera sled surveys were conducted around Tutuila by Pacific Islands Benthic Habitat Mapping Center (PIBHMC) in 2002 and 2004 that revealed the presence of high concentrations of scleractinian corals in several areas (Brainard et al. 2008). The completion of multibeam echosounder surveys in 2006 provided bathymetric and acoustic backscatter data sets that feature nearly 100% coverage of seafloor mapping between depths of 20 m and 3,000 m (Brainard et al. 2008). This high-resolution depiction of the banks, coupled with past video and still imagery confirming high coral cover and ecosystem diversity, spurred greater interest in these features and led to additional camera sled surveys in 2008, targeting the insular shelf and deep-bank coral reef habitats. The objectives of the study presented here were to: (1) quantitatively describe the percent cover of benthic assemblages and scleractinian coral colony morphology in depth ranges considered as MCEs around the island of Tutuila, American Samoa; (2) tentatively identify the most commonly observed scleractinian corals to the highest taxonomic resolution possible from video frame grabs; and (3) determine patterns of benthic assemblage distribution at various depths and locations.

Materials and methods

Camera sled surveys were conducted around Tutuila from 10 February to 4 March 2002, 19–26 February 2004 and 15–25 February 2008 using a Towed Aquatic Resource Assessment System (TARAS), also known as TOAD, which was designed and built by Deep Ocean Engineering. The frame housed a Deep Sea Power and Light (DSP&L) Multi SeaCam 2060 low-light color video camera, a Canon PowerShot G1 still camera slaved to an Ikelite DS-50 strobe (only in 2002), two 500 W DSP&L Multi-SeaLite model 1050 underwater lights, a Tritech PA200/20-PS sonar altimeter, a DSP&L SeaLaser 100 pair of parallel lasers, a fluxgate compass, and a depth sensor. The video feed from the sled was sent via a coaxial conductor within an umbilical cable to a topside control unit.

The TARAS topside control console included a video display used to monitor the real-time position of the sled relative to the seafloor. Data outputs from the compass, clock, depth sensor, and altimeter were incorporated into the video feed using a Deep Ocean Engineering OSD-379 On-Screen Display. Video data were recorded to MiniDV cassettes using a Sony Videowalkman Video Cassette Recorder and were later backed up to another MiniDV cassette or DVD format. Integrated into the console was a Garmin GPSMAP 198C with an external antenna to determine vessel positions and a dual frequency 200/50 kHz transducer that provided water column depth. Hypack (version 6.2b) hydrographic survey software was used to record the vessel's position as well as data from the other instruments on the TARAS. All clocks were synchronized and recorded in Coordinated Universal Time (UTC).

Upon arrival at each predetermined location, the TARAS was deployed and lowered to approximately 1–2 m above the seafloor. The TARAS is able to collect reasonable quality data with speeds over the seafloor up to 1.5 knots, and thus the vessel aimed to drift at that speed for the duration of the survey. The TARAS operator monitored the vehicle via the real-time video feed, recorded observations and maintained the sled's altitude just above the seafloor.

Collected navigation data were post-processed using Hypack's Single Beam editor. Hypack's survey software features a caternary function that incorporates offsets between the GPS antenna and sheave (over which the umbilical of the sled is paid out), the length of umbilical out and towing vessel's track to provide a refined position for the TARAS. The caternary function failed to operate reliably during the 2008 field effort, so camera sled positioning was refined during post-processing. After obtaining the tow vessel offsets, depth of the water column, and vessel's track, a modified version of the Pythagorean Theorem was used within Microsoft Visual Basic in Excel to calculate a more accurate camera sled positioning.

Video and still imagery were classified at five points spaced equidistant across the monitor at 30-s intervals, or a horizontal spacing of ca. 20 m between classification locations. Substrate type (rock, rubble, sand, etc.), living cover (coral, macroalgae, coralline algae, etc.), coral morphology (massive, plate-like, branching, etc.), and other benthic characteristics were recorded in the classification process within a Microsoft Access database. Each classified camera sled position and the associated benthic classifications were imported into ArcGIS to create shapefiles that were later symbolized to feature percent cover of scleractinian coral.

Since MCEs are defined as those ecosystems occurring at depths deeper than 30 m, only data points classified ≥30 m were used in the analyses presented here. Classified data were also divided into 10 m depth intervals (e.g., depths between 30.0 m and 39.9 m were included in the 30 m depth bin) in an attempt to identify the dominant substrate type, living cover, as well as scleractinian coral colony morphology across depth. Percent cover of each category discussed is a mean of the total percent cover values found within each depth interval.

