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COMMUNITY STRUCTURE OF HERMATYPIC CORALS AT MARO REEF IN THE NORTHWESTERN HAWAIIAN ISLANDS: A UNIQUE OPEN ATOLL

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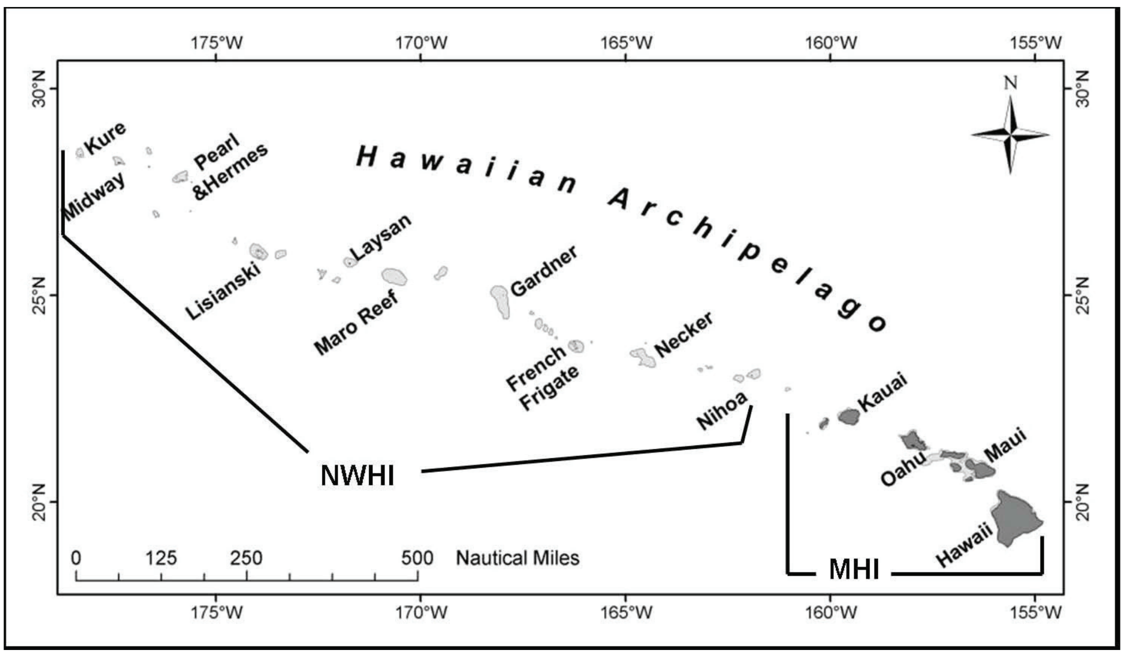

Figure 1. The Hawaiian Archipelago. NWHI = Northwestern Hawaiian Islands; MHI = main Hawaiian Islands. Lightly shaded areas represent 100-fathom isobaths.

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ABSTRACT

Percent cover of shallow-water (< 20m) scleractinian corals at Maro Reef, an open atoll with no perimeter reef in the Northwestern Hawaiian Islands (NWHI), was quantified from analysis of imagery recorded along more than 81 km of benthic habitat by towed divers and at 18 sites surveyed with video transects and photoquadrats. Colony densities and size class distributions were determined from censuses within belt transects at the same sites. All three methods showed statistically significant differences in total coral cover and relative abundance of coral genera among four geographic sectors characterized by different exposure to prevailing wave regimes. Massive and encrusting growth forms of *Porites* dominated coral cover and density throughout all sectors, with *Montipora* the next most dominant genus. Patterns of highest coral cover differed from that of most other classic and open atolls in the NWHI. Populations of *Pocillopora*, though contributing little to percent cover, attained the largest colony sizes of any reef system in the NWHI surveyed with similar methods. Numerous indicators, including coral percent cover, recovery from bleaching, low coral disease prevalence, rarity of crown-of-thorns seastars, and high larval recruitment rates suggest healthy coral communities at Maro Reef, although the predicted accumulation of marine debris from outside sources remains problematic. These data enable the most comprehensive quantitative description of coral communities at Maro Reef produced to date and are a valuable baseline for assessing change.

INTRODUCTION

The unique structure of Maro Reef (25º22'N, 170º35′W) in the Northwestern Hawaiian Islands (NWHI) (Fig. 1) has not been reported from anywhere else in the world (Rooney et al., 2008). Maro is composed of series of patch reefs, submerged pinnacles, and intricate linear and reticulated (forming a network) reef complexes. Described as an open atoll (Maragos and Gulko, 2002; NOAA, 2003; Rooney et al., 2008), Maro lacks the emergent or very shallow perimeter reef around a deeper lagoon that characterizes a

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classic atoll. Instead, the innermost area of the reef complex, with characteristics of a protected lagoon, is separated from the open ocean by the surrounding mesh of reticulate, linear, and patch reefs. Nonetheless, gaps throughout the neighboring reef structure enable wave energy to penetrate into the lagoonal waters and to keep fine sediments suspended in the water column much of the time. Deep water channels with highly irregular bottom relief lie between the shallower reef structures. A few blocks of reef rock exposed at low tide constitute the only emergent land. Elsewhere in the NWHI, Lisianski/Neva Shoal and French Frigate Shoals (Fig. 1) are also described as open atolls, the former with limited perimeter reef and the latter lacking perimeter reef to the west (Maragos and Gulko, 2002). With their perimeter reefs more completely surrounding a central lagoon, the most northern reef systems in the NWHI (Pearl and Hermes, Midway, and Kure; Fig. 1), are described as classic atolls (Maragos and Gulko, 2002; Rooney et al., 2008).

Executive Order 13178 in 2000 created the Northwestern Hawaiian Islands Coral Reef Ecosystem Reserve (CRER), which was superseded by the creation of Papahânaumokuâkea Marine National Monument by Presidential Proclamation 8031 in 2006. Prior to the inception of the CRER, biological resources at Maro Reef received scant research attention aside from commercially exploited lobster populations (e.g., Uchida et al., 1980; DeMartini et al., 1993), lobster trap bycatch (Moffitt et al., 2006), or benthic features associated with lobster habitat (e.g., Parrish and Polovina, 1994; Parrish and Boland, 2004). With a new era of political and management authority comes a resurgence of interest in acquiring scientific information needed to support ecosystem approaches to management of coral reefs in the NWHI (Brainard et al., 2008). With ~188 km^2 of shallow (< 20 m) shelf area (NOAA, 2003; Parrish and Boland, 2004) and 1508 km^2 of shelf shallower than 100 m, potential coral reef habitat at Maro is the second largest in the NWHI (Rooney et al., 2008).

