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**COMMUNITY STRUCTURE OF HERMATYPIC CORALS AT MIDWAY
ATOLL IN THE NORTHWESTERN HAWAIIAN ISLANDS: A LEGACY OF
HUMAN DISTURBANCE**

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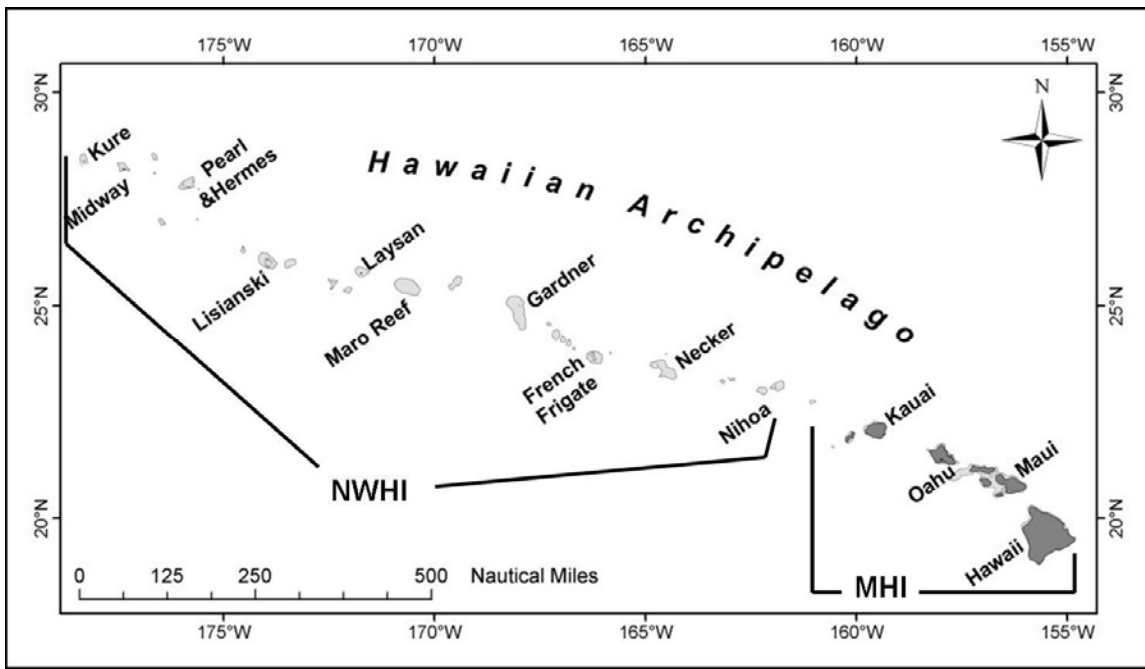


Figure 1. The Hawaiian Archipelago. NWHI = Northwestern Hawaiian Islands; MHI = main Hawaiian Islands. Lightly shaded areas are within the 100-fathom isobaths.

COMMUNITY STRUCTURE OF HERMATYPIC CORALS AT MIDWAY ATOLL IN THE NORTHWESTERN HAWAIIAN ISLANDS: A LEGACY OF HUMAN DISTURBANCE

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JEAN C. KENYON,¹ CASEY B. WILKINSON,¹ AND GRETA S. AEBY²

ABSTRACT

Percent cover of shallow-water (< 20 m depth) scleractinian corals at Midway Atoll, a classic atoll in the Northwestern Hawaiian Islands (NWHI), was quantified from analysis of imagery recorded along more than 49 km of benthic habitat by towed divers and at 26 sites surveyed with video transects and photoquadrats during 2002 and 2003. 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 three habitats (fore reef, back reef, and lagoon). Mean coral cover was sparse (< 1.6%) on both the fore reef, which was dominated by massive and encrusting growth forms of *Porites*, and in the lagoon (< 1.2%), which was dominated by *Pocillopora*. Mean coral cover was highest on the back reef (> 13.5%), which was dominated by *Montipora*. All taxa showed habitat-specific differences in colony density while the two most widespread genera, *Porites* and *Pocillopora*, showed differences in habitat-specific size class distributions. Midway has the lowest system-wide and habitat-specific mean coral cover of the seven reef systems in the NWHI that have been surveyed with similar methods during a comparable time period, which is likely related to its history of human use and modification. Bleaching history, disease prevalence, crown-of-thorns seastars, marine debris, larval recruitment, and alien benthic invertebrates are discussed as other influential factors shaping the observed coral community. As the most comprehensive description of Midway coral communities produced to date, these data provide a valuable baseline for assessing future change.

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INTRODUCTION

Charles Darwin conceived the subsidence theory of atoll formation during the voyage of the *Beagle* (Darwin, 1842). Supportive evidence was found in 1965 when two holes drilled at Midway Atoll through reef limestone and sediments reached volcanic basalt at depths of 152 m and 381 m, respectively (Ladd et al., 1967). Earlier, as a result of the decisive Battle of Midway in World War II, this remote atoll in the Northwestern Hawaiian Islands (NWHI) in the Hawaiian Archipelago (Fig. 1) became well known beyond the insular Pacific. Despite its fame, Midway Atoll remains poorly documented with regards to its contemporary shallow-water (≤ 30 m depth) benthic biological resources. Reports of the worldwide decline of coral reefs because of climate change, degraded water quality, and overexploitation (e.g., Nyström et al., 2000; Hughes et al., 2003; Pandolfi et al., 2005; Hoegh-Guldberg et al., 2007) hasten the need for comprehensive, quantitative baseline studies by which future trajectories of change can be assessed. With regards to coral communities, habitat-specific metrics (including percent cover of live coral, species diversity, colony density, and size-class distributions) collectively describe community structure, while supplemental factors of coral bleaching history, distribution and prevalence of other disease states, coral recruitment rates, and stressors (including corallivorous crown-of-thorn seastars, accumulation of marine debris, and alien marine species) provide a context of conditions to which coral communities have responded and continue to be shaped. Far more than other islands and atolls in the NWHI, Midway Atoll has been extensively modified for commercial and military purposes, thereby generating human disturbances to benthic habitats in addition to those occurring more naturally.

Midway Atoll (28°15'N, 177°20'W) was first recorded by western explorers in 1859 and claimed by the United States. The atoll includes two main islands, Sand Island and Eastern Island, and is encircled by a roundish atoll rim approximately 10 km in diameter with a pass on the western side (Fig. 2). The U.S. Navy began construction of a channel into the lagoon in 1870 but abandoned the effort until 1940, when the harbor and its entrances between Sand Island and Eastern Island were dredged to allow passage of large naval vessels. In the interim, the Pacific Commercial Cable Company developed Sand Island at Midway as a station for a cable between Guam and San Francisco that was completed in 1903. In 1935, Pan American Airways built an airport on Sand Island which became a refueling stop on the Manila to San Francisco route for its floatplanes. More than 8000 tons of topsoil were imported to Midway as part of these commercial ventures. In the years leading to World War II, Midway served as a critical base of naval operations, and the Midway Naval Air Station was commissioned in 1941. The station was bombed several months after the attack on Pearl Harbor, and the naval battle near Midway 6 months later was the turning point of the war in the Pacific theater. After World War II, the naval facility continued to be used as an important refueling stop for both ships and aircraft. In 1996, the Navy turned over control of Midway to the U.S. Fish and Wildlife Service which managed the atoll as Midway Atoll National Wildlife Refuge. In 2006, President George W. Bush created the NWHI Marine National Monument, renamed the Papahānaumokuākea Marine National Monument in 2007, to be co-managed by the U.S. Fish and Wildlife Service, the National Oceanic and Atmospheric Administration, and the State of Hawaii. Midway was delineated as a Special

Management Area where recreational activities are permitted, and it continues to be used as a port of call by both aircraft and ships, though not to the extent of its former usage.

