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COMMUNITY STRUCTURE OF HERMATYPIC CORALS AT PEARL AND HERMES ATOLL, NORTHWESTERN HAWAIIAN ISLANDS: UNIQUE CONSERVATION CHALLENGES WITHIN THE HAWAIIAN ARCHIPELAGO

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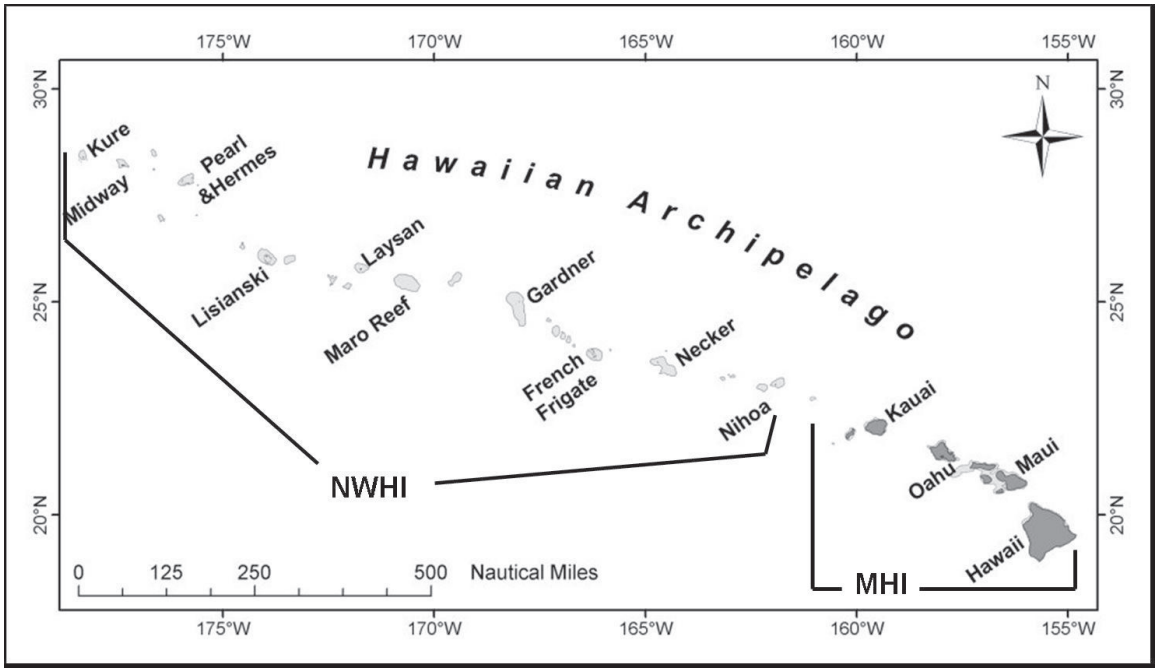

Figure 1. The Hawaiian Archipelago. NWHI = Northwestern Hawaiian Islands; MHI = main Hawaiian Islands. Lightly shaded areas represent 100-fathom isobaths.

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ABSTRACT

The distribution and abundance of scleractinian corals at Pearl and Hermes Atoll (PHA), Northwestern Hawaiian Islands, were determined by georeferenced towed-diver surveys that covered more than 85,000 m^2 of benthic habitat and site-specific surveys at 34 sites during 2000 – 2002. Three complementary methods (towed-diver surveys, videotransects, and photoquadrats) were used to quantify percent cover of corals by genus or species in the fore reef, back reef, lagoon, and channel habitats. Three genera —*Porites*, *Montipora*, and *Pocillopora*— account for 97% of the coral cover throughout the atoll, though their relative abundances vary considerably according to habitat and geographic sector within habitats. Fore-reef communities are dominated by massive and encrusting *Porites*, while the back reef is dominated by *Montipora* and the lagoon by *Porites compressa*. All taxa show habitat-specific differences in colony density and size-class distributions as assessed through colony counts within belt transects at fixed sites. These demographic data, which provide the most thorough quantitative description of the coral communities at PHA to date, are used to focus a discussion on risks of reef degradation from salient contemporary hazards, including bleaching, disease, marine debris, and *Acanthaster* predation. Coral communities at PHA may be the most vulnerable in the Hawaiian Archipelago to bleaching and accumulation of marine debris, thus warranting special management attention. These data also provide a detailed baseline to which population parameters determined from long-term monitoring surveys can be compared to assess the direction, pace, and drivers of change.

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INTRODUCTION

As a world-wide trend towards reef degradation continues (Gardner et al., 2003, Hughes et al., 2003, Bellwood et al., 2004, Palumbi 2005, Pandolfi et al., 2005, Hughes et al., 2005) and the differential responses of corals to various stressors become better known (Branham et al., 1971, Aeby 2004, Kenyon et al., 2006a, Kenyon and Brainard 2006), determining a reef's community composition becomes not just a descriptive exercise but a useful tool for assessing its risk to the influence of stressors (Kenyon et al., 2006 b,c). Conventional as well as emerging approaches to sustaining and repairing marine ecosystems, such as coral reefs, depend on knowledge of an ecosystem's biotic composition and the essential processes supported by key functional groups (Hughes et al., 2005). Hermatypic corals play a vital role in the development and maintenance of coral-reef ecosystems by providing the basic structural framework as well as the shelter and food requirements of numerous species that inhabit the reef (Grigg and Dollar 1980).

The Hawaiian Archipelago spans 2450 kilometers across the north Pacific from the island of Hawaii in the southeast (19° N 154° W) to Kure Atoll in the northwest (29° N 178° W) (Fig. 1). Originating over a relatively fixed point of upwelling lava ("hotspot") in the Pacific Plate, the islands, banks and atolls of the Archipelago have developed over at least 27 million years (Dalrymple et al., 1977) through gradual erosion and subsidence as they slowly drift to the northwest by sea-floor spreading (Wilson 1963, Grigg 1982, 1997). Grigg (1983) discerned several trends in coral community structure across the Hawaiian Archipelago, including a decrease in coral cover tending northward in the chain and a varying degree of dominance by species that are widely distributed throughout the chain. Grigg's surveys throughout the Archipelago were conducted primarily along southwest seaward reefs at depths close to 10 m, however, and do not necessarily characterize coral communities subject to different regimes of salient environmental parameters, including wave energy, temperature, light and sedimentation. In addition, more widespread surveys conducted by Maragos et al. (2004) throughout the Northwestern Hawaiian Islands (NWHI, Fig. 1) indicate that the relatively uniform species inventories reported by Grigg (1983) at southwest seaward sites simplify a richer and more spatially complex coral fauna. At Pearl and Hermes Atoll, for example, 12 species were observed by Grigg (1983) while 32 were reported by Maragos et al. (2004).

Detailed descriptions of the coral communities of individual islands, atolls and banks in the Hawaiian Archipelago have been limited historically by the vast shallow-water areas available for reef development relative to the resources available to characterize them. More than 1,350 km^2 of shallow (0–20 m) shelf area exist in the NWHI alone (NOAA, 2003; Parrish and Boland, 2004). In 2000, Presidential Executive Order No. 13178 (http://hawaiireef.noaa.gov) set in motion a process to extend federal management actions to submerged areas of the NWHI not included in extant state or federal mandates and rekindled a drive to assess more comprehensively the resources of the NWHI. Modern technologies, including GPS (global positioning system), GIS (geographic information system), digital imagery and remote sensing, have facilitated the development of methods by which benthic communities can be surveyed and characterized more extensively than was possible even a decade ago.