Hermatypic corals are a fundamental component of reef ecosystems as they underlie the structural architecture of the reef and provide shelter or food for many other reef inhabitants (Grigg and Dollar, 1980). Only two previous studies have provided data describing coral communities at Maro Reef. Grigg (1983) surveyed southwestern seaward reefs throughout the Hawaiian Archipelago and analyzed coral diversity and percent cover data with respect to the geographic distribution of key environmental variables. Maragos et al. (2004) compiled coral species inventories for 10 reef systems in the NWHI based on more spatially widespread surveys in a greater range of habitats and examined geographic trends in diversity, endemism, and abundance. In this paper we describe the community structure of the shallow-water (< 20 m) scleractinian corals at Maro Reef, based on reef-wide surveys conducted in 2000 to 2004. We assessed percent cover using towed-diver surveys accompanied by digital video documentation over extensive areas, as well as on finer spatial and taxonomic scales using video transects and photoquadrats at numerous sites. Coral density and size class distributions were assessed concurrently at the same sites where video transects and photoquadrats were conducted. These results are then discussed within the context of salient factors for which data exist from Maro Reef that are known to influence coral community structure, including wave stress, bleaching history, coral disease, marine debris, crown-of-thorns seastar abundance, and coral recruitment rates. They provide the most detailed and comprehensive portrait to date of coral communities at Maro Reef that is both of current value to scientists and managers as well as a solid baseline for future generations of stakeholders.

MATERIALS AND METHODS

Benthic Surveys

Non-overlapping towed-diver surveys were conducted in 2000 (17–20 September), 2001 (21–24 September), and 2002 (1–2 October) according to the methods of Kenyon et al. (2006a). Habitat digital videotapes were sampled at 30-sec intervals (interframe distance ~ 26 m) and quantitatively analyzed for coral percent cover using the methods of Kenyon et al. (2006a). The coral categories that could be distinguished were *Pocillopora*, massive and encrusting *Porites* (e.g., *P. lobata*, *P. evermanni*), *Porites compressa*, *Montipora*, *Acropora*, and other live coral (e.g., *Pavona*, *Fungia*, faviids). Laser-projected dots used to calibrate image size did not appear on videographic imagery recorded during 2002 surveys because of mechanical problems. Average depth was calculated for the photo-documented portion of each towed-diver survey from an SBE 39 temperature/pressure recorder (Sea-Bird Electronics, Inc.) mounted on the habitat towboard, and survey distances were calculated using global positioning system (GPS) and ArcView geographic information system (GIS) 3.3.

Site-specific belt-transect surveys, along with digital video recording of benthic cover along the transect lines, were conducted by three separate teams of divers from 15 September to 2 October 2002 according to the general methods described by Maragos et al. (2004) for 2002 Rapid Ecological Assessments. Four additional sites were surveyed with the same suite of methods on 22–23 September 2004. Locations of site-specific surveys were determined on the basis of (1) filling gaps in the locations of baseline assessments conducted during an expedition to the NWHI in 2000; (2) depths that allowed three dives/day/diver; (3) constraints imposed by other ship-supported operations; and (4) sea conditions. Detailed methods for recording videographic and size class data are presented in Kenyon et al. (2006b).

Twelve (35 cm x 50 cm) photoquadrats were concurrently photographed with spatial reference to the same two 25-m transect lines (i.e., six photoquadrats per transect) at each site according to the methods of Preskitt et al. (2004).

Data Extraction and Analysis

Capture, sampling, and analysis of frames from video transects are described in Kenyon et al. (2006b). The taxa that could be identified were *Acropora valida*, *Pocillopora meandrina, P. ligulata*, *Porites lobata, P. compressa, Montipora capitata, Montipora* sp., *Leptastrea* sp., *Fungia* sp., and *Pavona duerdeni*. Detailed methods for determining coral percent cover from photoquadrat imagery are also presented in Kenyon et al. (2006b).

Transect site locations and tracks of towed-diver surveys georeferenced with nondifferentially corrected GPS units (Garmin® model 12) were mapped using ArcView GIS 3.3. For analytical purposes, towed-diver and site-specific surveys were grouped spatially according to one of four geographic sectors (northeast, southeast, southwest, northwest) so as to examine coral cover and relative abundance based on exposure to or shelter from the direction of primary wave regimes. Northern and southern sections were delineated based on the latitude (25º26.791′N) of the shallow (~10 m) lagoonal area where a NOAA Coral Reef Early Warning System (CREWS) buoy was deployed in 2001. Eastern and western sections were delineated based on the eastern longitude (170º35.694′W) where the networks of reticulate reefs that protect the lagoon appear to coalesce on IKONOS imagery (Fig. 2). Towed-diver surveys that spanned more than one geographic sector were subdivided into separate sections using the time stamp that linked GPS position to recorded imagery.

Differences in total percent coral cover among sectors were examined using one-way ANOVA on non-transformed data; nonparametric Kruskal-Wallis tests were used when the data were not distributed normally, even with transformations. Differences in the relative abundance of coral genera among sectors were examined using the chi-square test of independence among two or more samples, pooling taxa as necessary to provide minimum expected values. Statistical analyses were conducted using SigmaStat® software.

Maragos et al. (2004) provide two indices of the relative occurrence and abundance of 37 coral species at Maro Reef based on qualitative Rapid Ecological Assessment surveys at 39 sites. Methods described in Kenyon et al. (2006b), which involved the generation of a single ranking using the separate occurrence and abundance indices, were used to compare these indices with the relative abundance of coral species as determined by percent cover analysis of photoquadrats in this study.

RESULTS

Towed-diver Surveys

The distance between frames sampled at 30-sec intervals from benthic tow videos depends on the tow speed; the average interframe distance ranged from 20.3 m to 34.0 m (mean = 25.8 m, n = 34 tows). The average benthic area captured in laser-scaled frames was 4517 cm^2 (SE = 129 cm^2, n = 1019 frames). Towed divers surveyed 81.0 km of benthic habitat (Table 1, Fig. 2), from which 3036 frames were analyzed. Given the 3:4 aspect ratio of the captured frames and extrapolating to the total number of consecutive, non-overlapping still frames that compose the benthic imagery, this benthic analysis area (3036 frames x 0.4517m^2/frame = 1371 m^2) samples a total survey area of 62,827 m^2 (Table 1). Survey effort was highest in the southeast sector (Table 1), where the greatest expanse of shallow-water (< 30 m) reef is found (Fig. 2).

Average total coral cover across the reef system was moderately low, ranging from 10.8% in the northwest sector to 16.8% in the northeast sector, with a reef-wide average of 14.0% (Table 1, Fig. 3a). The differences among the four sectors in their average total percent coral cover were statistically significant (Kruskal-Wallis test, $H = 29.67$, df = 3, $p < 0.001$). The differences among the four sectors in the relative abundance of coral taxa present were also statistically significant (chi-square test, $X^2 = 25.8$, df = 12, $p = 0.011$). Massive and encrusting *Porites* (e.g., *P. lobata, P. evermanni*) dominated across the reef system, accounting for more than 59% of the coral cover in all sectors. *Montipora* or *P. compressa* was the next most dominant taxon in all sectors except the southwest, where *Acropora* was the second most dominant taxon. *Pocillopora* contributed little to coral cover across the reef system (Table 1, Fig. 3a).