After the mean percent cover of benthic and living cover was calculated within each depth interval, the coral colony morphology was quantified as a mean relative percent of scleractinian coral. This distinction between total percent benthic cover and percent scleractinian coral cover values reported here is made with the use of the words "percent of coral cover" written after values given for coral colony morphology. The different colony morphologies recorded included encrusting, columnar, massive, branching, free-living and plate-like, as well as an unclassified category when coral morphology was not recognizable given image quality or distance from the seafloor.

The cruise and dive reports from the three *Pisces V* submersible dives at Fagatele Bay and Taema Bank (Wright 2005) were reviewed in an attempt to compare coral species and cover observed to the results of data collected during the camera sled surveys. Lastly, a suite of still images and video frame grabs were extracted from the collected optical data and used for taxonomic identification. Those images of the most frequently observed coral genera and colony morphologies were tentatively identified to the highest taxonomic resolution possible (mostly genus) given image quality. Image quality is dependent on, and often degraded by, several factors including insufficient illumination, high camera sled drift speeds (which affect camera focus), turbid water conditions, and very high camera sled altitudes. Also, frame grabs extracted from videos are typically less than 0.4 mega pixels in size, and image quality is degraded further by the video interlacing process.

Results

Eighty-nine TOAD camera sled tows were conducted by PIBHMC in 2002, 2004, and 2008, covering a total distance of 109.7 km of benthic habitat (Fig. 1). Video collection occurred at depths between 11.5 m and 105 m with the majority of surveys between 40 m and 60 m. Over 37 h of video imagery, including 4,958 framegrabs, and 131 still images were analyzed during the classification process to quantify benthic composition. Camera sled surveys revealed high coral cover in multiple locations along the slopes and tops of the banks and patch reefs inside the insular shelf (Fig. 1).

Vertical distribution of MCE components

Hard bottom comprised a majority of the substrate type observed for most depths (41.4–100%), except at 80 m depth where it was observed at 14.6% (Table 1; Fig. 2). Sand was the next most commonly observed substrate, typically covering 32.3–56.0% for most depths; however, mean sand cover was particularly high in the 80 m depth interval with 82.5 ± 30.7% (Mean ± SD) cover. While the data show a mean of 100 ± 0% hard bottom coverage in the 100 m depth interval (Table 1; Fig. 2), it is important to note that a single tow accounted for 95% of the total data classified for that interval, and thus those values represent a small fraction of the overall seafloor around Tutuila. Living cover resources, including macroalgae, reef-building (scleractinian) corals, and other colonizers (sponge, bryozoans, giant clams, coralline algae, non-scleractinian corals, and other non-mobile invertebrates) were also quantified (Table 1; Fig. 2). Mean percent cover of macroalgae was highest in the 50–70 m depth ranges and tapered off in shallower, as well as deeper, waters (Table 1; Fig. 2). Scleractinian coral cover was highest in the 30 m depth interval with a mean coverage of 15.5 ± 26.0% and gradually decreased to 3.3 ± 7.7% cover at 100 m depth. Other colonizers' mean percent cover ranged from 13.4 to 19.6% until the 80–100 m depth intervals where a larger drop down to 5.8–4.4% coverage occurred (Table 1; Fig. 2). Soft coral colonies of the genera *Sacrophyton* and *Lobophyton* constituted a large portion of this "other colonizers" category.

In the 30 m depth interval, where scleractinian coral coverage was highest (Table 1; Fig. 2), encrusting corals (33.8 ± 19.7% of coral cover) belonging to the genus