Along with Kure Atoll and Midway Atoll, Pearl and Hermes Atoll (PHA) is one of the three most northerly atolls in the NWHI (Fig. 1). In shallow-water (0-20 m) shelf area, PHA is second in size in the NWHI only to French Frigate Shoals, an open atoll farther south in the chain (407.2 vs. 468.5 km^2, respectively) (Parrish and Boland, 2004). Thirty-two species of scleractinian corals have been reported (Maragos et al., 2004) from the variety of habitats (e.g., fore reef, back reef, lagoon patch and reticulated reefs) delineated by the atoll's morphology. Recent research suggests that while coral communities at PHA are spared from considerable anthropogenic disturbance that frequently accompanies reefs close to population centers (e.g., pollution, dredging, nutrient overload), they may be the most vulnerable in the entire Hawaiian Archipelago to more indirect stressors such as thermally-induced bleaching (Kenyon et al., 2006a; Kenyon and Brainard 2006) and marine debris (Donohue et al., 2001, Boland and Donohue 2003, Dameron et al., 2006). This paper describes the community structure of the shallow-water (< 20 m) scleractinian corals at Pearl and Hermes Atoll, based on atoll-wide surveys conducted in 2000 – 2002 using three complementary methods. These data are then discussed in relation to other contemporary research at PHA that focuses on factors known to affect the physical condition of coral communities, including bleaching, disease, marine debris, and *Acanthaster* predation. They also serve as a detailed baseline for comparing results from ongoing monitoring activities that are part of a multi-agency effort to enhance long-term conservation and protection.

MATERIALS AND METHODS

Benthic Surveys

Towed-diver surveys were conducted in 2000 (25 September–5 October) and 2002 (18–28 September) according to the methods of Kenyon et al. (2006d). Laser-projected dots used to calibrate image size did not appear on videographic imagery recorded during 2002 surveys because of mechanical problems. Habitat digital videotapes were sampled at 30-sec intervals (inter-frame distance ~ 25m) and quantitatively analyzed for coral percent cover using the methods of Kenyon et al. (2005), in which the coral categories that could be distinguished were *Pocillopora*, massive and encrusting *Porites* (e.g., *P. lobata*, *P. evermanni*), *P. compressa*, *Montipora*, *Pavona*, and faviids. Average depth was calculated for 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 GPS and ArcView GIS 3.2.

Site-specific belt-transect surveys, along with digital video recording of benthic cover along the transect lines, were independently conducted by three separate teams of divers on 17–28 September 2002 according to the general methods described by Maragos et al. (2004) for 2002 Rapid Ecological Assessments. 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., 2006c.

Twelve (35 cm x 50 cm) photoquadrats were concurrently photographed with spatial reference to the same two 25 m transect lines (i.e., 6 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 videotransects are described in Kenyon et al., 2006c. The taxa that could be identified were *Pocillopora meandrina, P. eydouxi, P. damicornis, P. ligulata*, massive and encrusting *Porites (*e.g., *P. lobata, P. evermanni), Porites compressa, Montipora, Pavona, Fungia* and Faviidae. Detailed methods for determining coral percent cover from photoquadrat imagery are also presented in Kenyon et al., 2006c.

Transect site locations and tracks of towed-diver surveys georeferenced with non-differentially-corrected GPS units (Garmin® model 12) were mapped using ArcView GIS 3.2. For analytical purposes, towed-diver and site-specific surveys were grouped spatially according to habitat (fore reef, back reef, lagoon, channel) and geographic sector (N, NE, E, etc.).

Differences in total percent coral cover among habitats, and among sectors within habitats, were examined using one-way ANOVA or a *t*-test. Kruskal-Wallis or Mann-Whitney rank sum tests were used with percent cover data from surveys where the data were not distributed normally, even with transformations, or showed unequal variances. 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, aggregating all taxa other than *Porites*, *Pocillopora*, and *Montipora*. Statistical analyses were conducted using SigmaStat® software.

Maragos et al. (2004) provide two indices of the relative occurrence and abundance of 32 coral species at PHA based on qualitative Rapid Ecological Assessment surveys at 69 sites. Methods described in Kenyon et al., 2006c 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 sample frames captured at 30-sec intervals from benthic tow videos depends on the tow speed; the average inter-frame distance ranged from 19.1 m to 35.6 m (mean = 25.5 m, n = 43 tows). The average benthic area captured in laser-scaled frames was 4260 cm^2 (SE = 80 cm^2, n = 1052 frames). Towed divers surveyed 113.9 km of benthic habitat (Table 1, Fig. 2) of which 4251 captured 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 (4251 frames x 0.426m^2/frame = 1811 m^2) samples a total survey area of 85,843 m^2 (Table 1). Survey effort in 2000 emphasized the fore-reef habitat, as towed divers were able to work in conditions of high swell or strong current that were too extreme for roving divers to survey safely. Surveying the back-reef habitat was emphasized in 2002 so as to document a novel coral bleaching event in progress that was most pronounced in this habitat. Estimates of coral cover along the north fore reef and east back reef (Table 1) were derived from *in situ* diver observations rather than recorded imagery because of video camera problems during those surveys. Total average coral cover across the atoll was low-to-moderate, ranging from 5.2% at the southern end of the opening ("channel") on the western side of the atoll (Fig. 2) to 19.1% in the lagoon (Table 1, Fig. 3a). The differences among the four habitats in their average total percent coral cover were not significant statistically (Kruskal-Wallis test, $H = 7.24$, df = 3, $p = 0.65$). However, a significant difference existed among habitats in the relative abundance of coral genera present (chi-square test, $X^2 = 233.93$, df = 9, $p = 0.00$). 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* co-dominated the back-reef habitat, along with lesser and roughly equal proportions of *Pocillopora* and *Porites*. Lagoon assemblages were dominated by *Porites compressa* (Table 1, Fig. 3a).

The average coral cover across 40,095 m^2 surveyed along the fore reef was 6.8% (Table 1). Although the differences among the average total percent coral cover in the seven video-recorded fore-reef sectors were not significant statistically (Kruskal-Wallis test, $H = 10.92$, df = 6, $p = 0.09$), there were significant differences among sectors in the relative abundance of coral genera present (chi-square test, $X^2 = 249.40$, df = 18, $p = 0.00$). With the exception of south and southwestern exposures, *Porites* dominated all fore-reef sectors, usually accounting for more than two-thirds of the coral cover. Pocilloporids dominated south and southwestern exposures and were the next most dominant member of the coral fauna on all other fore-reef sectors. The most varied coral fauna was found along the southwest sector, where *P. compressa* and *Pavona* each made a modest contribution (7–9% of total) to coral cover. *Montipora* and faviids contributed little to coral cover on the fore reef (Table 1, Fig. 3a).

The average coral cover across 30,900 m^2 surveyed along the back reef was 10.5% (Table 1). Although the differences among the average total percent coral cover in the seven video-recorded back reef sectors were not significant statistically (Kruskal-Wallis test, $H = 9.54$, df = 6, $p = 0.145$), there were significant differences among sectors in the relative abundance of coral genera present (chi-square test, $X^2 = 708.42$, df = 18, $p = 0.00$). Patterns of coral dominance by geographic sector were more variable in the back-reef habitat than in the fore-reef habitat. North, northeast and southwest back-reef exposures were dominated by *Montipora*; northwest and west exposures were dominated by *Porites*; south and southeast exposures were dominated by *Pocillopora* (Table 1). The most varied coral fauna was found along the west sector where *P. compressa* and *Pavona* each made a modest contribution (10 – 14% of total) to coral cover. Faviids contributed little to coral cover on the back reef (Table 1, Fig. 3a).