Table 1. Coral cover determined from towed-diver surveys conducted at Maro Reef, NWHI, 2000–2002.

					Proportion of total coral cover[b]					
Geographic sector	Distance surveyed (km)	Area surveyed[a] (m^2)	Range of average depth (m)	Average % total coral cover	Massive & encrusting *Porites*	*Porites compressa*	*Pocillopora*	*Acropora*	*Montipora*	Other corals
ALL	81.0	62827	6.9–17.8	14.0	65.9	13.8	3.4	5.7	9.1	2.1
NE	5.3	4114		16.8	59.7	25.1	1.7	4.1	9.3	0.1
SE	45.2	35112		14.4	69.4	15.2	3.2	3.2	8.5	0.4
SW	10.9	8405		16.6	63.3	7.3	4.1	13.3	10.6	1.5
NW	19.6	15196		10.8	62.6	12.0	3.5	9.3	8.0	4.6

[a]Area surveyed is based on average area of laser-calibrated frames captured at 30-sec intervals.

[b]Proportions are graphically presented by sector in Fig. 3a.

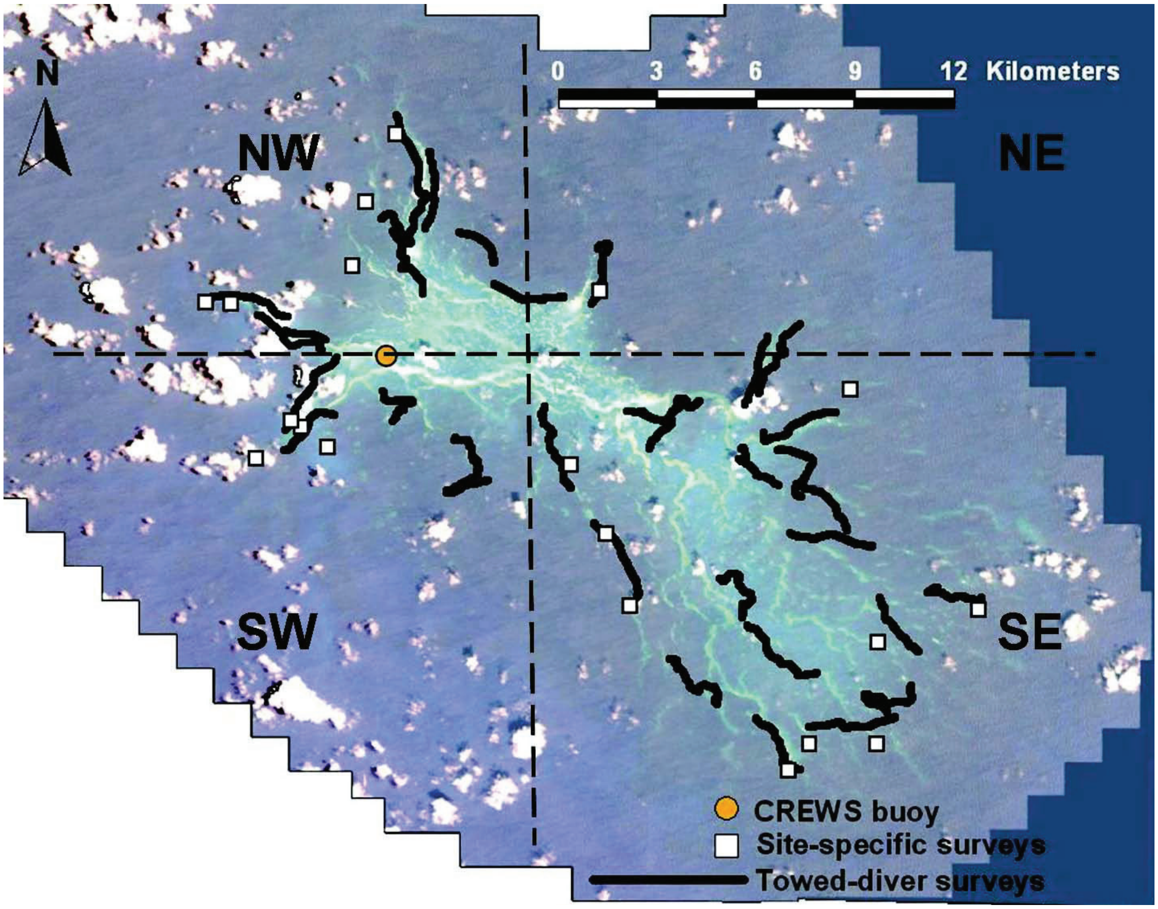

Figure 2. Location of towed-diver and site-specific surveys at Maro Reef, NWHI, using IKONOS satellite imagery as a basemap. Irregular white and gray shapes overlying the lagoon are clouds and their shadows.

Site-specific Surveys: Video Transects

A total of 544 m^2 at 17 sites (32 m^2/site) was quantitatively assessed from transect videotapes. Average coral cover ranged from 21.9% in the southeast sector to 54.8% in the northeast sector, with a reef-wide average of 33.8% (Table 2, Fig. 3b). Survey effort was highest in the southeast sector (Table 2), where the greatest expanse of shallow-water (< 30 m) reef is found (Fig. 2). Survey effort was low in the northeast sector due to the relatively limited expanse of shallow-water reef. The differences among the four sectors in their average total percent coral cover were statistically significant (one-way ANOVA, $F = 6.6$, df = 2, 13, $p = 0.011$).

Ten scleractinian taxa were seen in Maro Reef video transects (*Acropora valida*, *Pocillopora meandrina, P. ligulata*, *Porites lobata, P. compressa, Montipora capitata, Montipora* sp., *Leptastrea* sp., *Fungia* sp., and *Pavona duerdeni*). The differences among the four sectors in the relative abundance of coral genera present were statistically significant (chi-square test, $X^2 = 15.19$, df = 6, $p = 0.019$). Massive and encrusting *Porites* dominated across the reef system, accounting for more than 63% of the coral cover in all sectors. *Montipora* was the next most dominant taxon in all sectors, with its greatest relative abundance in the northwest sector. *Porites compressa* and *Pocillopora* contributed a small amount (≤ 5.4%) and *Acropora* contributed little (< 1%) to coral cover in all sectors.

Table 2. Coral cover determined from video transects and photoquadrats conducted at Maro Reef, NWHI, in 2002 and 2004.

Exposure	# Sites surveyed	Average total percent coral cover[a]	Range of transect depths (m)	Proportion of total coral cover[b]					
				Massive & encrusting *Porites*	*Porites compressa*	*Pocillopora*	*Acropora*	*Montipora*	Other coral
VIDEO TRANSECTS									
ALL	17	33.8	5.5–15.5	74.3	2.9	4.3	0.1	17.1	1.3
NE	1	54.8		75.1	0.0	5.4	0.0	15.8	3.7
SE	8	21.9		80.4	5.4	5.3	0.0	8.9	0.1
SW	3	51.0		80.5	0.8	3.2	0.0	14.9	0.5
NW	5	37.8		63.4	3.1	4.0	0.3	26.8	2.3
PHOTOQUADRATS									
ALL	18	32.4	5.0–15.5	73.1	1.5	3.7	1.0	19.6	1.1
NE	1	53.0		81.8	0.0	4.4	0.0	13.8	0.0
SE	8	22.1		84.1	1.6	5.5	2.5	4.0	2.4
SW	4	43.6		84.8	0.6	0.9	0.0	13.6	0.2
NW	5	35.7		48.2	2.8	4.7	0.7	42.6	1.0

[a]Values are means of replicate transects (2/site) or photoquadrats (12/site).