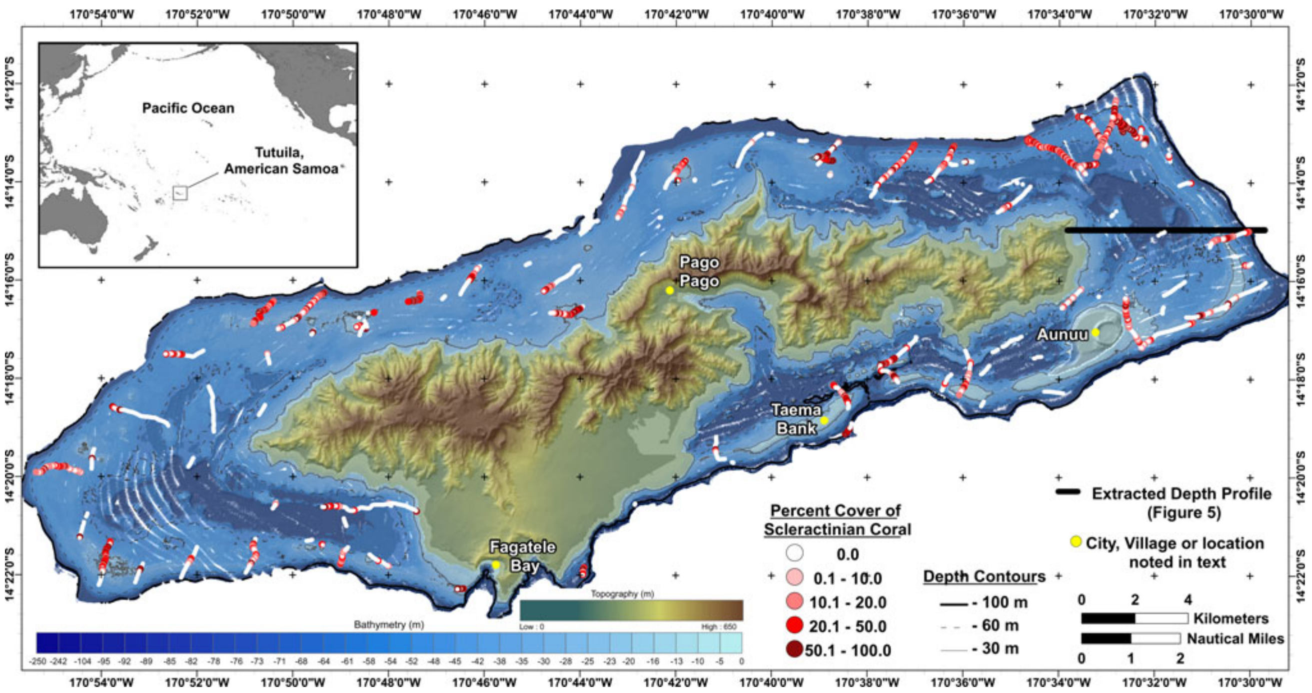

Fig. 1 Map of Tutuila Island, American Samoa, with bathymetry data depicting the insular shelf and camera sled tracks collected in years 2002, 2004, and 2008. The *straight*, *black line* on the eastern side of the island shows the location of the profile exhibited in Fig. 5. Coral cover and depth contours are also shown

Montipora (Table 1; Figs. 3, 4a) dominated. A few colonies of encrusting *Porites* spp. were also observed from the video and still imagery. Massive corals exhibited the second most common morphology and had a mean percent of coral cover of 32.4 ± 21.0, including colonies of *Porites* spp. (Table 1; Fig. 3). Plate-like corals dominated the depth intervals of 40–70 m, ranging from 40.3 to 64.7% of coral cover (Table 1; Fig. 3). Generic composition of these reefs was dependent on depth. Shallow, plate-like reefs (<50 m) were comprised mostly of *Acropora* spp., possibly *A. clathrata, A. speciosa,* and *A. crateriformis* (Fig. 4b). Deeper, plate-like reefs (>50 m) included *Leptoseris*, possibly *L. striata* or *Pachyseris* spp. (Fig. 4c). Branching colony coverage was relatively low between 30 m and 70 m, ranging from 5.9 to 10.7% of coral cover but increased to 27.3 ± 20.0% of coral cover in the 80 m depth interval and continued to increase to 109.9 m (Table 1; Fig. 3). Images of branching coral colonies were tentatively identified as *Acropora austera, A. humilis, A. nasuta,* and/or *A. robusta* (Fig. 4d). The two other scleractinian coral colony morphologies quantified constituted small percentages of coral cover. Columnar colonies were observed in the 40 m depth interval at 0.2 ± 1.3% cover, possibly including *Stylophora pistillata* or *Pavona* spp. (Fig. 4e). Free-living corals observed in the 50 m and 60 m depth ranges with 1.0 ± 2.7 and 1.5 ± 6.2% cover, respectively (Table 1; Fig. 3), were tentatively identified as *Sandalothia dentata* and *Ctenactis echinata* or *C. crassa* (Fig. 4f).

Example of landward-to-seaward distribution

A model of near-shore and vertical community zonation was fashioned by extracting a profile running from the shoreline across the insular shelf on the eastern side of the island from multibeam bathymetric data (Figs. 1, 5). Beginning near the shoreline at approximately 20 m depth (A) and moving down the reef slope, the benthic substrate consisted primarily of hard bottom, including rock, rubble, and boulders with roughly 45–65% cover (Table 1; Figs. 2, 5). Large expanses of sand were observed further down on the reef slope (ca. 30–55% cover). Occasional scatterings of rubble were observed, along with large macroalgal beds whose cover increased to ca. 20% in the 50 m depth range (Table 1; Fig. 2).