Table 1. Coral Cover determined from Towed-Diver Surveys done at Pearl and Hermes Atoll, Northwestern Hawaiian Islands, 2000 - 2002.

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	*Porites compressa*	*Pocillopora*	*Montipora*	*Pavona*	Faviidae
Fore Reef	ALL	53.2	40095	4.6 - 15.4	6.8	69.8	3.0	23.1	1.1	2.4	0.6
	NW	8.8	6632		5.5	87.7	0.3	8.6	0.4	2.8	0.2
	N	2.8	2110		27.5[c]	NA	NA	NA	NA	NA	NA
	NE	5.0	3768		24.2	89.8	2.1	4.9	1.0	2.1	0.1
	E	7.4	5577		5.9	71.2	1.1	27.1	0.4	0.2	0.0
	SE	7.6	5728		2.0	54.1	3.0	42.9	0.0	0.0	0.0
	S	9.7	7310		2.9	21.4	4.4	74.2	0.0	0.0	0.0
	SW	9.3	7009		7.5	38.0	7.8	42.3	3.1	8.6	0.2
	W	2.6	1960		7.7	98.4	0.0	0.7	0.0	0.8	0.1
Back Reef	ALL	41.0	30900	0.5 - 4.0	10.5	28.4	6.8	24.2	36.9	3.5	0.2
	NW	2.6	1960		7.7	77.7	13.2	7.0	1.4	0.7	0.0
	N	7.2	5426		17.6	9.1	3.2	22.7	65.0	0.0	0.0
	NE	2.7	2035		11.7	3.9	12.8	3.9	79.4	0.0	0.0
	E	2.8	2110		2.4[c]	NA	NA	NA	NA	NA	NA
	SE	3.6	2713		2.8	16.4	0.0	83.6	0.0	0.0	0.0
	S	6.0	4522		3.6	8.6	3.3	85.9	0.0	2.1	0.1
	SW	5.2	3919		11.0	13.6	0.1	38.3	45.4	2.5	0.1
	W	10.9	8215		10.7	61.6	13.1	13.0	1.6	10.6	0.1
Lagoon	ALL	17.1	12888	3.2 - 11.0	19.1	0.3	99.4	0.2	0.1	0.0	0.0
	E	14.4	10853		22.2	0.2	99.7	0.0	0.1	0.0	0.0
	W	2.7	2035		0.3	33.4	3.5	63.1	0.0	0.0	0.0
Channel	W	2.6	1960	9.4	5.2	19.3	0.2	68.4	10.4	1.8	0.0

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

[b] Proportions are graphically presented by habitat in Figure 3*a*.

[c] Estimates are from in situ diver observations

The average coral cover across 12,888 m^2 surveyed in the lagoon habitat was 19.1% (Table 1). Although the differences between the average total percent coral cover in the east and west lagoon sectors were not significant (Mann-Whitney rank sum test, $T = 1.00$, $p = 0.29$), there were significant differences in the relative abundance of coral taxa (chi-square test, $X^2 = 187.35$, df = 2, $p = 0.00$). Nearly all (99.7%) of the coral cover in the eastern lagoon was *Porites compressa*, whereas both *Pocillopora* and massive and encrusting *Porites* comprised most of the sparse coral cover in the western lagoon (Table 1, Fig. 2).

Coral cover along the single tow survey conducted in the opening ("channel") on the western side of the atoll (Fig. 2) was low (5.2%), and consisted mainly of *Pocillopora* (Table 1).

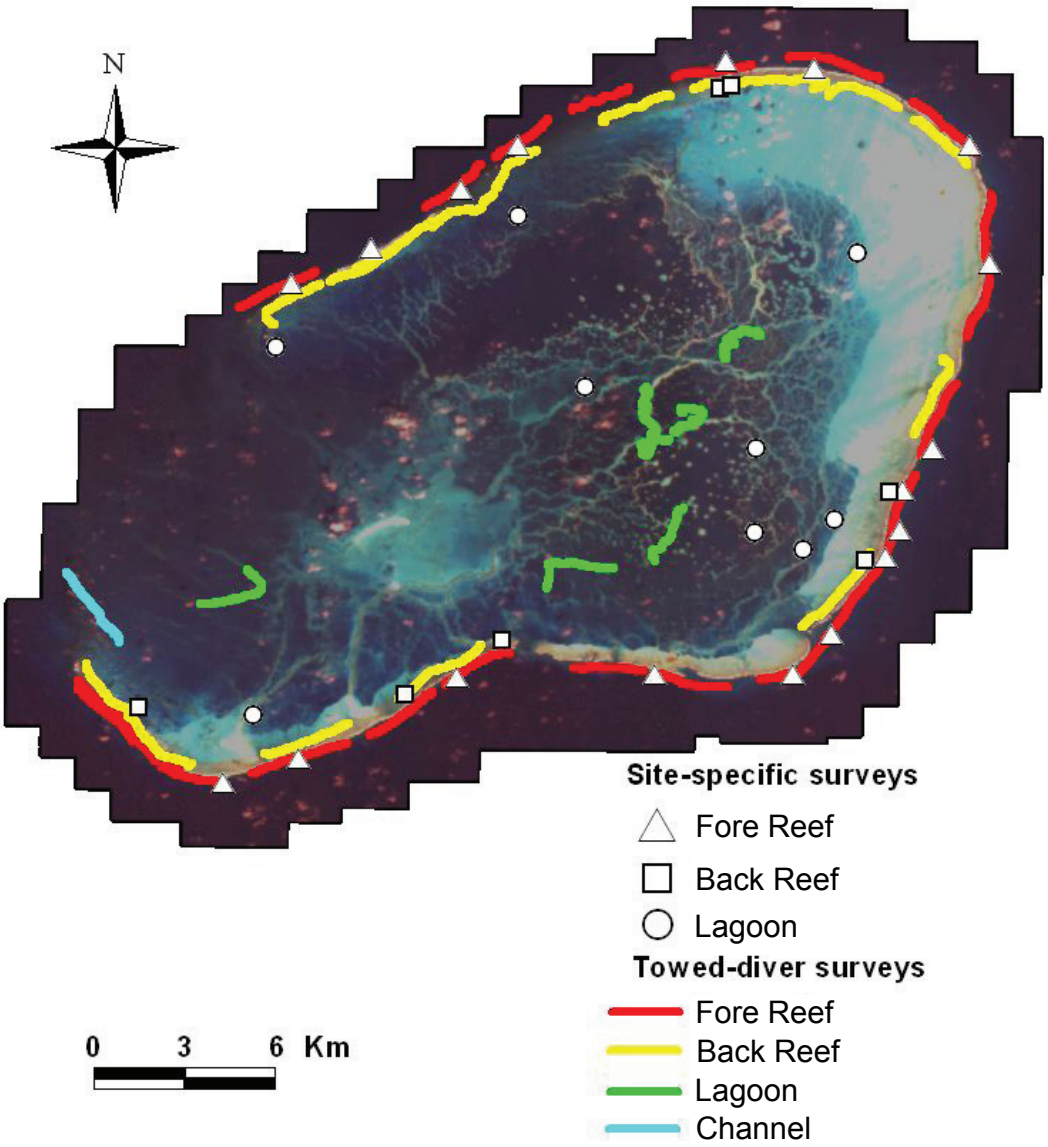

Figure 2. Location of towed-diver and site-specific surveys at Pearl and Hermes Atoll, NWHI, using IKONOS satellite imagery as a basemap.