[b]Proportions are graphically presented by sector in Figs. 3b,c.

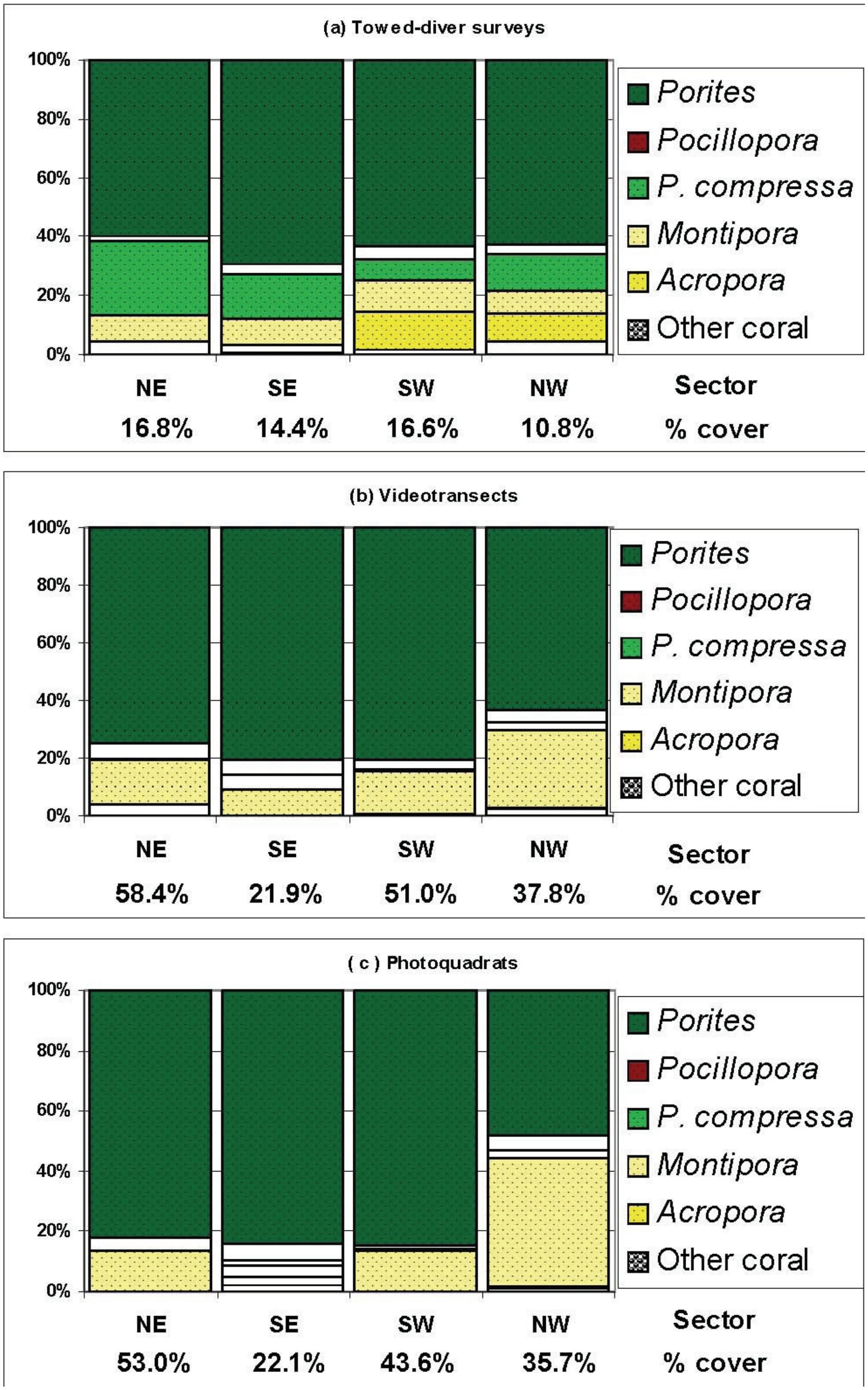

Figure 3. a–c. Relative abundance of primary coral taxa by sector at Maro Reef, NWHI, derived from three different methods. Values below sector labels are total coral percent cover within each sector. *Porites* = massive and encrusting *Porites*.

Site-specific Surveys: Photoquadrats

Video transects and photoquadrats were recorded concurrently at 16 sites with one additional site surveyed for percent cover by video transects alone and two additional sites surveyed for percent cover by photoquadrats alone. Survey effort was highest in the southeast sector (Table 2), where the greatest expanse of shallow-water (< 30 m) reef is found (Fig. 2). Survey effort was low in the northeast sector due to the relatively limited expanse of shallow-water reef. Of the 16 sites where both methods were applied, the maximum difference in total coral cover calculated with the two methods was 10.2%; the average of the absolute values of the difference between video transect and photoquadrat total coral cover was 6.3%. The overall patterns of coral cover were highly similar to those derived from video transects (Table 2, Figs. 3b,c). Average coral cover ranged from 22.1% in the southeast sector to 53.0% in the northeast sector, with a reef-wide average of 32.4%. The greatest difference in total coral cover between the photoquadrat and video transect methods was in the southwest sector (51.0% vs 43.6%, respectively). The differences among the four sectors in their average total percent coral cover were statistically significant (Kruskal-Wallis test, $H = 27.10$, df = 3, $p < 0.001$).

Twelve scleractinian taxa were seen in Maro Reef photoquadrats (*Acropora valida*, *Pocillopora meandrina, P. ligulata, Porites lobata*, *P. evermanni*, *P. compressa*, *Montipora capitata*, *M. patula*, *M. flabellata, Leptastrea purpurea, Cyphastrea ocellina and Pavona duerdeni*) (Table 3). The differences among the four sectors in the relative abundance of coral taxa present were statistically significant (chi-square test, $X^2 = 67.6$, df = 6, $p < 0.001$). The overall patterns of coral composition were also similar to those derived from video transects (Table 2, Figs. 3b,c) with the exception of the northwest sector, where the relative contribution of *Montipora* to coral cover (42.6%) nearly equaled that of massive and encrusting *Porites* (48.2%). Massive and encrusting *Porites* dominated in all sectors, and *Montipora* was the next most dominant taxon with the exception of the southeast sector, where *Pocillopora* slightly exceeded the contribution of *Montipora*. *Porites compressa* and *Pocillopora* contributed a small amount (≤ 5.5%) and *Acropora* contributed little (< 2.5%) to coral cover in all sectors.