Moving offshore (B), midshelf patch reefs occurred from depths of ca. 50–80 m (Fig. 5). Many of the coral species at these depths, for example, plate-like corals belonging to the genus *Acropora*, were the same as in shallow reefs and boasted high percent cover (ca. 50–65%) (Table 1; Fig. 3). Interspersed between the midshelf patch reefs, in depths of ca. 80–95 m (C), expanses of sand were observed on the shelf (coverage up to ca. 80%) with very

Table 1 Mean percent cover of selected substrate types, living cover, and scleractinian coral colony morphology within each 10 m depth interval. The standard deviation is shown in parentheses: Mean (SD)

Depth interval (m)	Frames analyzed (n)	Substrate type and living cover (%)						Scleractinian coral colony morphology (%)						
		Scleractinian coral	Macroalgae	Other colonizers	Uncolonized hard bottom	Sand	Total hard bottom	Encrusting	Plate-like	Branching	Massive	Free-living	Columnar	Unclassified
30–39.9	543	15.5 (26.0)	3.1 (11.6)	14.7 (26.2)	24.1 (34.9)	32.3 (38.2)	67.0 (38.3)	33.8 (19.7)	23.1 (19.4)	10.7 (14.6)	32.4 (21.0)	0	0	0
40–49.9	1,181	8.8 (20.7)	7.5 (18.9)	13.4 (23.2)	11.3 (22.2)	53.4 (41.2)	44.9 (41.0)	21.5 (13.6)	40.3 (24.4)	10.5 (12.4)	26.1 (19.0)	0	0.2 (1.3)	1.4 (5.1)
50–59.9	1678	4.7 (14.6)	20.3 (29.1)	17.0 (25.9)	11.8 (23.0)	45.0 (39.9)	54.4 (39.9)	19.1 (13.6)	53.8 (22.3)	6.9 (8.1)	19.1 (15.5)	1.0 (2.7)	0	0
60–69.9	978	6.6 (16.5)	16.9 (28.2)	19.6 (28.7)	9.9 (21.7)	40.9 (44.1)	54.6 (44.7)	14.6 (11.2)	67.5 (21.4)	4.6 (6.7)	11.1 (16.1)	1.5 (6.2)	0	0.6 (2.1)
70–79.9	359	6.7 (16.2)	15.4 (29.1)	14.1 (26.4)	4.1 (11.6)	56.0 (44.9)	41.4 (44.5)	20.2 (15.1)	64.7 (20.3)	5.9 (7.9)	8.4 (8.8)	0	0	0.8 (2.5)
80–89.9	114	1.9 (7.5)	3.2 (11.5)	5.8 (17.6)	3.5 (12.5)	82.5 (30.7)	14.6 (28.1)	27.3 (22.4)	45.5 (33.8)	27.3 (20.0)	0	0	0	0
90–99.9	87	4.8 (14.6)	3.0 (11.6)	5.3 (18.7)	12.6 (27.0)	47.8 (46.8)	48.7 (46.8)	0	14.3 (20)	23.8 (28.1)	0	0	0	61.9 (72.3)
100–109.9	18	3.3 (7.7)	0	4.4 (14.6)	12.2 (19.6)	0	100.0 (0)	0	0	33.3 (11.5)	0	0	0	66.7 (16.3)

few coral (ca. 2% cover) or algal (ca. 3% cover) species present (Table 1; Figs. 2, 5).

Approaching the submerged bank tops, depth decreased, and at approximately 50 m–75 m (D), a distinct change in the substrate was observed (Fig. 5). Crustose coralline algal-covered rock and rubble, with coverage ca. 50%, with intermittent species of *Halimeda* (macroalgae coverage as high as ca. 20% in 50 m depth interval) and scleractinian coral colonies (5–7% cover) were common (Table 1; Fig. 2). Reefs were observed with many coral colony morphologies (five different morphologies observed), high species diversity (14 species tentatively identified from still images), and the highest scleractinian coral cover (ca. 15%) along the tops and sides of the submerged banks (E) between 30 m and 50 m depth (Table 1; Figs. 1, 2, 3, 5). The tops of the banks often times occurred in depths as shallow as 10 m; however, these analyses were focused on the deeper bank tops and sides that occurred in the mesophotic depth ranges. Colonies of plate-forming species of *Acropora* (Fig. 4b) were particularly common along the top of the northeastern and east banks.

Moving down the offshore slope of the banks to depths of ca. 60 m–80 m (F) (Fig. 5), the shallow-water reef receded and gave way to a deeper, diverse reef with scleractinian corals of plate-like morphology possibly including *Montipora, Pachyseris, or Leptoseris* spp. (Fig. 4c). The frequency of these plate-like coral colonies increased with depth; however, densities appeared to diminish around 80 m (ca. 2% cover), with a few colonies still present at 95 m (ca. 5% cover). Continuing offshore from ca. 80 m–100 m (G) (Fig. 5), the substrate returned to unconsolidated fine grain sediments with several patches of high cover of macroalgae, possibly including *Halimeda* spp.