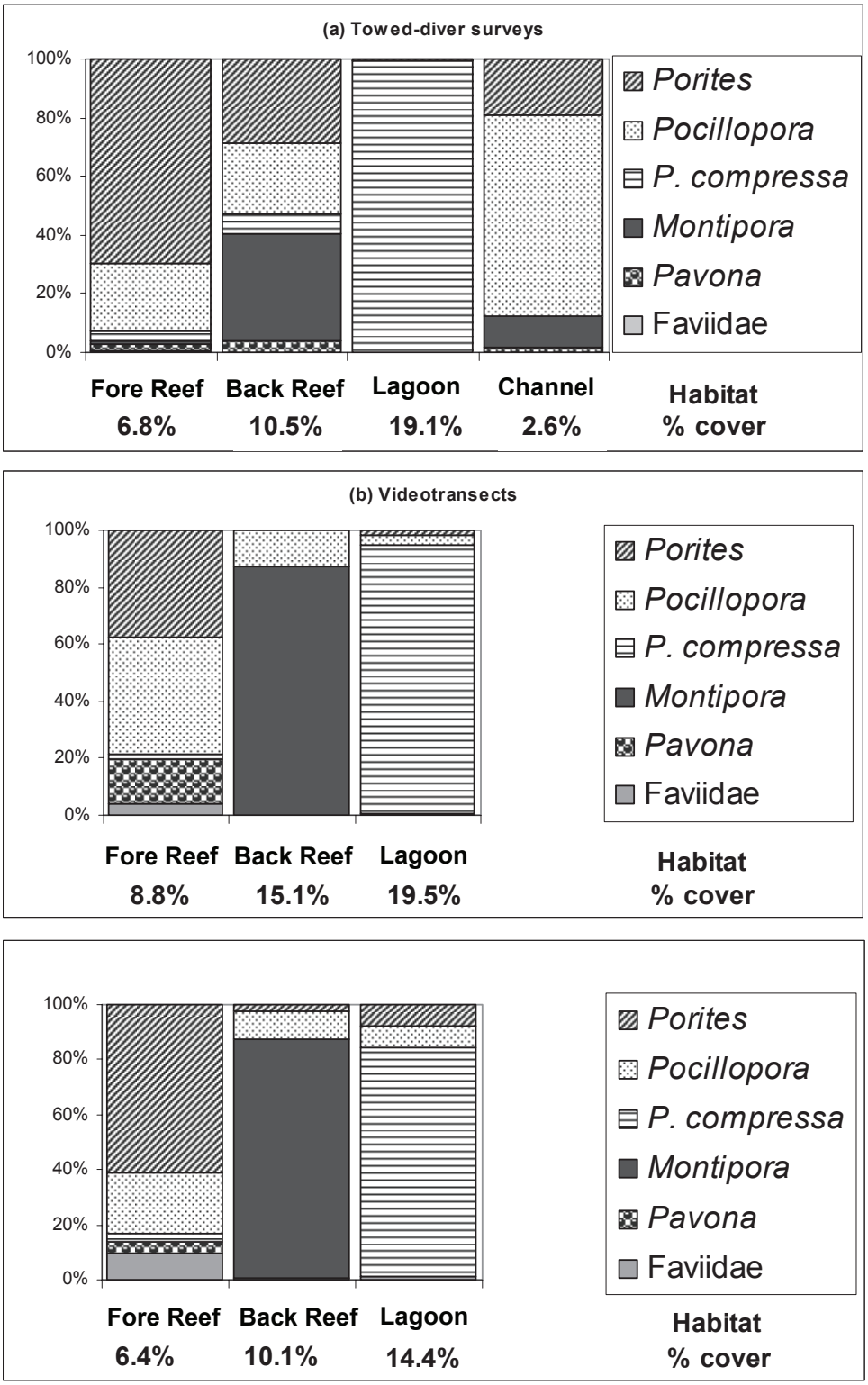

Figure 3. *a – c.* Relative abundance of primary coral taxa by habitat at Pearl and Hermes Atoll, NWHI, derived from three different methods. Values below habitat labels are total coral percent cover within each habitat. *Porites* = massive and encrusting *Porites*.

Site-specific Surveys: Video Transects

A total of 800 m^2 at 25 sites (32 m^2/site) was quantitatively assessed from transect videotapes. Overall coral cover was lowest on the fore reef (8.8%) with progressively greater cover on the back reef (15.9%) and lagoon (19.5%) (Table 2, Fig. 3b). The differences among the three habitats in their average total percent coral cover were not statistically significant (one-way ANOVA, $F = 1.07$; df = 2, 22; $p = 0.36$).

Nine scleractinian taxa were seen in PHA video transects (*Pocillopora meandrina*, *P. eydouxi*, *P. ligulata*, *P. damicornis*, massive and encrusting *Porites*, *P. compressa*, *Montipora*, *Leptastrea*, *Pavona duerdeni*). A significant difference existed among the three habitats in the relative abundance of coral taxa present (chi-square test, $X^2 = 360.22$, df = 6, $p = 0.00$). The fore-reef habitat was co-dominated by pocilloporids and by poritiids with massive and encrusting growth forms (Table 2, Fig. 3b). Of the four distinguishable species of *Pocillopora* present in video transects, *P. meandrina* comprised 92.3% of the total pocilloporid cover throughout the atoll. The back-reef habitat was dominated by *Montipora*. Similar to results from towed-diver surveys, the lagoon was dominated by *Porites compressa* (Table 2, Fig. 3b) and faviids contributed little to coral cover in all habitats (Table 2, Fig. 3b). *Pavona* was most abundant on the fore-reef habitat.

Site-specific Surveys: Photoquadrats

Video transects and photoquadrats were recorded concurrently at 25 sites with an additional nine sites surveyed for percent cover by photoquadrats alone. Of the 25 sites where both methods were applied, the maximum difference in total coral cover calculated with the two methods was 14.7%; the average of the absolute values of the difference between video transect and photoquadrat total coral cover was 4.9%. Overall coral cover was lowest on the fore reef (6.4%) with progressively greater cover on the back reef (10.1%) and the lagoon (14.4%) (Table 2, Fig. 3c). The differences among the three habitats in their average total percent coral cover were not significant statistically (Kruskal-Wallis test, $H = 0.967$, df = 2, $p = 0.62$).

Fourteen scleractinian taxa were seen in PHA photoquadrats (Table 3). A significant difference existed among the three habitats in the relative abundance of coral taxa present (chi-square test, $X^2 = 284.77$, df = 6, $p = 0.00$). Relative abundances of coral taxa derived from photoquadrat methods in back-reef and lagoon habitats were highly similar to those derived from videotransect methods (Table 2, Fig. 3b,c). The fore-reef habitat was co-dominated by poritiids with massive and encrusting growth forms and by pocilloporids (Table 2, Fig. 3c). Of the four species of *Pocillopora* present in photoquadrats, *P. meandrina* comprised 83.1% of the total pocilloporid cover and *P. ligulata* comprised 12.0% of the cover throughout the atoll using this method. *Pavona* and faviids contributed relatively little to coral cover in all habitats but were best represented on the fore reef (Table 2, Fig. 3c).