Site-specific Belt-transect Surveys: Colony Density and Size Classes

A total of 3191 colonies were counted and classified by their maximum diameter within belt transects covering 775 m^2 at 18 sites. *Porites* was the most numerically abundant (i.e., highest density) taxon across the reef system followed by *Montipora*, *Pocillopora*, *Pavona,* and *Acropora* (Fig. 4). The average colony density for all taxa combined was 4.1 colonies m^{-2}.

Of the three primary coral taxa at Maro Reef (*Porites, Montipora, Pocillopora*), *Porites* and *Montipora* had similar size class distributions (Fig. 5), with more than a third of the colonies in each genus having maximum diameters > 40 cm (36.1% and 33.9%, respectively). Thirteen percent of *Pocillopora* colonies also attained large sizes (> 40 cm maximum diameter), as did 12.9% of faviid colonies. In contrast, no acroporids within belt transects measured > 40 cm maximum diameter, and only 6.6% of *Pavona* colonies attained these large sizes. Fungiid colonies (data not shown) did not exceed 20 cm maximum diameter.

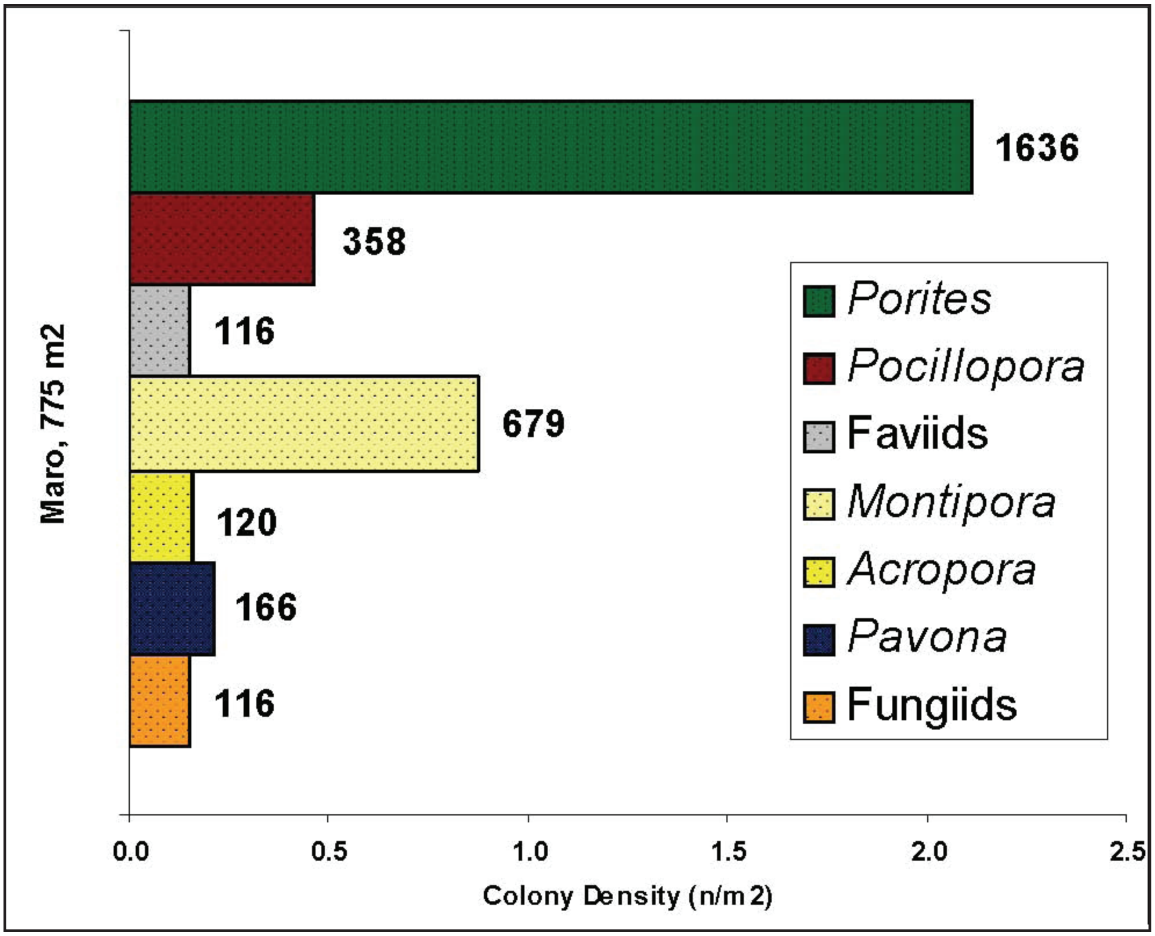

Figure 4. Colony density (no. m^{-2}) of seven coral taxa at Maro Reef, NWHI. Number of colonies (*n*) were determined from belt transect surveys. Values to the right of bars are the number of colonies of each taxon.