General horizontal distribution

The insular shelf on the north side of Tutuila consisted of large areas of unconsolidated sandy bottom with a high prevalence of macroalgae. Isolated, mid-shelf patch reefs with hard bottom substrate and abundant scleractinian corals were also observed in this region. The northeastern and eastern banks were dominated by high coverage of scleractinian corals, including species of *Acropora* (Fig 4b), with the highest abundance seen at the northeast corner. South of Aunu'u Island, the substrate shifted to a predominantly unconsolidated, sandy bottom. Continuing westward, toward Taema Bank and adjacent reef areas, the diversity of benthic substrates and faunal species increased. The seafloor throughout this area varied between sand, macroalgae, unconsolidated rubble, consolidated rocky/hard bottom areas, and reef assemblages dominated with scleractinian corals. Diversity in habitat and species along the outer shelf decreased moving west toward Fagatele Bay

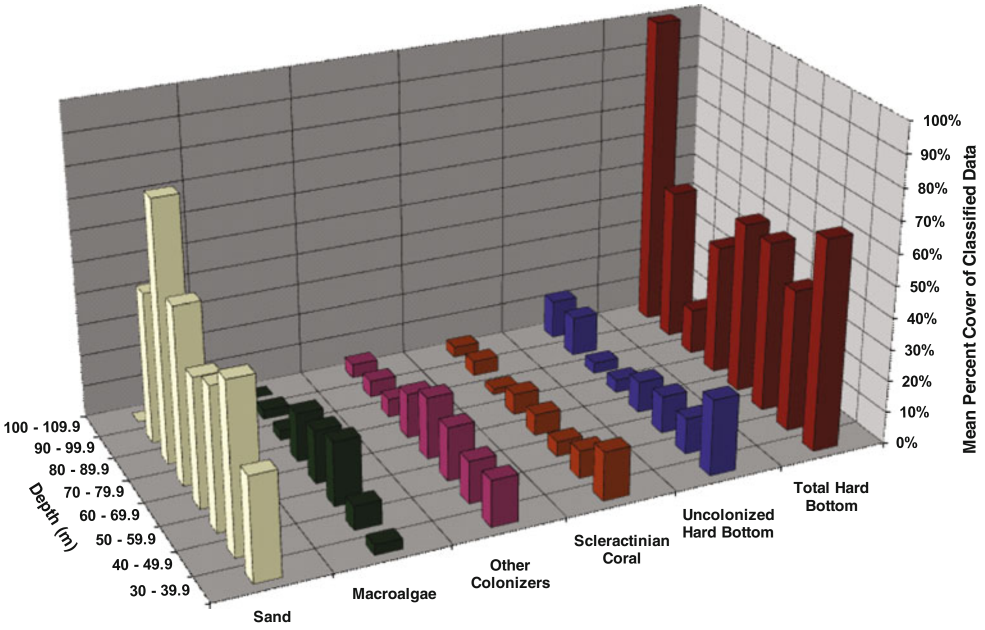

Fig. 2 Percent cover of classified benthic data at 10 m depth intervals showing substrate types and living cover values