Table 2. Coral Cover determined from Video Transects and Photoquadrats done at Pearl and Hermes Atoll, Northwestern Hawaiian Islands, in 2002.

Habitat	No. of Sites Surveyed	Average Total % Coral Cover[a]	Range of Transect Depths (m)	Proportion of Total Coral Cover[b]					
				Massive & encrusting *Porites*	*Porites compressa*	*Pocillopora*	*Montipora*	*Pavona*	Faviidae
Video transects									
Fore Reef	12	8.8	9.7 - 16.4	37.6	1.6	40.9	0.3	15.4	4.2
Back Reef	5	15.1	1.2 - 7.9	0.3	0.0	12.3	87.3	0.0	0.1
Lagoon	8	19.5	2.7 - 8.8	1.9	94.2	3.3	0.2	0.4	0.0
Photoquadrats									
Fore Reef	18	6.4	8.5 - 18.3	61.0	3.1	21.7	0.0	4.2	9.6
Back Reef	7	10.1	0.9 - 8.3	2.1	0.0	10.2	87.4	0.0	0.4
Lagoon	9	14.4	2.4 - 10.7	7.8	82.9	7.8	0.0	0.3	1.0

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

A total of 4188 colonies were counted and classified by size class within belt transects covering 1950 m^2 at 31 sites. *Porites* was the most numerically abundant (i.e., highest density) taxon across the atoll system followed by *Pocillopora*, Faviidae, *Montipora* and *Pavona* (Fig. 4, All Habitats). Only 40 colonies of *Fungia* and *Psammocora* (<1% of total) were not in these taxa. Relative densities of coral taxa followed a similar pattern within the fore-reef and lagoon habitat as across the atoll system (Fig. 4); i.e., in both habitats, *Porites*, followed by *Pocillopora* and faviids, was the most numerically abundant taxon. In the back-reef habitat, however, *Porites* was the least abundant taxon with substantially fewer colonies than *Montipora* or *Pocillopora*. Highest overall colony density occurred on the fore reef (3.7 colonies/m^2) and lowest on the back reef (0.5 colonies/m^2).

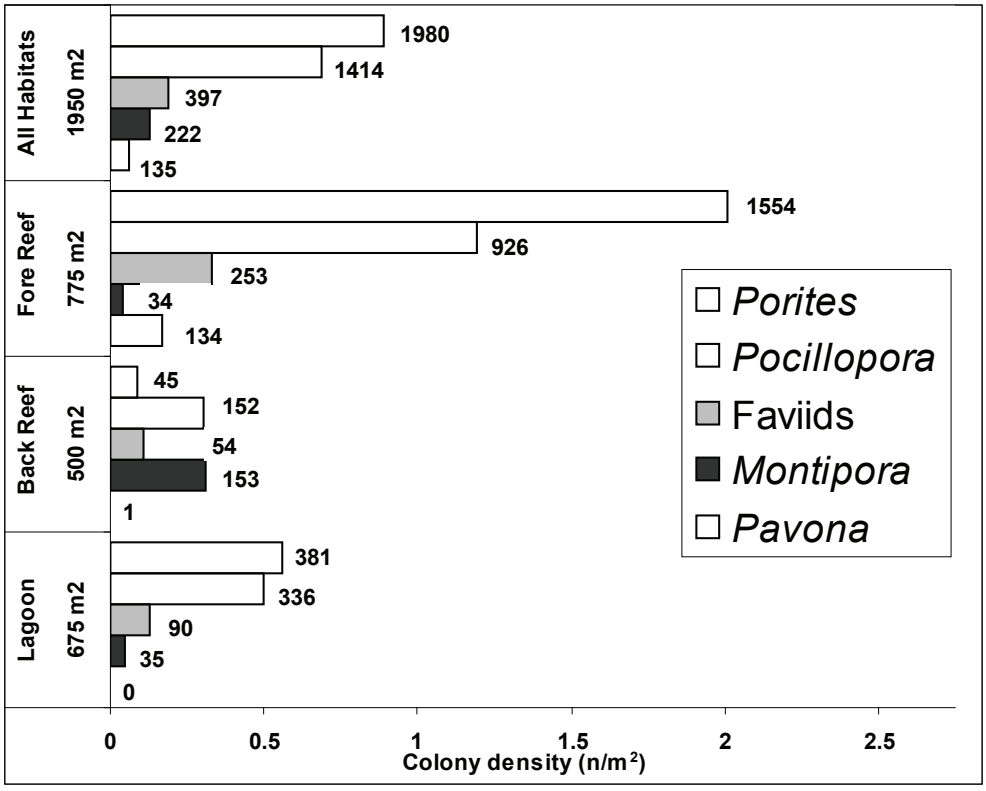

Figure 4. Colony density (n/m^2) of five coral taxa at Pearl and Hermes Atoll, NWHI, in the lagoon, back reef, fore reef, and the three habitats combined. Number of colonies (n) were determined from belt transect surveys; area (m^2) surveyed in each habitat is shown next to habitat label. Values to the right of bars are the number of colonies of each taxon.

Coral communities at PHA are primarily composed of small colonies; nearly three-quarters (72.7%) of all colonies measured < 20 cm maximum diameter. Although most taxa had distinctive size-class distributions in different habitats (Figs. 5, 6, 7), only *Montipora* in the back-reef habitat had more than 50% of colonies measuring > 20 cm maximum diameter (Fig. 6b).