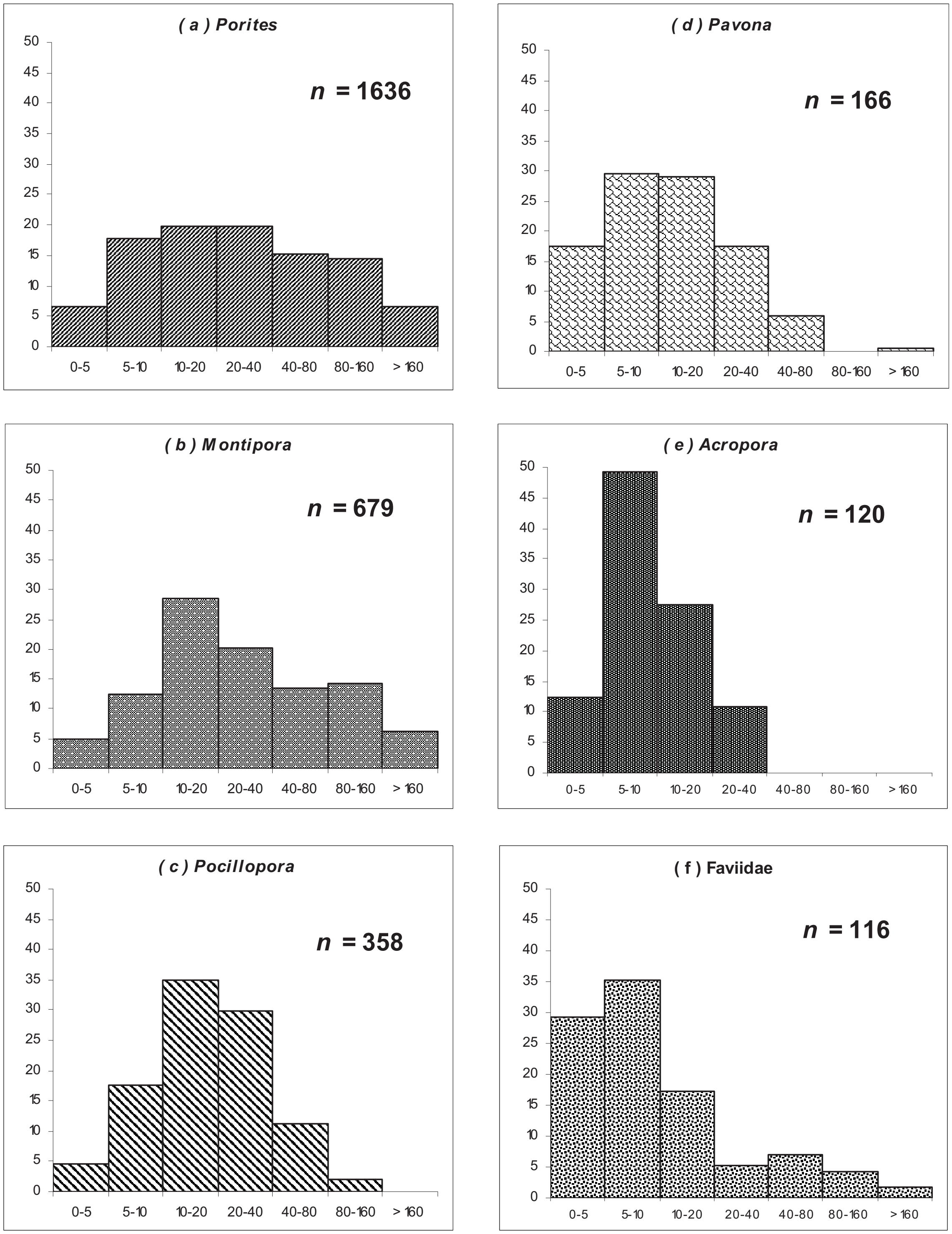

Figure 5. a–f. Size class (cm) distributions of select scleractinian corals at Maro Reef, NWHI. Y-axis is percent of colonies enumerated in each taxon.

DISCUSSION

Synopsis of Salient Results

Video transect and photoquadrat methodologies produced highly similar values for coral cover across the reef system and by sector, but these values were, with the exception of the southeast sector, 2 to 3.5 times higher than those produced by analysis of imagery recorded during towed-diver surveys (Tables 1,2; Fig. 3). Site-specific surveys sampled by the video transect and photoquadrat methods targeted hardbottom communities, while towed divers surveyed along track lines defined by the general contours of the linear and reticulate reefs that typify the structure of the shallow-water reef system at Maro. These track lines included numerous breaks in the reef structure characterized by soft bottom and unconsolidated substrate (i.e., sand and/or rubble), resulting in lower estimates of live coral cover than those produced from site-specific surveys. Despite the magnitude of the difference in coral cover values, all three methods showed statistically significant differences in coral cover among the four sectors, with highest coral cover in the northeast sector and second-highest in the southwest sector. The rank order for coral cover in the remaining two sectors (northwest and southeast) differed between the towed-diver and site-specific methods.

All three methods showed statistically significant differences in the relative abundance of coral taxa among sectors. Massive and encrusting *Porites* (e.g., *P. lobata*, *P. evermanni*) dominated all sectors. Towed-diver surveys indicated *Porites compressa* was generally the next most dominant taxon, but site-specific surveys indicated *Montipora* was the next most dominant taxon. All three methods indicated that *Pocillopora*, *Acropora*, and other corals (e.g., *Pavona*, fungiids, faviids) contributed relatively little to coral cover. *Acropora*, which is most abundant in the NWHI at French Frigate Shoals and Maro Reef (Grigg, 1981), made the greatest contribution to coral cover along the western sectors (Table 1, Fig. 3a). Unlike French Frigate Shoals, however, where more than a third of *Acropora* colonies (primarily *A. cytherea*) in the lagoon and back reef habitats exceeded 40 cm maximum diameter (Kenyon et al., 2006b), no *Acropora* colonies censused in the present study attained such large sizes (Fig. 5e). Conversely, *Pocillopora* populations attained larger sizes than at other NWHI reef systems where comparable studies have been conducted (Kenyon et al., 2006c; 2007a, b; in review), i.e., 13% of pocilloporids at Maro had a maximum diameter > 40 cm (n = 358) versus the next highest of 5.2% at Kure Atoll (n = 1539).

Comparison with Previous Surveys

Grigg (1983) reported 21 species from southwest seaward sites at Maro Reef. Maragos et al. (2004) reported 37 species from 39 survey sites but provided no demographic data pertaining to their distribution across the reef system. In the present study, 12 species were distinguished in photoquadrats (Table 3); 1 additional taxon (*Fungia* sp.) was seen in a video transect. Of these 13 taxa, 11 are included among the top 12 species ranked with the use of occurrence and abundance indices developed by Maragos et al. (2004) (Table 3). Seven of the 11 species ranked by Grigg (1983) on southwest seaward reefs were observed in photoquadrats in the present study.

Table 3. Relative abundance of scleractinian coral species at Maro Reef ranked by photoquadrats in present study, Maragos et al. (2004), and Grigg (1983).

Rank	Present study	Maragos et al. (2004)	Grigg (1983)
1	*Porites lobata*	*Porites compressa*	*Porites lobata*
2	*Montipora patula*	*Porites lobata*	*Porites compressa*
3	*Montipora capitata*	*Pocillopora meandrina*	*Montipora patula*
4	*Pocillpora meandrina*	*Pavona duerdeni*	*Pocillopora meandrina*
5	*Porites compressa*	*Montipora capitata*	*Montipora verrucosa*[b]
6	*Porites evermanni*[a]	*Cyphastrea ocellina*	*Montipora flabellata*
7	*Acropora valida*	*Montipora patula*	*Cyphastrea ocellina*
8	*Pocillopora ligulata*	*Porites evermanni*[a]	*Pavona (Pseudocolumnastraea)*
9	*Pavona duerdeni*	*Pocillopora damicornis*	*Porites (Synarea) convexa*[d]
10	*Montipora flabellata*	*Pocillopora ligulata*	*Montipora dilatata*
11	*Leptastrea purpurea*	*Montipora flabellata*	*Leptastrea bottae*
12	*Cyphastrea ocellina*	*Leptastrea purpurea*	N.A.[e]

[a] Considered to be *Porites lutea* by Fenner (2005).

[b] Revised as *Montipora capitata* (Maragos, 1995).

[c] Synonymized with *Pavona maldivensis* (Cairns et al., 1999).

[d] Synonymized with *Porites hawaiiensis* (Maragos, 1977).

[e] Not available; data only provided for eleven scleractinian species by Grigg (1983).