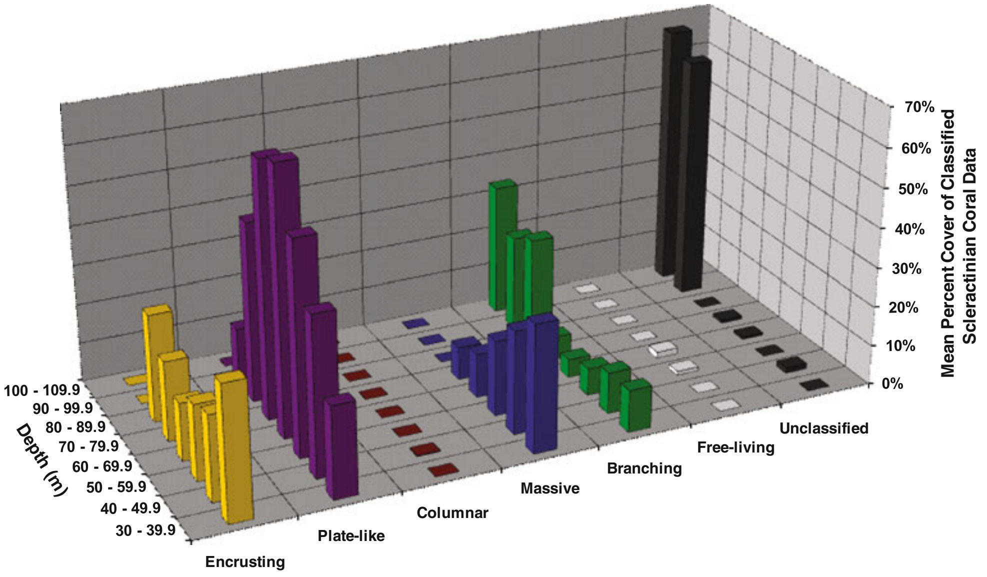

Fig. 3 Percent cover of classified coral data at 10 m depth intervals for each scleractinian coral colony morphology

National Marine Sanctuary (FBNMS). Continuing clockwise, past FBNMS, deeper locations on the shelf off southwestern Tutuila consisted of bottom types dominated by sand and macroalgae, with occasional coral-rich areas. The substrate along the western shelf was predominantly unconsolidated mixed with rubble and macroalgae. Macroalgae of various types (blade-like, filamentous, calcareous, etc.) were common around the entire island. Species of *Halimeda* showed highest cover on the inner and outer slopes of the submerged banks, while filamentous and blade-like morphologies of algae became dominant closer to shore. A common pattern of plate-like corals, most likely belonging to the genus *Acropora,* was also observed with more corals on the inside slope of the submerged banks to the north. To the south, however, plate-like corals appeared to be more abundant on the outside slopes of the submerged banks, particularly at Taema Bank.

The three Pisces V submersible dive reports from 2005 around Taema Bank and Fagatele Bay were reviewed in an attempt to compare species lists with the current study's tentatively identified coral species. However, the species lists from those dive reports only included fishes and invertebrates not including scleractinian corals. While these data were not useful for the current study, future