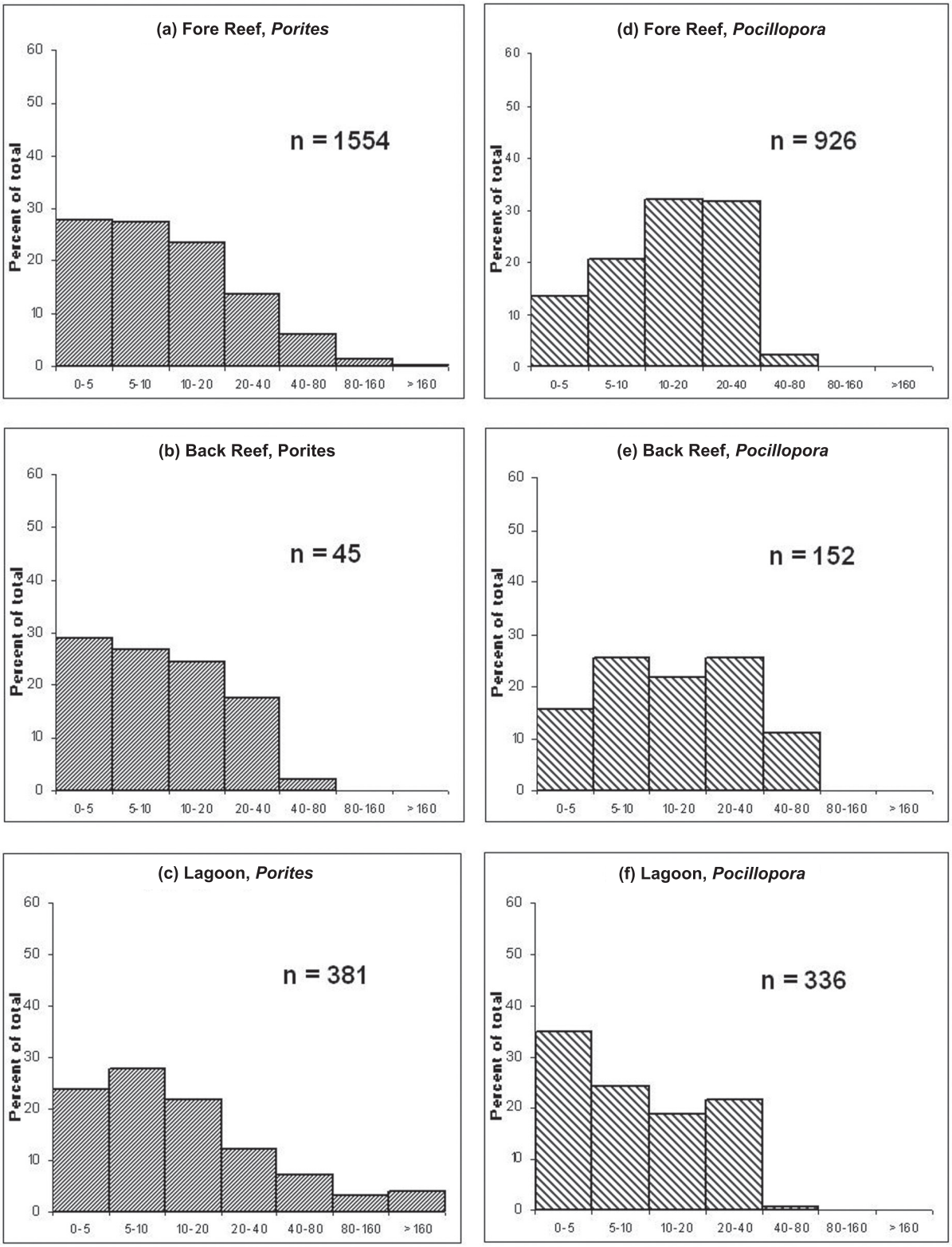

Figure 5. Size class (cm) distributions, by habitat, of scleractinian corals at Pearl and Hermes Atoll, NWHI. *a – c Porites*, *d-f Pocillopora*.

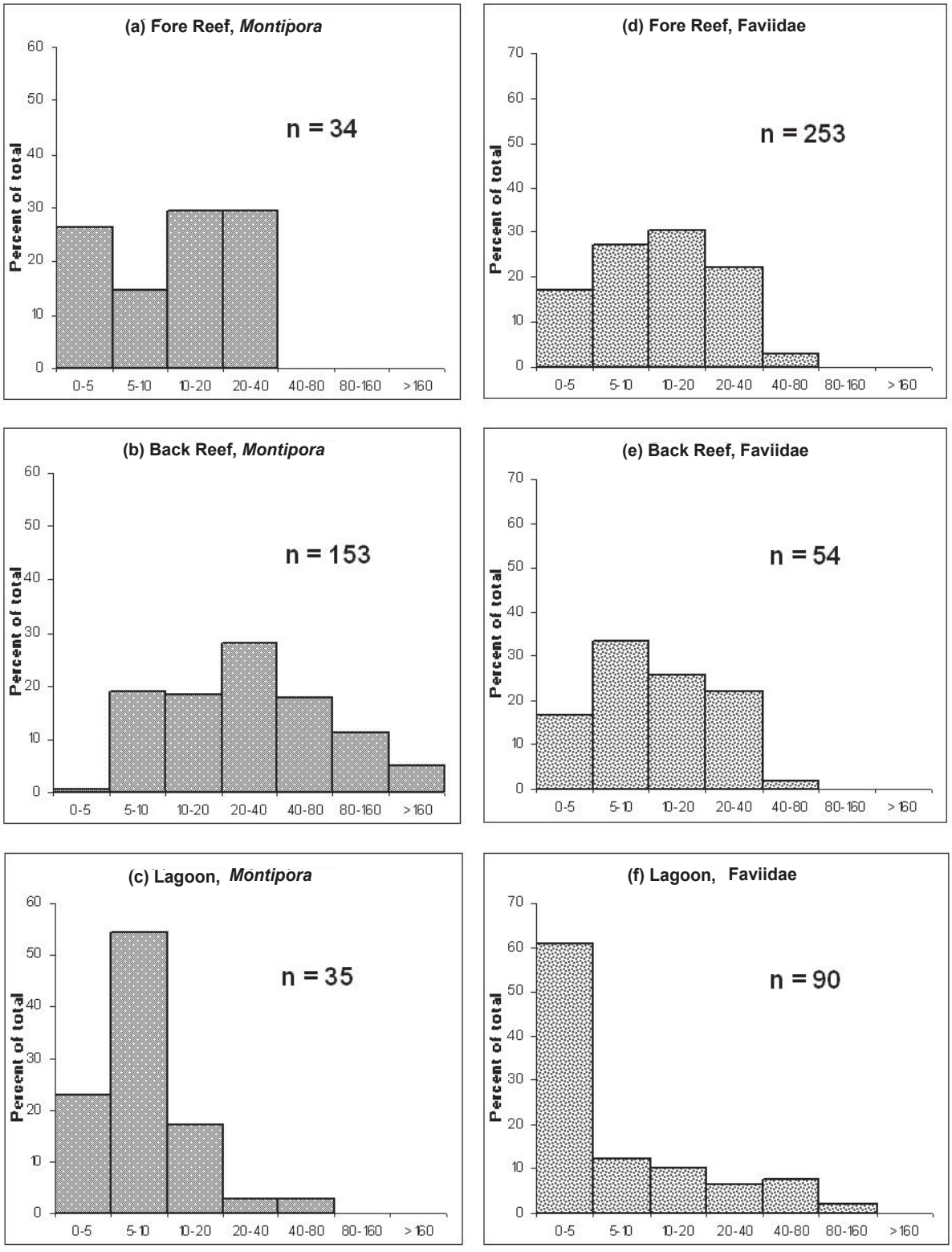

Figure 6. Size class (cm) distributions, by habitat, of scleractinian corals at Pearl and Hermes Atoll, NWHI. *a – c Montipora*, *d-f* Faviidae.

Porites' size-class distributions on the fore reef and back reef are highly similar (Fig. 5a, b) despite the taxon's disparate representation in the two habitats both in coral cover (Fig. 3) and density (Fig. 4). In the lagoon, this genus is largely represented by *P. compressa* (Fig. 3), whose tendency to form large thickets by clonal propagation (Hunter 1993) accounts for the increased proportions in larger-size classes (Fig. 5c).

Pocilloporids are more dense (Fig. 4) and make a greater contribution to coral cover (Fig. 3) on the fore reef than on the back reef or in the lagoon. Their density is lowest on the back reef, but a greater proportion of larger (> 20 cm maximum diameter) colonies is found here compared to other habitats (Fig. 5d–f).

Montiporids dominate the back reef both in terms of density (Fig. 4) and contribution to coral cover (Fig. 3) but are rare on the fore reef and lagoon (Fig. 3, 4). On the back reef, as noted above, the proportion of *Montipora* colonies in larger size classes (> 20 cm maximum diameter) exceeds that of other taxa throughout the atoll.

More than 75% of faviids in all habitats measure < 20 cm maximum diameter (Fig. 6d–f); their small size and low densities (Fig. 4) account for their small contribution to total coral cover.

At belt-transect survey sites, *Pavona* (primarily *P. duerdeni*) was only common enough on the fore reef to construct a size-class distribution (Fig. 7). There, the taxon ranked second only to back reef *Montipora* in the proportion of colonies measuring > 20 cm diameter (43.3% vs. 62.1%, respectively).