Midway is the smallest of the three classic atolls (Pearl and Hermes, Midway, and Kure) and three open atolls (French Frigate Shoals, Maro Reef, Lisianski/Neva Shoal) in the Hawaiian Archipelago (Maragos and Gulko, 2002; Rooney et al., 2008) with 85.4 km² inside the 10-fathom depth curve (Rohmann et al., 2005). Four previous peer-reviewed studies provide data on contemporary coral communities at Midway Atoll. 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. From the shallow eastern lagoon at Midway, Coles (1998) provided the first record of the reef coral *Montipora turgescens* in Hawaii. Maragos et al. (2004) compiled coral species inventories for 10 reef systems in the NWHI and examined geographic trends in diversity, endemism, and abundance. Schroeder and Parrish (2006) provided coral diversity and cover data for four patch reefs in the southwestern lagoon. These important contributions, however, are spatially limited and only address one or two elements of the coral community.

In this paper we describe the community structure of the shallow-water (< 20 m depth) scleractinian corals at Midway Atoll, based on reef-wide surveys conducted in 2002 and 2003. We assessed percent cover using towed-diver surveys accompanied by digital video documentation over extensive areas. Documentation at finer spatial and taxonomic scales was provided by 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. The results are discussed within the context of factors known to influence coral community structure and for which data are available for Midway Atoll, including bleaching history, coral disease, marine debris, crown-of-thorns seastar abundance, coral recruitment rates, and introduced benthic marine species. We provide the most comprehensive baseline assessment to date that describes coral communities at Midway Atoll in the early years of the 21st century, which can serve as an important and useful standard for future generations of scientists, managers, and other stakeholders.

MATERIALS AND METHODS

Benthic Surveys

Non-overlapping towed-diver surveys were conducted in 2002 (20–25 September and 4–6 December) according to the methods of Kenyon et al. (2006a). Three additional surveys were conducted in 2003 (6–8 August) to examine areas that had not been assessed on earlier surveys. On 2002 surveys, a digital video camera inside an underwater housing with a wide-angle port was used to continuously record benthic imagery. On the 2003 surveys, a digital still camera (Canon EOS-10D, EF 20 mm lens) in a customized housing with strobes was used to photograph the benthos automatically at 15-sec intervals. Habitat digital videotapes recorded in 2002 were sampled at 30-sec intervals (interframe distance ~ 24 m) and quantitatively analyzed for coral percent cover using the methods of Kenyon et al. (2006a). Digital photographs recorded in 2003 were sampled at 30-sec intervals and quantitatively analyzed for coral percent cover using point-count

software (Coral Point Count with Excel Extension, Kohler and Gill, 2006) and using 50 randomly stratified points per frame. The coral categories that could be distinguished were *Pocillopora*, massive and encrusting *Porites* (e.g., *P. lobata*, *P. evermanni*), *Porites compressa*, *Montipora*, and other live coral (e.g., *Pavona*, *Fungia*, faviids). Laser-projected dots used to calibrate image size did not appear on photographic imagery because of mechanical problems; consequently, scaling data from imagery recorded elsewhere throughout the NWHI with the same methods (Kenyon et al., 2006b, 2007a, 2007b, 2008a, 2008b) were used to calculate average benthic area in captured frames. 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 a global positioning system (GPS) and ArcView GIS 3.3.

Site-specific belt-transect surveys, along with digital video recording of benthic cover along two 25-m-long transect lines, were conducted by three separate teams of divers from 20 to 25 September 2002 according to the general methods described by Maragos et al. (2004) for the 2002 Rapid Ecological Assessments. At four lagoon sites only one 25 m transect could be recorded and analyzed because of the small size of the patch reefs. Three additional sites were surveyed with the same suite of methods on 7 August 2003. Locations of site-specific surveys were determined on the basis of (1) maximizing spatial coverage within the allotted number of survey days; (2) establishing depths that allowed three dives/day/diver; (3) providing benthic data for sites at which a time series of reef fish survey data existed; (4) working within constraints imposed by other ship-supported operations; and (5) 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 all but four sites according to the methods of Preskitt et al. (2004). At the four lagoon sites where only one, 25-m transect line could be deployed, only six photoquadrats were recorded.

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 *Pocillopora meandrina*, *P. damicornis*, *P. eydouxi*, *P. ligulata*, *Porites lobata*, *P. compressa*, *Montipora capitata*, *Montipora* sp., *Pavona varians*, and *Psammocora stellata*. 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 habitat (fore reef, back reef, and lagoon) and geographic sector (N, NE, E, etc.) (Fig. 2). Towed-diver surveys that spanned more than one habitat or 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 habitats and among sectors within habitats were examined using nonparametric Kruskal-Wallis tests as the data were not distributed normally, even with transformations. Differences in the percent cover of coral genera among habitats and among sectors within habitats 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 28 coral species at Midway Atoll based on qualitative Rapid Ecological Assessment surveys that were conducted at 51 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 imagery depends on the tow speed; the average interframe distance ranged from 15.0 m to 32.5 m (mean = 24.1 m, $n = 24$ tows). The average benthic area captured in laser-scaled frames from imagery recorded elsewhere throughout the NWHI with the same methods was 5832 cm² (SE = 58 cm², $n = 6398$ frames). Towed divers surveyed along 49.4 linear km of benthic habitat (Table 1, Fig. 2), from which 2080 frames were analyzed. Given the 3:4 aspect ratio of the captured frames and extrapolating to the total number of consecutive, nonoverlapping still frames that compose the benthic imagery, this benthic analysis area (2080 frames \times 0.5832 m²/frame = 1213 m²) samples a total survey area of 43,565 m² (Table 1). Survey effort in the lagoon was limited to the northwest and west sectors (Fig. 2), as other portions of the lagoon bottom are primarily composed of sand with widely scattered patch reefs.

Average total coral cover across the atoll was low, ranging from 0.2% in the northwest lagoon to 15.2% on the north back reef (Table 1, Fig. 2). The differences among the three habitats in their average total percent coral cover were statistically significant (Kruskal-Wallis test, $H = 118.65$, $df = 2$, $p < 0.001$). Moreover, a significant difference existed among habitats in the relative abundance of coral genera present (chi-square test, $X^2 = 211.15$, $df = 4$, $p < 0.001$). Considering each habitat as a whole throughout the atoll, the fore reef was dominated by massive and encrusting *Porites* (e.g., *P. lobata*, *P. evermanni*). *Montipora* dominated the back-reef habitat, while *Pocillopora* dominated in the lagoon (Table 1, Fig. 3a).

The average coral cover across 22,664 m² surveyed along the fore reef was 1.6% (Table 1). The differences among the eight fore-reef sectors in the average total percent coral cover were statistically significant (Kruskal-Wallis test, $H = 49.71$, $df = 7$, $p < 0.001$), and there were significant differences among sectors in the relative abundance of coral genera present (chi-square test, $X^2 = 225.58$, $df = 8$, $p < 0.001$). Coral cover was highest (2.1%) in the north sector. Massive and encrusting growth forms of *Porites*

Table 1. Coral cover determined from towed-diver surveys conducted at Midway Atoll, NWHI, 2000–2003.