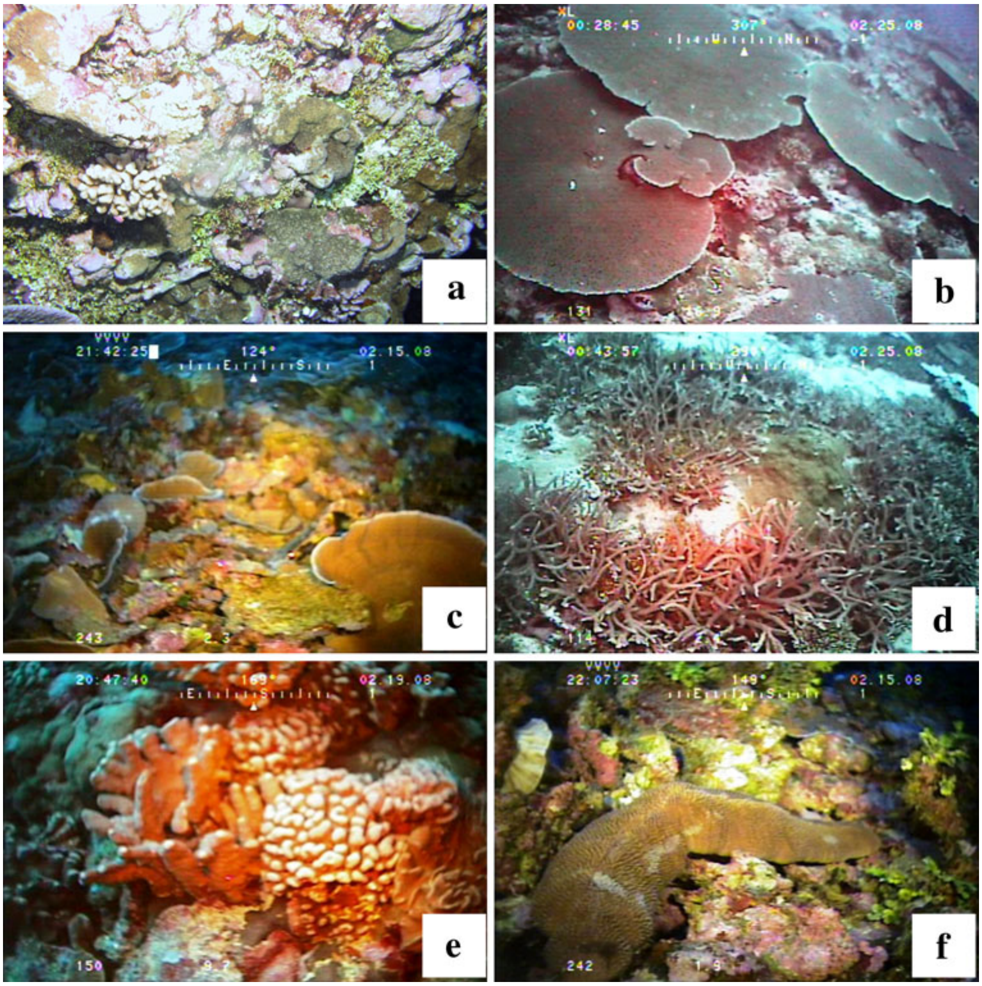

Fig. 4 Selected still images and video frame grabs depicting dominant scleractinian coral colony morphology and tentative taxonomic identification, where possible. **a** Encrusting coral, *Montipora sp.* 46 m. **b** Plate-like *Acropora clathrata* 44 m. **c** Plate-like *Leptoseris sp.* 59 m. **d** Branching *Acropora robusta* 36 m. **e** Columnar *Stylophora pistillata* or *Pavona* spp. 40 m. **f** Free-living *Ctenactis echinata* or *C. crassa* 67 m

analyses of fish populations within MCEs around Tutuila may be better identified and understood by comparing camera sled data with the previous submersible dive data.

Discussion

Total hard bottom percent cover composed a majority of the substrate type observed within several of the MCE depth intervals analyzed (Table 1; Fig. 2), and also most of the reef slope (A) (Fig. 5). Total hard bottom included rubble, rock, boulders, or man-made material, and also included any type of living cover (e.g., macroalgae, coralline algae, coral, and other invertebrates). Uncolonized hard bottom was separated from total hard bottom to show the percent cover of bare hard bottom or pavement observed. As expected, uncolonized hard bottom cover began increasing in the 90 m and 100 m depth ranges where light penetration is reduced and the ability of light-dependent organisms to occupy the substrate also declines (Table 1; Fig. 2). However, these values are based on only two camera sled tows, one of which occupied 95% of the total data for that depth range. Observations from the video suggest that hard bottom percent cover continued to decrease after the 80 m depth interval and gave way to unconsolidated sediment consisting of mud and sand (G) (Fig. 5).

In addition, the 80 m depth interval exhibited a very low percent cover of hard bottom relative to the values observed for the other depth intervals. The low hard bottom value in this depth range was countered by a very high value for sand percent cover. With little hard bottom available for colonization, it is not surprising that this depth range also yielded the lowest percent cover of scleractinian coral. Scleractinian coral cover ranged from 1.9 to 15.5% over the entire 30 m to 110 m depth ranges analyzed

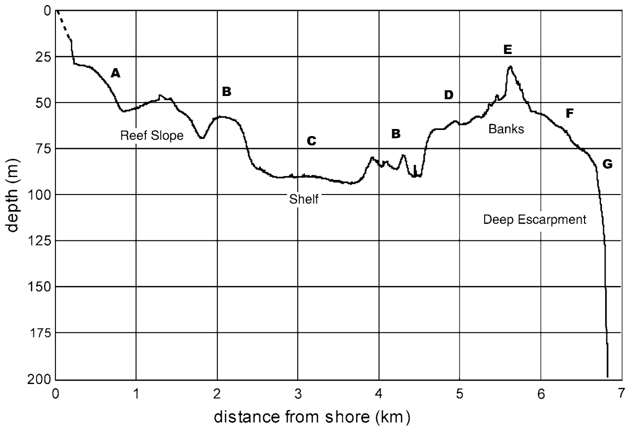

Fig. 5 Depth profile extracted from bathymetric data from the eastern coast of Tutuila. This figure, adapted from Fenner et al. (2008), represents the idealized landward-to-seaward and vertical distribution of benthic communities. Labeled locations include the near-shore slope (*a*), midshelf patch reefs (*b*), sediment basins (*c*), *inner slopes* to submerged banks (*d*), submerged banks (*e*), *outer slopes* of banks marking the edge of the insular shelf (*f*), and the steep drop into deeper water (*g*)

(Table 1). The highest coral cover values were seen in the shallowest depths, especially on the shallow bank tops and slopes and patch reefs (B and E) (Fig. 5). At these shallow depths, high light penetration, water temperature and wave action, along with a high cover of rocky substrate (approximately 55–65%; Table 1) provide ideal conditions to support coral growth. Macroalgae ranged from 0 to 20.3% cover and was highest on the deep reef slope and also approaching the bank tops (A and D) (Fig. 5). These areas of deep reef slope and the sides of the banks were also covered with large patches of rubble, which may have aided the growth of the often-seen sprawling *Halimeda* spp. Other colonizers ranged from 4.4 to 19.6% cover (Table 1). Similar to the steep decline in scleractinian coral cover when the total hard bottom cover decreased drastically in the 80 m depth interval, the other colonizers' percent cover also decreased at these depths (Fig. 2). Probably, the largest component of the other colonizers category was the soft corals that were seen mostly on hard substrate. Large expanses of sand with little living cover were observed in the videos along the inner shelf around 80 m depth (C) (Fig. 5; Table 1).