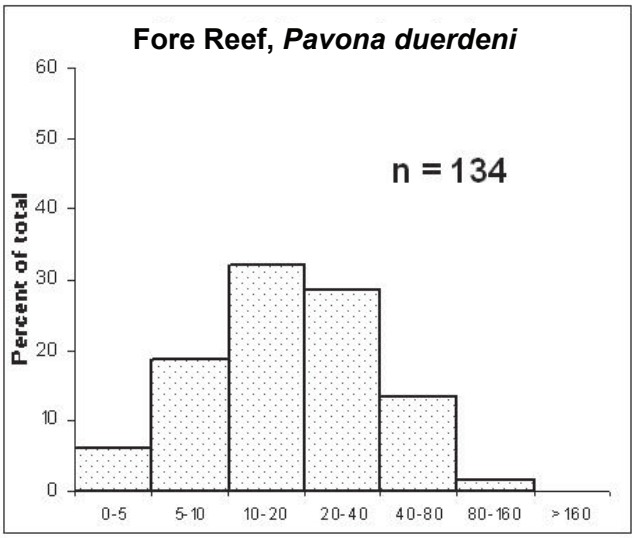

Figure 7. Size class (cm) distribution of Pavona in the fore-reef habitat at Pearl and Hermes Atoll, NWHI. Too few colonies were found in other habitats to construct distributions.

DISCUSSION

Comparison with Previous Surveys

The three survey methods used in the present study produced highly congruent patterns in the atoll-wide distribution and abundance of coral taxa. The chief discrepancy among the methods in coral cover was found in the back-reef habitat where videotransects and photoquadrats yielded similar results but overestimated *Montipora* compared to towed-diver surveys (Tables 1, 2, Fig. 3). The dominance of *Porites* with massive and encrusting growth forms on the fore reef (Tables 1, 2, Fig. 3) is consistent with the top ranking of *Porites lobata* by Maragos et al. (2004) and by Grigg (1983) along the southwest fore reef (Table 3), but in the present study back-reef and lagoon habitats were dominated by *Montipora* and *Porites compressa*, respectively.

Table 3. Relative Abundance of Coral Species at Pearl and Hermes Atoll Ranked by Photoquadrats in This Study, in Maragos et al. (2004), and in Grigg (1983)

Rank	This Study	Maragos et al. (2004)	Grigg (1983)
1	*Porites lobata*	*Porites lobata*	*Porites lobata*
2	*Porites compressa*	*Pocillopora damicornis*	*Porites compressa*
3	*Montipora capitata*	*Porites compressa*	*Pavona duerdeni*
4	*Pocillopora meandrina*	*Leptastrea purpurea*	*Pocillopora meandrina*
5	*Montipora flabellata*	*Pocillopora ligulata*	*Montipora verrucosa* [a]
6	*Leptastrea purpurea*	*Pocillopora meandrina*	*Leptastrea purpurea*
7	*Pocillopora ligulata*	*Cyphastrea ocellina*	N.A.[b]
8	*Pavona duerdeni*	*Montipora capitata*	N.A.[b]
9	*Pocillopora damicornis*	*Psammocora stellata*	N.A.[b]
10	*Pocillopora eydouxi*	*Fungia scutaria*	N.A.[b]
11	*Pavona varians*	*Porites evermanni*	N.A.[b]
12	*Fungia scutaria*	*Montipora flabellata*	N.A.[b]
13	*Psammocora stellata*	*Montipora turgescens*	N.A.[b]
14	*Cyphastrea ocellina*	*Pavona varians*	N.A.[b]

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

[b] Not available; data only provided for 6 species by Grigg (1983).

Grigg (1983) reported a mean coral cover of 19% from two 50-m seaward transects off the southwest sector of PHA. This value is consistent with coral cover obtained from videotransects and photoquadrats at one southwest fore-reef site in our study (21.9% and 17.1%, respectively). However, Grigg's value is high relative to the average coral cover (7.5%) obtained from analysis of 9.3 km surveyed by towed-divers along the southwest fore reef (Table 1, Fig. 2) as well as coral cover obtained from photoquadrats at a second southwest fore-reef site (6.3%). These comparisons highlight the need for broad survey coverage in characterizing a habitat.

Galtsoff (1933), working primarily in the lagoon with samples collected by free-divers and observing from the surface through a glass-bottom box, recorded nine coral species: *Porites lobata*, *P. compressa*, *Pocillopora ligulata P. damicornis*, *P. meandrina*, *Montipora verrucosa*, *M. verrilli*, *Pavona varians*, and *Cyphastrea ocellina*. Grigg (1983) reported 12 species from southwest seaward reefs (Table 3). Maragos et al. (2004) reported 32 species from 69 survey sites but provided no demographic data pertaining to their distribution across the atoll. In the present study, 14 species were distinguished in photoquadrats (Table 3). Of these 14 species, 11 are included among the top 14 species ranked with the use of occurrence and abundance indices developed by Maragos et al. (2004) (Table 3). All six species recorded by Grigg (1983) on southwest seaward reefs were observed in photoquadrats in the present study.

In comparing coral abundance throughout the Hawaiian Archipelago, Grigg (1983) noted that "the most significant difference in community structure between islands in the archipelago as represented by stations off southwest exposures is the degree of dominance by individual species". The present study, along with analyses of coral community structure at French Frigate Shoals (FFS) reported by Kenyon et al. (2006c), supports Grigg's statement and extends it to additional exposures and habitats. With the exception of *Acropora*, which had not been observed at PHA (Grigg 1981, Maragos et al., 2004, this study) until 2006 (Kenyon et al., unpublished data), the same suite of species are the major contributors to coral community structure, but their relative abundances as assessed through percent cover and density vary between these two atolls. At both atolls, massive and encrusting *Porites* along with *Pocillopora* dominate or co-dominate all sectors of the fore reef. *Montipora*, rare at FFS, dominates several back-reef sectors at PHA. Lagoon reefs at PHA are largely made up of *Porites compressa*, which is much less prevalent on FFS lagoon reefs than massive and encrusting *Porites*.

Unique Challenges

Jokiel and Rodgers (2005) 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. PHA along with Lisianski (Fig. 1) ranked second to FFS in this integrated index of reef condition. Much of PHA's composite score derived from its top scores in the reef-fish biomass and endemism categories, whereas it ranked 12th in the coral-cover category. While this ranking implies that PHA is presently among the least disturbed reef systems in the Hawaiian Archipelago, due in part to distance from population centers, recent research suggests its coral communities are the most vulnerable in the Archipelago to stressors, including mass coral bleaching and marine debris accumulation, whose reaches extend well beyond populated areas.