Habitat	Geographic sector	Distance surveyed (km)	Area surveyed ^a (m ²)	Range of average depth (m)	Average % total coral cover	Proportion of total coral cover ^b				
						Massive & encrusting <i>Porites</i>	<i>Porites compressa</i>	<i>Pocillopora</i>	<i>Montipora</i>	Other coral
Fore reef	ALL	25.7	22664	9.0–15.8	1.6	77.8	0.7	20.4	0.1	1.3
	NW	3.9	3439		1.7	47.0	2.3	44.2	0.3	6.3
	N	2.3	2028		2.1	87.8	0.6	11.9	0.0	0.0
	NE	2.2	1940		1.1	93.7	0.0	6.1	0.0	0.0
	E	4.3	3792		1.9	80.1	0.2	19.1	0.0	0.5
	SE	3.8	3351		1.3	53.1	0.8	46.0	0.0	0.0
	S	2.8	2469		1.1	99.2	0.6	0.4	0.0	0.0
	SW	2.5	2205		1.1	99.1	0.0	1.2	0.0	0.0
	W	3.9	3439		1.6	94.7	0.4	4.4	0.2	0.0
	ALL	19.9	17549	0.3–1.8	6.4	4.9	0.0	0.0	72.1	0.1
	NW	1.4	1235		8.2	0.5	0.0	7.5	92.0	0.0
	N	4.2	3704		15.2	2.3	0.0	12.5	85.2	0.0
	NE	2.8	2469		2.6	0.5	0.0	28.2	70.1	0.0
	E	3.1	2734		6.8	22.1	0.0	23.5	53.4	1.0
Lagoon	SE	1.9	1676		1.0	22.9	0.0	70.8	6.3	0.0
	S	1.2	1058		2.5	49.5	0.0	47.2	3.1	0.0
	SW	4.4	3880		1.2	5.1	0.0	90.0	4.8	0.0
	W	0.9	794		3.1	0.0	0.8	97.1	2.0	0.0
	ALL	3.8	3351	1.2–3.7	0.3	34.7	0.0	63.6	0.0	0.0
	NW	2.5	2205		0.2	0.0	0.0	100.0	0.0	0.0
	W	1.3	1146		0.6	60.0	0.0	40.0	0.0	0.0

^aArea surveyed is based on average area of laser-calibrated frames captured at 30-sec intervals.

^bProportions are graphically presented by habitat in Fig. 3a.

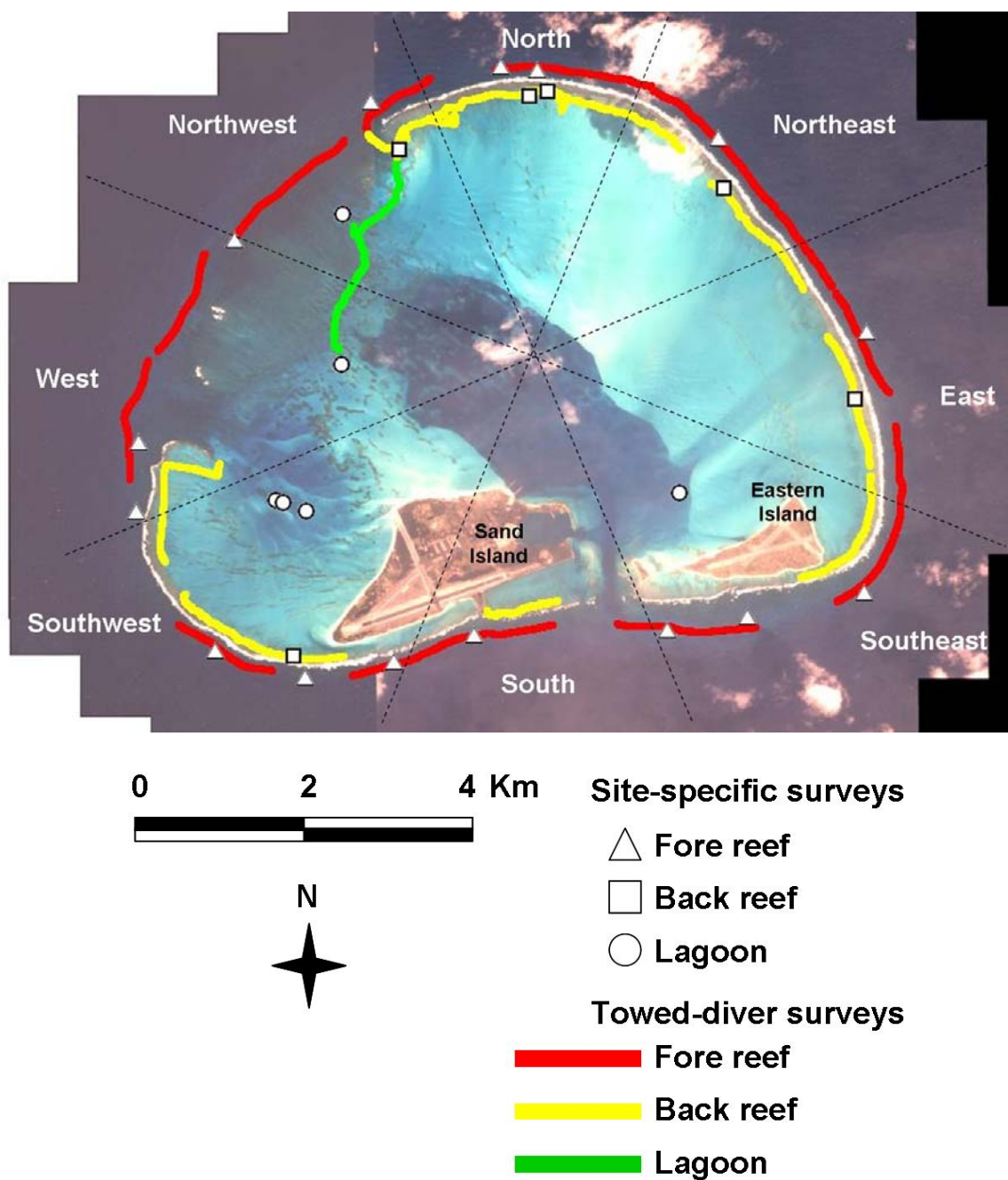


Figure 2. Location of towed-diver and site-specific surveys at Midway Atoll, NWHI, using IKONOS satellite imagery as a basemap. Irregular white and gray shapes overlying the lagoon are clouds and their shadows.