Grigg (1983) reported a mean coral cover of 54% from four 50-m transects off the southwest sector of Maro. This value is consistent with average coral cover in the southwest sector derived from video transects (51.0%) and photoquadrats (43.6%) in the present study (Table 2, Figs. 3b,c). However, these southwest sector values are high compared to the average reef-wide coral cover on hardbottom substrate derived from video transects and photoquadrats (33.8% and 32.4%, respectively), which in turn are high compared to the more spatially comprehensive estimates derived from towed-diver surveys (14.0%, Table 1). The dominance of *Porites* with massive and encrusting growth forms (Tables 1, 2, Fig. 3) is consistent with the top ranking of *Porites lobata* by Grigg (1983) at southwest sites but differs from the top ranking of *Porites compressa* by Maragos et al. (2004) (Table 3). Four taxa ranked among the top 11 by Grigg (1983) (*Pavona* [*Pseudocolumnastraea*] *pollicata, Porites* [*Synarea*] *convexa, Montipora dilatata, Leptastrea bottae*; Table 3) were not distinguished in imagery recorded by any of the three methods in the present study.

Coral Cover and Wave Disturbance

The most significant wave disturbance to Hawaiian reefs comes from large waves approaching from the north or northwest that are generated by the North Pacific winter swell between November and March (Grigg, 1998; Friedlander et al., 2005; Rooney et al., 2008). Wave exposure, in turn, is a major factor influencing the development of Hawaiian coral reefs, with moderate coral cover developing in areas directly exposed to winter wave regimes and high coral cover developing in sheltered embayments and areas protected from direct swells (Dollar, 1982; Storlazzi et al., 2005; Jokiel, 2006). More benign wave regimes in the summer (May–September) are primarily driven by northeast trade winds, with wave stress greatest along northeast and east exposures. NOAA Wave Watch III data at Maro Reef from January 1997 to December 2006 show the greatest winter wave stress originates primarily from the northwest (e.g., on average a wave event with a 12–14 second period from 310^{o} has a height of 4 m and occurs 20 or more days in a season) and secondarily from the northeast (e.g., on average a wave event with a 12–14 second period from 60º has a height of 4 m and occurs 7 or more days in a season) (Rooney et al., 2008). Summer wave regimes are dominated by smaller, shorter-period waves from the east (e.g., on average a wave event with a 8–10 second period from 90º has a height of 1.5 m and occurs 30 or more days in a season) (Rooney et al., 2008). Reef-wide patterns of coral cover at Maro Reef vary from those at other locations in the NWHI. At Pearl and Hermes Atoll, coral cover was highest on the fore reef in the northwest and north sectors (~ 24–28%; Kenyon et al., 2007a); at Kure Atoll, coral cover was highest on the fore reef along the arc extending counterclockwise from north to west (~ 11–16%; J. Kenyon, unpubl. data). At French Frigate Shoals, an open atoll lacking perimeter reef to the west, coral cover on the fore reef was highest in the northwest sector (~ 26%; Kenyon et al., 2006b). In contrast, at Lisianski/Neva Shoal, an open atoll with limited perimeter reef (Maragos and Gulko, 2002), coral cover was highest in the southeast and southwest sectors (~25–27%; Kenyon et al., 2007b). At Maro Reef, an open atoll with no perimeter reef (Maragos and Gulko, 2002; Rooney et al., 2008), all three methods showed the highest coral cover was along the northeast exposure, closely followed by the southwest exposure (Tables 1, 2). Both Lisianski/Neva Shoal and Maro Reef are classified as open atolls, but their complex structure of reticulate reef with little to no enclosure by perimeter reef likely generates a more complicated pattern of wave exposure than that experienced by atolls more clearly delineated by a perimeter reef, and accordingly they are characterized by different patterns of highest coral cover.

Health Status of Maro Reef Coral Communities

Jokiel and Rodgers (2007) used five, equally weighted metrics of coral-reef biological "health" or "value" (reef-fish biomass, reef-fish endemism, coral cover, endangered monk seal [*Monachus schauinslandi*] population, and numbers of female green sea turtles [*Chelonia mydas*] nesting annually) to rank the condition of 18 islands/atolls throughout the Hawaiian Archipelago. Of the 10 reef systems in the NWHI, Maro ranked fifth. Like most reef systems in the NWHI, Maro outranked all eight islands in the populated main Hawaiian Islands. However, two of the metrics (number of nesting green sea turtles and monk seal population) are tied to the presence of emergent land, which resulted in a score of zero for those metrics at Maro. With regards to coral cover on hardbottom substrate, Maro ranked highest of all 18 islands/atolls throughout the Hawaiian Archipelago. This scoring was based on visual estimates of coral cover during 2002 at the suite of sites reported in the present study and elsewhere in the NWHI. Maro's status as the reef system with the highest coral cover on hardbottom substrate is in agreement with results from the more detailed, rigorous data extraction methods presented here and at other island/atoll systems in the NWHI where a similar suite of methods has been applied (Kenyon et al., 2006b; 2007a,b; 2008). Other indicators of the health status of coral communities include bleaching history, prevalence of coral disease, presence of marine debris, density of the crown-of-thorns seastar *Acanthaster planci*, and rates of coral recruitment.

Two episodes of mass coral bleaching have been documented in the NWHI, in 2002 and 2004, with the northernmost atolls (Pearl and Hermes, Midway, and Kure) most severely affected during both episodes (Aeby et al., 2003; Kenyon et al., 2006c; Kenyon and Brainard, 2006). Nonetheless, in 2002, 24.8% of the coral cover sampled along 16.4 km surveyed by towed divers at Maro Reef was bleached, and 2.9% of colonies enumerated within belt transects at nine sites were bleached (Kenyon et al., 2006c), with *Pocillopora* and *Montipora* showing the greatest differential susceptibility to bleaching. In 2004, 14.7% of colonies enumerated within belt transects at eight sites at Maro were bleached (Kenyon and Brainard, 2006), with *Montipora patula, Porites evermanni*, and *Pocillopora damicornis* showing the greatest differential susceptibility to bleaching (68.8%, 35.2%, and 25.7% of colonies, respectively). Both episodes of bleaching were accompanied by prolonged periods of elevated sea surface temperature (Hoeke et al., 2006; Kenyon and Brainard, 2006). Average percent coral cover from six sites surveyed in both 2004 and 2006 declined from 40.2 to 34.0%, but this decrease was not statistically significant (J. Kenyon, unpubl. data). However, the distributions of colony sizes from the six sites surveyed in both 2004 and 2006 were significantly different (J. Kenyon, unpubl. data); the 2006 distribution was more strongly skewed towards smaller size classes, suggesting partial mortality of colonies affected by bleaching in 2004. Bleaching can have other long-term effects on coral communities as well, including increased susceptibility to disease (Harvell et al., 1999; Whelan et al., 2007) and diminished reproductive capacity (Michalek-Wagner and Willis, 2001; Omori et al., 2001).