Encrusting coral colony morphology composed the highest percent of coral cover in the 30 m depth interval and decreased with depth until a sudden increase in cover in the 70 m depth interval (Fig. 3). However, there were no points classified with encrusting coral in the 90 m and 100 m depth intervals (Table 1; Fig. 2). This is probably due to small sample size and inability to correctly identify morphology at these depth intervals. In general, due to lower ambient light, a decrease in video quality tends to occur at deeper depths. This fact most likely also explains the very high values for the unclassified and branching categories of coral colony morphology percent cover in the 90 m and 100 m depth ranges (Table 1; Fig. 3). Massive corals, belonging mostly to the genus *Porites*, followed an expected decrease in relative abundance with depth (Fig. 3). Plate-like corals displayed an almost-normal distribution across depth, with the highest percent cover of coral being in the 60 m depth interval (Fig. 3). It would be expected that plate-like morphology cover would have increased with depth, since light capture is maximized with this morphology; however, the data collected show a steady decline in cover starting at 70 m.

The horizontal distribution of benthic assemblages was not quantitatively described in this study, but it may be worthwhile to complete this task in the future to better determine the locations and abundances of important mesophotic coral ecosystem resources. In general, the northeastern bank tops exhibited the highest coral cover observed, dominated by shallow-water corals of the plate-like morphology such as *Acropora* spp. (Fig. 4b). All bank tops around the island had the highest coral cover relative to other regions of the insular shelf. Moving north around FBNMS, the deep shelves consisted of unconsolidated sediments with less hard bottom than that observed to the north and south of Tutuila. Differences in macroalgal morphology were observed with filamentous and blade-like morphology cover most abundant closer to shore where softer sediments occurred. Calcareous *Halimeda* spp. were observed on the reef slopes approaching bank tops where rubble abundance was higher. Another trend observed was a high cover of plate-like corals on the outside slopes of the submerged banks to the south of Tutuila. However, similar plate-like corals appeared more abundant on the inside slopes to the north. The dominant wind direction at Tutuila is east–southeast (Fenner et al. 2008). An increase in coral growth rate as a result of clear offshore waters along the outer slope may explain this trend.

Understanding mesophotic reefs has particular importance, since it is hypothesized that moderate depth reefs may serve as refugia for their shallower counterparts (Glynn 1996; Reigl and Piller 2003). During times of increased environmental stress, corals at depth could potentially be sheltered from the varying conditions that affect shallow reefs. Bak et al. (2005) suggested that deep reefs do not necessarily follow the same trends as shallow reefs; most factors that cause deterioration of shallow reefs are not yet effective at depth. For example, deep corals may be more protected from bleaching events related to temperature rise of the surrounding seawater. Similarly, deeper reefs are most likely further from shore; thus, land-based effects such as sedimentation, eutrophication, and chemical pollution may be dramatically reduced. Reigl and

Piller (2003) proposed that moderate depth corals may potentially serve as “regeneration batteries” for denuded shallow reefs.

Besides potentially providing a source of coral larvae for shallow reefs, MCEs may be important for reef fish populations. Shallow reef fish species are often seen at mesophotic depths where corals provide small cavities and overhangs that shelter reef fish. This suggests that MCEs enhance habitat suitability, particularly for some smaller fish species and perhaps juveniles. In addition, MCEs are partially insulated by their depth from scuba or free diving-based spearfishing and netting activities. The same textural complexity that provides shelter for reef fish may also hinder hook and line fishing. The extent at which shallow-water and mesophotic reefs are connected is still unknown; however, it appears that mesophotic coral reefs are usually extensions of the adjacent shallow reef and are important factors in the overall coral reef ecosystem (Lesser et al. 2009). The present study was optimized for optically sampling benthic communities rather than demersal fish populations, and therefore, fish assemblages and species observed are not discussed here. However, frequent observations of fish in the vicinity of MCEs around Tutuila suggest that they may offer refugia to targeted fishery species and provide additional incentive for including MCEs in marine protected areas.

Further studies of MCEs around Tutuila are needed to better understand their distribution, community structure, connectivity to shallow-water reefs, and their roles in the larger coral reef ecosystem. An explicit consideration of MCEs, both for Tutuila and for other islands, is recommended to improve the effectiveness of coral reef management plans.

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