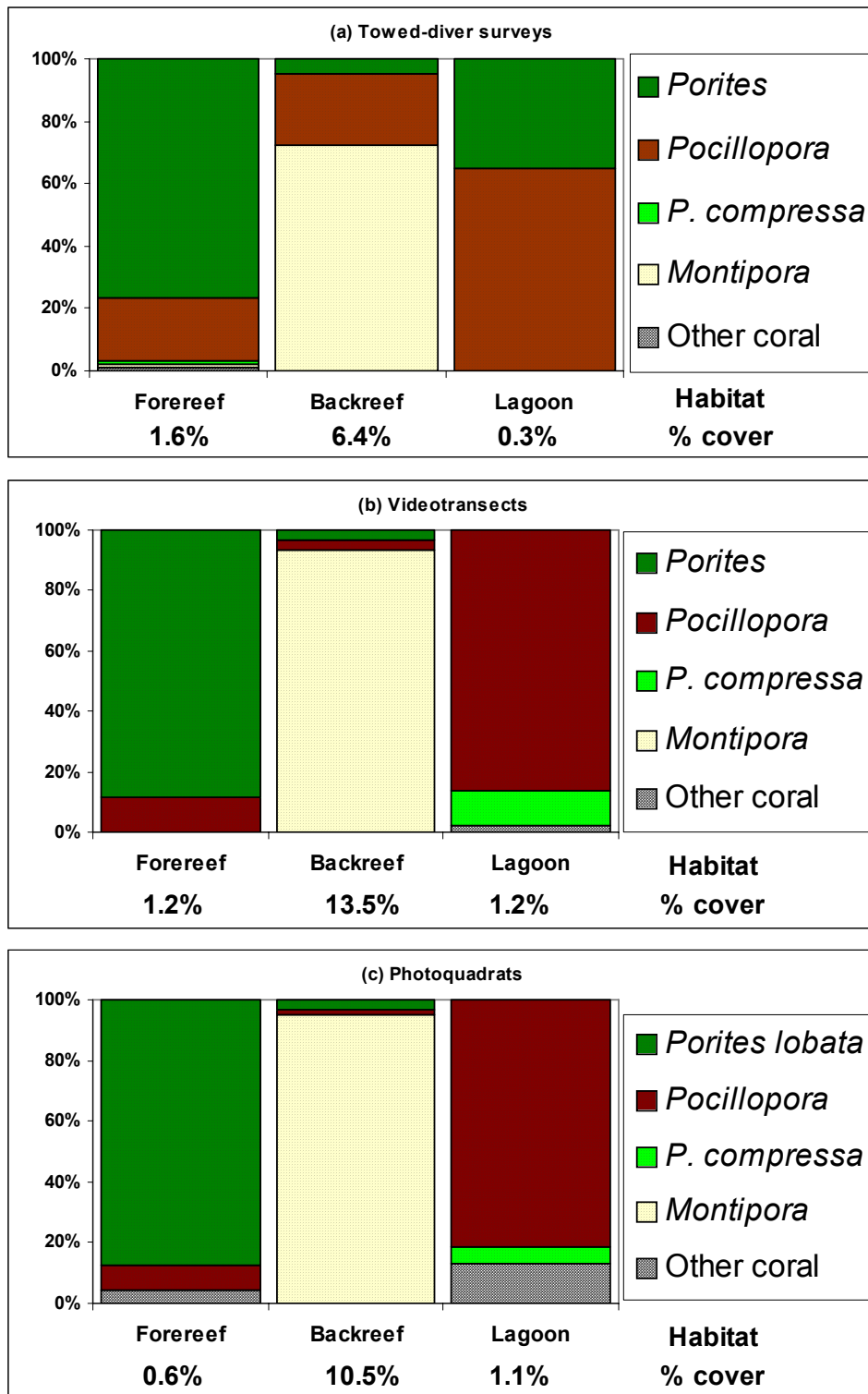


Figure 3. a–c. Relative abundance of primary coral taxa by habitat at Midway Atoll, NWHI, derived from three different methods. Values below sector labels are total coral percent cover within each habitat. Porites = massive and encrusting Porites.

dominated all sectors except the northwest and southeast, which were codominated by *Pocillopora*. *Porites compressa*, *Montipora*, and other taxa contributed little to coral cover on the fore reef (Table 1, Fig. 3a).

The average coral cover across 17,549 m² surveyed along the back reef was 6.4% (Table 1). The differences among the six back-reef sectors in the average total percent coral cover were statistically significant (Kruskal-Wallis test, $H = 148.79$, $df = 7$, $p < 0.001$), and there were significant differences among sectors in the relative abundance of coral genera present (chi-square test, $X^2 = 627.76$, $df = 14$, $p < 0.001$). Total coral cover was highest (15.2%) in the north sector but lower (< 8.2%) in all other sectors. *Montipora* dominated along the arc of back reef extending clockwise from the northwest to east sectors. *Pocillopora* dominated the remaining sectors except for the south, where this genus codominated with massive/encrusting *Porites*. *Porites compressa* and other taxa contributed little to coral cover on the back reef (Table 1, Fig. 3a).

The average coral cover across 3351 m² surveyed in the north and northwest sectors of the lagoon was 0.3% (Table 1, Fig. 3a). *Pocillopora* dominated the sparse coral cover in the northwest sector while massive and encrusting forms of *Porites* codominated with *Pocillopora* in the west sector (Table 1).

Site-specific Surveys: Video Transects

A total of 608 m² at 21 sites (16 or 32 m²/site) were quantitatively assessed from transect videotapes. The differences among the three habitats in their average total percent coral cover were statistically significant (Kruskal-Wallis test, $H = 157.25$, $df = 2$, $p < 0.001$). Average total coral cover was highest on the back reef (13.5%) and low (1.2%) in both the lagoon and fore reef (Table 2, Fig. 3b).

At least ten scleractinian species were seen in Midway video transects (*Pocillopora meandrina*, *P. damicornis*, *P. eydouxi*, *P. ligulata*, *Porites lobata*, *P. compressa*, *Montipora capitata*, *Montipora* sp., *Pavona varians*, and *Psammocora stellata*). *Montipora flabellata* could not be reliably distinguished from *M. turgescens* in videographic imagery. The differences among the three habitats in their relative abundance of coral taxa were statistically significant (chi-square test, $X^2 = 439.95$, $df = 4$, $p < 0.001$). The fore reef was dominated by *Porites lobata*, while the back reef was dominated by *Montipora* and the lagoon was dominated by *Pocillopora* (Table 2, Fig. 3b). Of the four species of *Pocillopora* present in video transects, *P. meandrina* composed 61.9% of the total pocilloporid cover throughout the atoll.

Site-specific Surveys: Photoquadrats

Video transects and photoquadrats were recorded concurrently at 19 sites with an additional 7 sites sampled by photoquadrats alone. Of the 19 sites where both methods were applied, the maximum difference in total coral cover calculated with the two methods was 6.0%; the average of the absolute values of the difference between video transect and photoquadrat total coral cover was 1.1%. The differences among the three habitats in their average total percent coral cover were statistically significant (Kruskal-Wallis test, $H = 223.28$, $df = 2$, $p < 0.001$). Average total coral cover was highest on the

Table 2. Coral cover determined from video transects and photoquadrats conducted at Midway Atoll, NWHI, in 2000 and 2003.

Habitat	# Sites surveyed	Average total % coral cover ^a	Range of transect depths (m)	Proportion of total coral cover ^b			
				<i>Porites lobata</i>	<i>Porites compressa</i>	<i>Montipora</i>	Other coral
Video transects							
Fore reef	10	1.2	9.4–15.0	88.2	0.0	11.8	0.0
Back reef	5	13.5	0.6–1.0	3.3	0.0	3.1	93.6
Lagoon	6	1.2	4.0–8.0	0.0	11.5	86.5	0.0
Photoquadrats							
Fore reef	14	0.6	10.0–15.0	87.1	0.0	8.7	0.0
Back reef	6	10.5	0.6–1.0	3.2	0.0	1.9	94.9
Lagoon	6	1.1	4.0–8.0	0.0	5.2	81.2	0.0

^a Values are means of replicate transects (two per site) or photoquadrats (12 per site), except for four lagoon sites, where only one transect and six photoquadrats were recorded because of the small size of the patch reefs.