Coral disease is emerging as a problem worldwide and has been investigated in the NWHI since 2003. Baseline surveys at 73 sites throughout the NWHI in 2003 revealed the presence of 10 disease states, of which 5 states affecting the genera *Porites* and *Montipora* were recorded from 8 of the 9 sites surveyed (88.9%) at Maro Reef (Aeby, 2006). Maro had higher levels of montiporid disease compared to other islands/atolls in the NWHI in terms of both frequency of occurrence (percent of sites with disease) and prevalence (percent of colonies with disease). Surveys in 2004 found montiporid disease to occur at 5 of 7 sites (71.4%) at Maro as compared to other islands/atolls where montiporid disease was found at only 7 of 36 sites (19.4%). Similarly, the overall prevalence of montiporid disease at Maro was 2.8% compared to the overall prevalence of montiporid disease from the rest of the NWHI, which was 0.34% (G. Aeby, unpubl. data). Although *Montipora* is the second most common coral genus found on the reefs of Maro (Fig. 4), higher levels of montiporid disease cannot be explained purely by host abundance as *Montipora* is also common at many other islands/atolls (Kenyon et al., 2007a, b). However, suspended sediment is higher at Maro Reef compared to other regions as evidenced by low beam transmission values, a measure of water clarity (Rooney et al., 2008; Coral Reef Ecosystem Division, unpubl. data). Sediment stress on the encrusting montiporids (the dominant form at Maro) could leave corals more susceptible to disease.

From 2000 to 2007, NOAA's Pacific Islands Fisheries Science Center's Coral Reef Ecosystem Division removed 526 metric tons (MT) of marine debris, primarily derelict fishing gear, from the NWHI, which includes 57.1 MT from Maro (R. Brainard, unpubl. data). Marine debris is a persistent problem in the NWHI, as it accumulates in the North Pacific Subtropical Convergence Zone (STCZ) and is transported southward towards the NWHI by the seasonal migration of the STCZ and by prevailing wind and wave regimes (Pichel et al., 2007). Factors such as shallow water depth, high-relief reef structure, and low exposure to significant wave height within the sheltered lagoons enhance the potential of marine debris to settle on reefs in the NWHI, where mechanical damage ensues to benthic communities including corals (Donohue et al., 2001). Based on known accumulation rates calculated from areas where debris was prone to collect at two NWHI reef systems, Dameron et al. (2007) developed a "net habitat prediction model" to estimate future annual accumulation at reef systems with similar physical features conducive to debris deposition. Annual NWHI debris accumulation was estimated to be 52.0 MT, with 10.6 MT (20% of total) deposited in the lagoon and adjacent network of reticulate reefs at Maro. Further development of procedures to economically locate and remove derelict fishing gear at sea may eventually reduce its environmental damage to benthic reef habitat.

The crown-of-thorns seastar (*Acanthaster planci* Linnaeus) is a selective corallivore that has caused widespread destruction on numerous reefs throughout the Indo-Pacific (e.g., Chesher, 1969; Endean et al., 1973; Done, 1985). Outbreaks can result in significant loss of corals on reefs and it is still unclear what drives these population surges. Hypotheses include the role of nutrients in terrestrial runoff that in turn enhance phytoplankton food supply for larval seastars, particularly during periods of high rainfall when nutrients are flushed into the sea (Cameron et al., 1991). Population densities of *A. planci* are regularly monitored using towed-diver surveys conducted on shallow-water (≤ 30 m) reefs throughout the U.S. Pacific as part of NOAA's Pacific Reef Assessment and Monitoring Program (Brainard et al., 2008). In the NWHI, not a single crown-of-thorns seastar was recorded by towed divers surveying along 188.3 km of track lines at Maro Reef during annual surveys between 2000 and 2004 and a survey conducted in 2006. This was the lowest density observed in the NWHI, followed by Lisianski (2.0×10^{-6} seastars m^{-2}) and Laysan (2.8×10^{-6} seastars m^{-2}), with the highest density at Pearl and Hermes Atoll (1.6×10^{-4} seastars m^{-2}) (Coral Reef Ecosystem Division, unpubl. data). During site-specific surveys at Maro in 2003, 2004, and 2005, only one *A. planci* seastar was observed in a survey area totaling 11,500 m^2 (Coral Reef Ecosystem Division, unpubl. data).

The capacity of scleractinian corals to maintain or renew genetically diverse populations through sexual reproduction is a key attribute of reef resilience (West and Salm, 2003). Documenting the density, taxon, and size of coral recruits to settlement plates during known time intervals is a widely used method of quantifying coral recruitment. Four deployments of arrays of terra cotta recruitment plates were conducted at six locations in the NWHI (French Frigate Shoals, Maro Reef, Lisianski/Neva Shoal, Pearl and Hermes Atoll, Midway Atoll, and Kure Atoll; Fig. 1) at annual or biennial intervals between 2001 and 2006. Several locations, including Maro Reef, showed substantial interannual variability in the density of coral recruits. Maro had the highest average recruitment rate (265.3 recruits m^{-2} $year^{-1}$ (SE 87.0)) versus the next highest at French Frigate Shoals at 57.7 recruits m^{-2} $year^{-1}$ (SE 33.2) and a larger mean coral diameter (2.7 mm (SE 0.08)) versus the next highest at Kure of 2.4 mm (SE 0.16) than other locations (Dunlap and Kenyon, 2004; J. Kenyon, unpubl. data). The taxonomic composition of the recruits throughout the NWHI (96.1% Pocilloporidae, 2.8% Acroporidae, 1.1% Poritidae) did not reflect the composition of mature coral communities, as the genus *Porites* dominates in all locations (Kenyon et al., 2006b; 2007a,b; 2008). At Maro, 97.1% of the recruits were pocilloporids, though this genus contributed little to coral cover (Tables 1,2; Fig. 3) and had lesser colony density than *Porites* or *Montipora* (Fig. 4). At all locations, the arrays of recruitment plates were deployed at similar depths (~10 m) at wave-sheltered sites near coral-rich reefs; at Maro, the mesh of reticulate reefs adjacent to the lagoonal site where the plates were deployed in association with the CREWS buoy anchor (Fig. 2) may have facilitated retention of gametes and/or larvae compared to other NWHI locations where the neighboring reef structure was not as complex. These results reveal the need for further study of coral reproductive and recruitment processes in these remote areas, from where little data exist. In an era when numerous reefs throughout the world are reported to be in decline (Nyström et al., 2000; Hughes et al, 2003; Pandolfi et al., 2005), and even remote reefs are negatively impacted by natural and anthropogenic events that originate from far distant sources or are increasingly global in nature (Hoegh-Guldberg et al., 2007), coral communities at Maro appear to be in good condition based on the data presented and discussed here. Mean coral cover, a parameter often used in assessment of coral reef health (e.g., Jokiel and Rodgers, 2007), is the highest within the NWHI. The corals appear to have suffered few substantial long-term impacts from two episodes of coral bleaching. Coral disease prevalence is low; crown-of-thorns seastars are rare; preliminary coral recruitment rates based on limited data are the highest in the NWHI. No alien or invasive species have been reported from Maro Reef. Accumulation of marine debris that originates from distant sources, however, is a persistent problem with attendant damage to benthic reef habitats. The results presented here, derived from three complementary methods each with distinct spatial and taxonomic scales, can serve as an important baseline for assessing changes to Maro Reef's coral communities in the decades to come.

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