Mass coral bleaching occurred on reefs throughout the NWHI in 2002 and 2004; in both years, the incidence of bleaching was highest at PHA (Kenyon et al., 2006a, Kenyon and Brainard 2006). Bleaching was most pronounced in the back-reef habitat where 97% of M*ontipora* and *Pocillopora* colonies examined during 2002 surveys (n =

340) at PHA showed bleached tissue, as did 71% of colonies in these genera examined during 2004 surveys (n = 727). Both mass bleaching episodes coincided with periods of prolonged, elevated sea-surface temperatures (SST) detected by satellite remote sensing and *in situ* temperature recorders (Hoeke et al., 2006a,b; Kenyon and Brainard 2006). Analyses of historical SST datasets show a warming trend in the Hawaiian Archipelago (Jokiel and Brown 2004, Barton and Casey 2005) that is most pronounced at the northern end of the chain, suggesting the frequency and severity of thermally induced bleaching events may increase in the Hawaii region (Jokiel and Brown 2004) with shallow back reef corals at PHA potentially the most vulnerable. Quantification of coral mortality from the 2002 bleaching event, as assessed through photoquadrat analysis of sites surveyed in both 2002 and 2004, indicated a decrease of live *Montipora* cover by as much as 20% at some PHA back-reef sites (P. Vroom and J. Kenyon, unpublished data). The size class distribution of *Montipora* from back-reef sites surveyed in 2004 (n = 350 colonies) is also more right-skewed (J. Kenyon, unpublished data) than the 2002 distribution (n = 153, Fig. 6c), as partial mortality effectively fissions a genet into multiple ramets, which in following years become counted as separate, smaller colonies.

Elevated temperatures and associated bleaching have been shown to increase the incidence of numerous opportunistic coral diseases (Harvell et al., 1999, Kuta and Richardson 2002, Rosenberg and Ben-Haim 2002), which can contribute significantly to coral-reef degradation (Santavy et al., 2005). Six disease syndromes affecting *Porites*, *Pocillopora*, or *Montipora* have been documented at PHA (Aeby 2006). During surveys conducted throughout the NWHI in 2005, ~ 4% of colonies examined at PHA showed signs of disease with the highest prevalence of diseased colonies (~ 7%) at Maro Reef (Fig. 1). These levels are low compared to the main Hawaiian Islands (Aeby et al., 2006) and may represent baseline levels of coral disease normally found in an undisturbed system. Populations weakened by further stressors, such as additional bleaching events, could experience increased disease levels with deleterious consequences to the ecosystem as has occurred in the Caribbean and Florida Keys over the past two decades (Santavy et al., 2005).

Derelict fishing gear causes substantial damage to reefs throughout the NWHI (Donohue et al., 2001). Debris originating from North Pacific fisheries may accumulate in the region of the NWHI because of their location in a convergence zone associated with the North Pacific subtropical high (Kubota 1994, Brainard et al., 2000). Driven over northeast-facing reefs in the NWHI by prevailing winds, the debris begins a cycle of destruction, snagging on reefs, breaking off coral through wind-driven water motion, snagging and damaging additional coral, and so on. Most reef-hung derelict fishing gear occurs in shallow (< 10 m) water (Donohue et al., 2001). Based on quantified removal efforts at PHA and Lisianski (Fig. 1) in 1999, Donohue et al. (2001) suggested the oceanic convergence zone associated with the North Pacific subtropical high may intersect PHA more frequently than Lisianski, resulting in more debris accumulation at PHA. Re-survey of areas at Kure Atoll, PHA and Lisianski in 2001 that were cleaned of marine debris in 2000 indicated the highest accumulation rate (number of items/km^2/year) occurred at Kure Atoll (Boland and Donohue 2003) followed in order by PHA and Lisianski. Both studies focused on small areas (< 1.3 km^2) at each location frequently

used by endangered Hawaiian monk seals (*Monachus schauinslandi*) and did not purport to quantify accumulation rates on larger scales or in habitats characterized by different regimes of bathymetry, rugosity, or wave energy.

Marine debris removal efforts undertaken by NOAA's Coral Reef Ecosystem Division over more extensive areas including a greater diversity of habitats in the NWHI from 1999-to-2006 have removed 560 metric tons of fishing debris which includes 295 metric tons from PHA (R. Brainard, unpublished data). Weight analysis of debris removed in 2005 from shallow areas (< 4.5 m) that were cleaned of marine debris in 2004 at PHA and Kure Atoll indicates the mean accumulation density (kg/km^2) in areas of reticulated lagoon reef is ~ 2.5 times greater than accumulation in areas with a deeper, more homogeneous reef structure that are closer to a barrier reef (Dameron et al., 2006). When accumulation rates in these two types of "net habitat" are coupled to the area of each habitat in the NWHI, PHA emerges as the location with the greatest predicted future accumulation (kg/yr) of derelict fishing gear. PHA's predisposition to high accumulation densities derives both from the large area occupied by the labyrinth of shallow reticulated reefs in the eastern lagoon and the broad expanse of barrier reef exposed to prevailing northeast winds. Moreover, visual assessment of net density fields at PHA generated from plots of net locations reveals that nets tend to accumulate along the northeast and southwest back reef as well as a linear expanse of reticulated lagoon reefs extending from northwest to southeast across the atoll (Dameron et al., 2006). Examination of submerged debris during removal activities at PHA in 2002 and 2003 showed that live coral had recruited on or grown within the mesh of 32% of debris items (n = 4434) (Asher and Timmers 2004). Consistent with coral abundance data in the present study, *Montipora* and *Pocillopora* were the primary genera found on derelict gear from the back reef, and *Porites* and *Pocillopora* were prevalent on debris recovered from reticulated lagoon reefs.

The corallivorous sea-star *Acanthaster planci* occurs naturally at low densities on Hawaiian reefs (Chess et al., 1997) and only a single large-scale aggregation has been reported from Hawaii (Branham et al., 1971). While factors regulating population levels remain controversial, outbreaks have occurred in areas far from agricultural, industrial and urban development and can have significant ecosystem effects (Birkeland 1982, 1989). *In situ* observations of non-cryptic *Acanthaster* during towed-diver surveys conducted throughout the NWHI between the years 2000 and 2003 indicated their highest frequency of occurrence was at PHA relative to other atolls (1.9/tow) (Timmers et al., 2004). When different habitats within atolls were compared, frequency of sightings was highest on the fore reef, with the highest fore-reef frequency at PHA and Midway Atoll (3.8/tow). In the main Hawaiian Islands, *Montipora* and *Pocillopora* were reported as preferred prey by Branham et al. (1971) and Chess et al. (1997), respectively, even when more abundant *Porites* was present. Keenan et al. (2004) report more than 500 *Acanthaster* sightings during tows conducted in search of marine debris in the lagoon and back reef at PHA in 2003 and that the sea stars were commonly feeding on *Porites*. PHA might therefore be at greatest risk in the NWHI for sustaining future outbreaks given the extant highest frequency of *Acanthaster* at this location and the abundance, in different habitats, of all three genera reported as preferred *Acanthaster* prey in Hawaii.

The shallow-reef systems discussed in the present study politically come within

overlapping jurisdictions of the state of Hawaii and the U.S. Fish and Wildlife Service's National Wildlife Refuge system. Submerged lands seaward of state and other federal authority in the NWHI were given additional federal oversight through the creation of the NWHI Marine National Monument by presidential proclamation in 2006 (http://www.whitehouse.gov/news/releases/2006/06/20060615-18.html). Renewed political interest in the NWHI has accelerated the pace of scientific investigation in this remote region and helped generate the means by which long-term assessment and monitoring of biological resources and environmental parameters are being conducted. Demographic coral data shown in the present study and interpreted within the context of known risks to habitat integrity suggest that shallow-water (< 20 m) coral communities at PHA are especially vulnerable to stressors that have led to reef degradation in other regions and may therefore warrant special management attention. Our data serve as a detailed baseline to which population parameters along specific tow tracks and at 15 long-term monitoring sites established in 2003 can be compared in future years to better understand the direction, pace, and drivers of change.

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