^b Proportions are graphically presented by habitat in Fig. 3b,c.

back reef (10.5%) and low in the lagoon and fore reef (1.1% and 0.6%, respectively; Table 2, Fig. 3b).

At least ten scleractinian species were seen in Midway photoquadrats (Table 3). The differences among the three habitats in their relative abundance of coral taxa were statistically significant (chi-square test, $X^2 = 454.46$, $df = 4$, $p < 0.001$.) The fore reef was dominated by *Porites lobata*, while the back reef was dominated by *Montipora* and the lagoon was dominated by *Pocillopora* (Table 2, Fig. 3b). The three species of *Pocillopora* present in photoquadrats were fairly evenly divided in their contribution to the total pocilloporid cover throughout the atoll.

A total of 3220 colonies were counted and classified by size class within belt transects covering 1618 m² at 31 sites. *Porites* was the most numerically abundant (i.e., highest density) taxon across the atoll system followed by *Pocillopora*, *Montipora*, and *Pavona* (Fig. 4, All Habitats). Only 38 coral colonies (1.2% of total) in the fore-reef region did not represent species of these four genera, but were members of the genera *Leptastrea* and *Cyphastrea*. Relative densities of the major coral genera followed a similar pattern within the fore-reef habitat as across the atoll system (Fig. 4); i.e., *Porites*, followed by *Pocillopora*, was the most numerically abundant genus. In the back-reef and lagoon habitats, however, *Pocillopora* showed a higher density than *Porites*. *Montipora* was most abundant in the back-reef habitat, while *Pavona* was most abundant in the lagoon. Highest overall colony density occurred on the fore reef (2.9 colonies m⁻²) with lower colony densities in the back-reef (1.4 colonies m⁻²) and lagoon (1.0 colonies m⁻²) habitats.

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

Coral communities at Midway Atoll are primarily composed of small colonies, with 86.2% of all colonies being < 20 cm maximum diameter. There was a sufficient sample size to construct meaningful size-class distributions in all three habitats only for *Porites* and *Pocillopora* (Fig. 5). Both *Porites* and *Montipora* had more than 50% of colonies measuring > 20 cm maximum diameter in the back-reef habitat (Figs. 5b, 6a), but all other habitat-specific distributions indicated a majority of colonies had maximum diameters measuring less than 20 cm (Figs. 5, 6b).

A large number of small (< 20 cm) *Porites* colonies (Fig. 5a) accounts for the high density of this genus on the fore reef (Fig. 4). On the back reef, massive and encrusting forms of *Porites* largely account for the high proportion of larger (> 20 cm) colonies (Fig. 5b), as *P. compressa* is rare on the back reef (Fig. 3). In the lagoon, the *Porites* size class distribution (Fig. 5c) is largely represented by *P. compressa* (Fig. 3).

Pocilloporid density was highest on the fore reef, where a majority (84.4%) of colonies had a maximum diameter < 10 cm (Figs. 4, 5d). Pocilloporids were most sparsely distributed (i.e., least dense) on the back reef (Fig. 4), but the highest proportion of larger (> 20 cm) pocilloporid colonies was found in this habitat (Fig. 5e). Relative to the fore-reef and back-reef habitats, pocilloporid populations in the lagoon were moderate with respect to both colony density and size structure (Figs. 4, 5f).

Faviids, all recorded on the fore reef, measured < 10 cm maximum diameter.

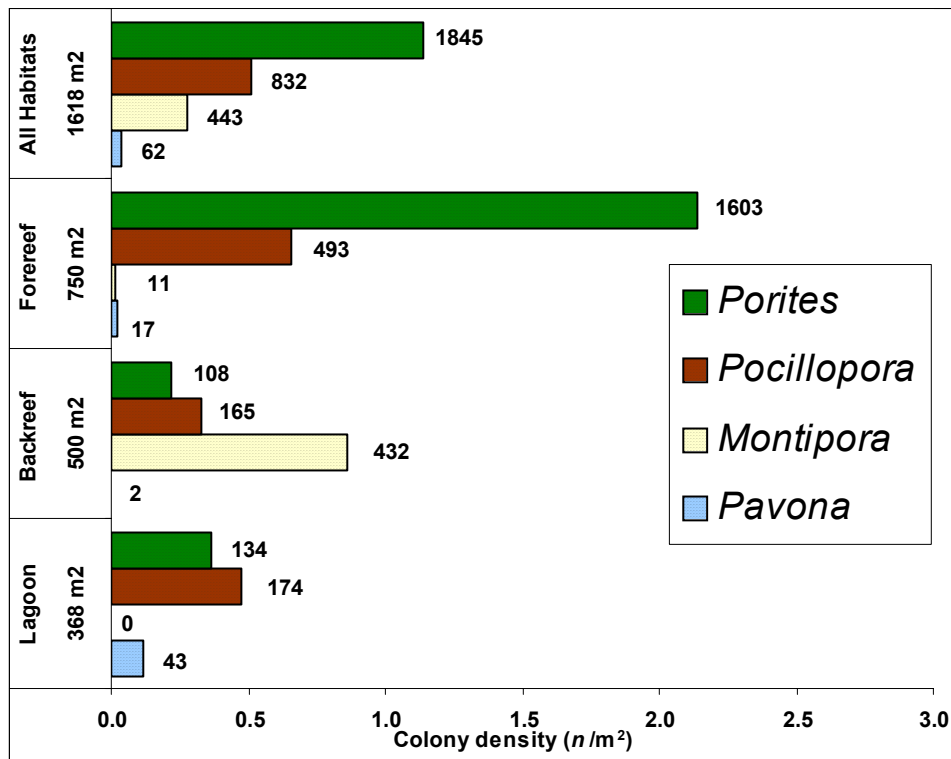


Figure 4. Colony density (no. m⁻²) of four coral genera at Midway Atoll, NWHI, in the lagoon, back reef, fore reef, and the three habitats combined. Number of colonies (n) was determined from belt transect surveys; area (m²) surveyed in each habitat is shown next to habitat label. Values to the right of bars are the number of colonies of each genus.

DISCUSSION

Synopsis of Salient Results

The three survey methods used in the present study produced similar patterns in the atoll-wide distribution and abundance of coral taxa. All three methods showed statistically significant differences among the three habitats in mean coral cover as well as the relative abundance of coral taxa. The chief discrepancy among the methods in mean coral cover was found in the back-reef habitat where estimates derived from video transect surveys (13.5%) were twice as great as those derived from towed-diver surveys (6.4%) (Tables 1, 2). Because towed divers survey substantially more area than free-swimming divers during site-specific surveys, values derived from towed divers likely provide a better measure of mean coral cover across large expanses of habitat than do site-specific surveys. Highest coral cover values derived from towed-diver surveys were found on the north and northwest back reef (Table 1). With regards to relative abundance, the chief discrepancy among the methods was found in the lagoon, where the towed-diver survey method showed a relatively greater contribution of massive and encrusting *Porites* to the sparse coral cover. All three methods showed that the sparse coral cover on the fore reef was dominated by massive and encrusting *Porites*, while the back reef was dominated by *Montipora* (Tables 1, 2, Fig. 3).

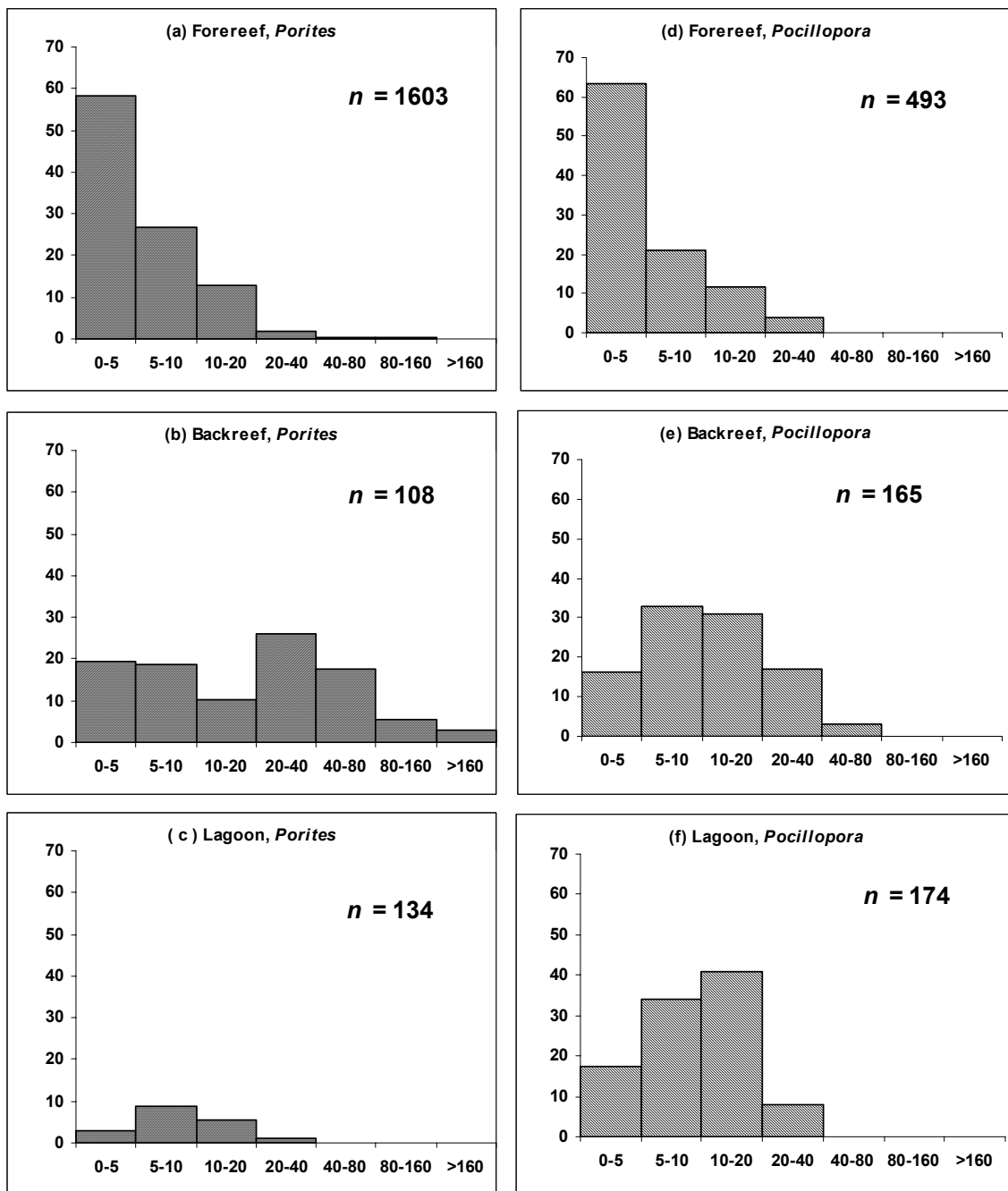


Figure 5. a–f. Size-class (cm) distributions, by habitat, of scleractinian corals at Midway Atoll, NWHI. a–c *Porites*, d–f *Pocillopora*. The x-axis is maximum diameter (cm). The y-axis is percent of colonies enumerated in each taxon.

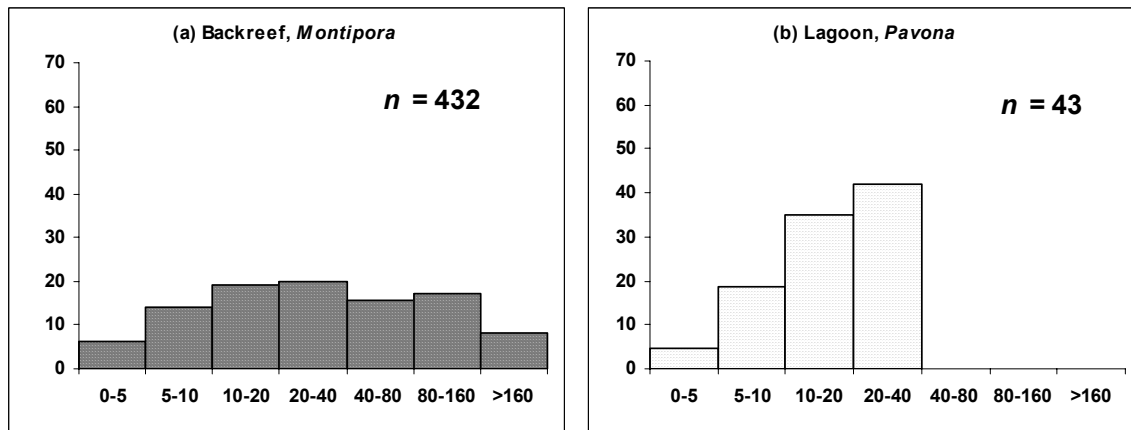


Figure 6. Size-class (cm) distributions of (a) *Montipora* in the backreef, and (b) *Pavona* in the lagoon, at Midway Atoll, NWHI. The x-axis is maximum diameter (cm). The y-axis is percent of colonies enumerated in each taxon.

Comparison with Previous Surveys

Grigg (1983) reported 14 coral species at Midway Atoll. Maragos et al. (2004) reported 28 species from 51 survey sites but provided no demographic data pertaining to their distribution across the reef system. In the present study, at least 10 species were distinguished in photoquadrats (Table 3); 2 additional species (*Pocillopora eydouxi* and *Psammocora stellata*) were seen in video transects. Of these, 7 are included among the top 10 species ranked with the use of occurrence and abundance indices developed by Maragos et al. (2004) (Table 3). Only 4 of the 8 species ranked by Grigg (1983) on south-west seaward reefs were observed in photoquadrats in the present study. Coles (1998) noted that *Montipora turgescens* was the dominant coral in shallow areas in the eastern lagoon, but this species could not be reliably distinguished from *M. flabellata* in the present study.

Grigg (1983) reported a mean coral cover of 11% from five 50-m transects off the south-west fore reef at Midway. This value is an order of magnitude greater than the mean coral cover along the south-west fore reef, as determined by towed-diver surveys in the present study (1.1%; Table 1) as well as an order of magnitude greater than the mean coral cover on the fore reef, as determined by video transects and photoquadrats (1.2% and 0.6%, respectively). The highest coral cover at any fore-reef site determined by video transects was 2.4% and the highest determined by photoquadrats was 1.7%. Grigg (1983) ranks *Porites compressa* as the most abundant coral at south-west fore-reef stations (Table 3), but this species was rarely documented on the fore reef in towed-diver surveys (Table 1) and not observed at all in video transects or photoquadrats on the fore reef (Table 2).

Schroeder and Parrish (2006) studied four patch reefs in the southwestern lagoon (Welles Harbor), reporting mean coral cover values of 7.3% and 6.9% in 1981 and 1985, respectively. Three of the patch reefs in the present study were located in this sector of the lagoon (Fig. 2), at which mean coral cover values of 1.8% and 1.7% were determined with videotransects and photoquadrats, respectively. Of the six species reported by

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

Rank	Present study	Maragos et al. (2004)	Grigg (1983)
1	<i>Montipora</i> sp. ^a	<i>Porites lobata</i>	<i>Porites compressa</i>
2	<i>Montipora capitata</i>	<i>Pocillopora damicornis</i>	<i>Porites lobata</i>
3	<i>Porites lobata</i>	<i>Pocillopora meandrina</i>	<i>Pocillopora meandrina</i>
4	<i>Pocillopora meandrina</i>	<i>Pocillopora ligulata</i>	<i>Pavona duerdeni</i>
5	<i>Pocillopora damicornis</i>	<i>Porites evermanni</i> ^b	<i>Montipora flabellata</i>
6	<i>Pocillopora ligulata</i>	<i>Cyphastrea ocellina</i>	<i>Porites (Synarea) convexa</i> ^c
7	<i>Pavona varians</i>	<i>Montipora flabellata</i>	<i>Cyphastrea ocellina</i>
8	<i>Pavona duerdeni</i>	<i>Montipora capitata</i>	<i>Leptastrea purpurea</i>
9	<i>Porites compressa</i>	<i>Porites compressa</i>	N.A. ^d
10	<i>Fungia scutaria</i>	<i>Montipora turgescens</i>	N.A. ^d

^a *Montipora flabellata* and *M. turgescens* could not be reliably distinguished in photoquadrats.

^b Considered to be *Porites lutea* by Fenner (2005).

^c Synonymized with *Porites hawaiiensis*, Maragos (1977).

^d Not available; data only provided for eight scleractinian species by Grigg (1983).

Schroeder and Parrish (2006), two (*Cyphastrea ocellina* and *Leptastrea purpurea*) of them were not observed on the three Welles Harbor patch reefs in the present study; conversely, two species (*Pocillopora ligulata* and *P. eydouxi*) not seen by Schroeder and Parrish (2006) were observed. Schroeder and Parrish (2006) note that two of the original patch reefs in their study were totally buried by progressive sand movement during winter storms of 1983–84, and that the area of the two unburied patch reefs declined by 10% and 55%, respectively, during the study period. Between 1985 and 2002, some patch reefs in Welles Harbor were greatly reduced in size, while others, initially very small, became several orders of magnitude larger as winter storms eroded sand away (R. Schroeder, pers. comm.). As a result of the absence of a well-developed perimeter reef in the west and northwest sectors of the atoll (Fig. 2) patch reefs in this sector of the lagoon are poorly protected from large winter wave events from the northwest and appear to be physically and ecologically dynamic over annual to decadal time scales.

Health Status of Midway Atoll 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. As one of the 10 reef systems in the NWHI, Midway ranked sixth. Like most reef systems in the NWHI, Midway outranked all eight islands in the populated main Hawaiian Islands. With regards to coral cover on hard-bottom substrate, Midway ranked ninth among the 10 islands/atolls in the NWHI,

with only the basaltic Necker Island (Fig. 1) having lower coral cover. 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. Midway's status as the reef system with the next-to-lowest coral cover on hard-bottom substrate in the NWHI is in agreement with results from the more detailed, rigorous data extraction methods presented here and at other island/atoll systems where a similar suite of methods has been applied (Table 4; Kenyon et al., 2006b; 2007a,b; 2008a,b). While all the reef systems associated with carbonate islands in the NWHI have experienced varying degrees of human usage and associated impacts (Friedlander et al., 2008), Midway has been the most extensively modified for commercial and military purposes throughout the 20th century. In the absence of baseline surveys preceding the current study, it cannot be determined to what extent the low coral cover documented at Midway Atoll is due to human disturbance over the past century. However, given the similar wave and temperature regimes experienced at Pearl and Hermes, Midway, and Kure Atolls (Rooney et al., 2008), it is reasonable to expect that coral cover values in the three habitats at these three closed atolls would be similar under natural circumstances. In contrast, coral cover in all three habitats is substantially lower at Midway than at Pearl and Hermes and at Kure, where coral cover values are comparable (Table 4). Channel and harbor dredging, landfill, construction of piers and navigational markers, waste disposal, and construction of a geological field station on the northern back reef in previous decades have all likely contributed to reduced coral cover at Midway relative to that at neighboring atolls.

Table 4. Comparison of coral cover, as determined from towed-diver surveys, at seven reef systems in the Northwestern Hawaiian Islands. NA = Not Applicable

Island/Atoll	Distance surveyed, km	Benthic area surveyed (m ²)	Average total percent coral cover			
			All habitats combined	Fore reef	Back reef	Lagoon
French Frigate Shoals ^a	88.9	101060	9.8	8.8	18.9	7.7
Maro Reef ^b	81.0	62827	14.0	NA	NA	NA
Laysan ^c	25.2	18566	5.3	NA	NA	NA
Lisianski/Neva Shoal ^c	43.2	33887	19.7	NA	NA	NA
Pearl and Hermes ^d	113.9	85843	10.2	6.8	10.5	19.1
Midway	49.4	43565	3.6	1.6	6.4	1.9
Kure ^e	39.1	26923	10.5	9.7	10.8	18.6

^a Kenyon et al.(2006b)

^b Kenyon et al.(2008a)

^c Kenyon et al.(2007b)

^d Kenyon et al.(2007a)

^e Kenyon et al.(2008b)

In addition to percent coral cover, other metrics useful as 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*, rates of coral recruitment, and the presence and impact of alien marine species.

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). During the 2002 event at Midway, 77% of the coral cover sampled along 8.7 km surveyed by towed divers in the back-reef habitat was bleached, and 56.1% of colonies enumerated within belt transects at six back-reef sites were bleached, with *Pocillopora* and *Montipora* showing the greatest differential susceptibility to bleaching (Kenyon et al., 2006c). In 2004, 21.5% of colonies enumerated within belt transects at four back-reef sites at Midway were bleached, with *Montipora capitata* and *M. turgescens* showing the greatest differential susceptibility to bleaching (100% and 66.3% of colonies, respectively) (Kenyon and Brainard, 2006). Both episodes of bleaching were accompanied by prolonged periods of elevated sea surface temperature (Hoeke et al., 2006; Kenyon and Brainard, 2006). Mean coral cover at the northernmost back-reef sites, where coral cover is highest (Fig. 2, Table 1), declined by 18% from 2002 to 2004, with *Montipora flabellata*, which was relatively resistant to bleaching, representing a larger proportion of the coral fauna in 2004 than in 2002 (Kenyon, unpubl. data). The lighter winds and higher summer sea surface temperatures experienced at the three northern atolls relative to elsewhere in the Hawaiian Archipelago (Hoeke et al., 2006) increase Midway's vulnerability to additional bleaching episodes, which are predicted to increase in frequency and severity both worldwide (Hoegh-Guldberg, 1999) and in the Hawaii region (Jokiel and Brown, 2004). Bleaching is known to have other potential long-term effects on coral communities as well, including increased susceptibility to disease (Harvell et al., 1999; Whelan et al., 2007) and reduced reproductive capacity (Michalek-Wagner and Willis, 2001; Omori et al., 2001).

Coral disease, which can have negative impacts on coral populations, has been investigated in the NWHI since 2003. Baseline surveys conducted at 73 sites throughout the NWHI during 2003 revealed the presence of 10 coral disease states, of which 2 diseases affecting the genus *Porites* (*Porites* trematodiasis, *Porites* tissue loss syndrome) and one disease affecting the genus *Montipora* (*Montipora* white syndrome) were recorded from Midway (Aeby, 2006). Midway had the lowest frequency of occurrence of disease relative to other locations in the NWHI, with disease only occurring at 3 of the 11 (27.3%) sites surveyed (Aeby, 2006). Midway has low coral cover compared to other regions in the NWHI and so it is not surprising that overall disease occurrence would also be low. However, disease occurrence also depends on a number of other factors, such as host susceptibility and environmental conditions, among others. We found the highest prevalence of disease (proportion of colonies affected) at Midway to be at two back-reef areas with a history of bleaching stress and which are dominated by montiporids. Environmental stress has been linked to coral disease with McClanahan et al. (2009) finding a strong relationship between coral bleaching and *Porites* growth anomalies and Bruno et al. (2007) reporting that both coral cover and thermal stress were factors contributing to the occurrence of white syndrome (tissue loss diseases) in several genera

of coral on the Great Barrier Reef. Within the NWHI, acroporids and montiporids are known to have the highest susceptibilities to disease (Aeby, 2006). Hence, the back reefs of Midway represent a combination of susceptible corals in an environment prone to environmental stress.

Marine debris is a chronic problem in the NWHI, where it accumulates in shallow-reef habitats following transport from the North Pacific Subtropical Convergence Zone (STCZ) by prevailing wind and wave regimes (Pichel et al., 2007). Corals become damaged as the debris becomes stranded, with shallow, high-relief reefs that experience little exposure to significant wave height being particularly susceptible to debris accumulation (Donohue et al., 2001). Between 2000 and 2008, the NOAA Pacific Islands Fisheries Science Center's Coral Reef Ecosystem Division and partners removed 583 metric tons (MT) of marine debris, primarily derelict fishing gear, from the NWHI, including 46 MT from Midway Atoll (R. Brainard, unpubl. data). Based on known accumulation rates calculated from areas where debris was prone to collect at Pearl and Hermes and Kure Atolls, Dameron et al. (2007) developed a "net habitat prediction model" to estimate future annual accumulation at other NWHI reef systems with similar physical features conducive to debris deposition. Annual NWHI debris accumulation was estimated to be 52.0 MT, with 6.4 MT (12% of total) deposited on the back reef at Midway. This significant threat posed to benthic habitats and marine biota may be mitigated by the development of economical and efficient methods to locate and remove masses of marine debris farther offshore before deposition occurs in shallow habitats.

Damage from the corallivorous seastar *Acanthaster planci* can differentially affect coral communities as adult *A. planci* are known to preferentially prey on the genera *Montipora* and *Pocillopora* more than other genera such as *Porites* (De'ath and Moran, 1998; Pratchett, 2007). Towed divers regularly monitor population densities of non-cryptic *A. planci* on shallow-water (≤ 30 m depth) reefs throughout the U.S. Pacific as part of the NOAA Pacific Reef Assessment and Monitoring Program (Brainard et al., 2008). Since 2000, *Acanthaster* density throughout the NWHI has consistently been at least an order of magnitude lower than that considered to be characteristic of an outbreak (≥ 1500 seastars km^{-2} ; Moran and De'ath, 1992). At Midway, the highest density in any survey year from 2000 to 2006 was 92 seastars km^{-2} . In support of his hypothesis that *Acanthaster* outbreaks are linked to terrestrial runoff following heavy rains, Birkeland (1982) noted that outbreaks of *A. planci* have a significant tendency to occur around high islands and rarely around atolls. While it is still unclear what drives *Acanthaster* population surges, the observation of the rarity of outbreaks around atolls suggests Midway and other atolls in the NWHI may be unlikely to experience these destructive population eruptions.

Recruitment patterns can be an important factor affecting the future coral community, including changes in coral cover (Coles and Brown, 2007). 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 (Mundy, 2000). 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. Recruitment rates at Midway were among the lowest in the NWHI for all four deployments, and the average annual recruitment rate across all years was lowest at

Midway ($8.5 \pm$ recruits $m^{-2} yr^{-1}$ (SE 2.8)) (Dunlap and Kenyon, 2004; Kenyon, in press). All of the recruits tallied on Midway plates ($n = 24$) were pocilloporids, which is consistent with the taxonomic composition of the recruits throughout the NWHI (96.1% Pocilloporidae, 2.8% Acroporidae, 1.1% Poritidae) which, in turn, is disharmonic with the *Porites*-dominated composition of mature coral communities (Kenyon et al., 2006b; 2007a,b; 2008a,b). At all locations, the arrays of recruitment plates were deployed at similar depths (~ 10 m) at wave-sheltered sites near coral-populated substrate. At Midway, the plates were deployed adjacent to a patch reef composed of two adjacent pinnacles in the southeastern lagoon (see REA site in Fig. 1) where the low coral cover (1.2%) was dominated by *Porites compressa*. Further study of recruitment processes in these remote areas, from where little data exist, is needed to better understand the capacity of coral populations for renewal and replenishment.

Following more than a century of exposure to humans and their cargo, Midway hosts more than 200 alien species of terrestrial plants and numerous insects (Rooney et al., 2008). Despite the potential for the unintentional introduction of marine species through ships' hull fouling and ballast water discharge, a 1997 survey of invertebrate fouling communities on artificial substrates found only three invertebrate species considered to be nonindigenous in the Hawaiian Islands. No introduced invertebrates were found in natural habitats, and the threat to the native reef community by established nonindigenous species was considered minimal (DeFelice et al., 1998). Alien algae have not been reported from Midway (P. Vroom, pers. comm.).

Hawaii is an isolated archipelago with high levels of marine endemism (Kay and Palumbi, 1987), and its reefs may be especially vulnerable to local and global threats (Carpenter et al., 2008). Midway has been under the protection of federal resource management agencies since 1996, but the footprint of prior environmental rearrangements due to commercial and military activities appears to have been left in the distinctive reduction of coral cover relative to other locations in the NWHI, including those experiencing similar climatic and oceanographic regimes. The oceanographic setting of coral communities at Midway, particularly those in the back reef and lagoon habitats, is prone to thermally induced coral bleaching and accumulation of marine debris, disturbances with anthropogenic undercurrents despite the remoteness of the atoll from population centers. Conversely, stressors that have compromised coral populations elsewhere globally are not currently problematic at Midway: disease prevalence is low and spatially limited; no alien algae have been introduced; and the few introduced marine benthic invertebrates have not shown invasive characteristics. 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 coral communities at Midway Atoll in the decades to come.

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