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COMMUNITY STRUCTURE OF HERMATYPIC CORALS AT KURE ATOLL IN THE NORTHWESTERN HAWAIIAN ISLANDS:STEMMING THE SHIFTING BASELINE

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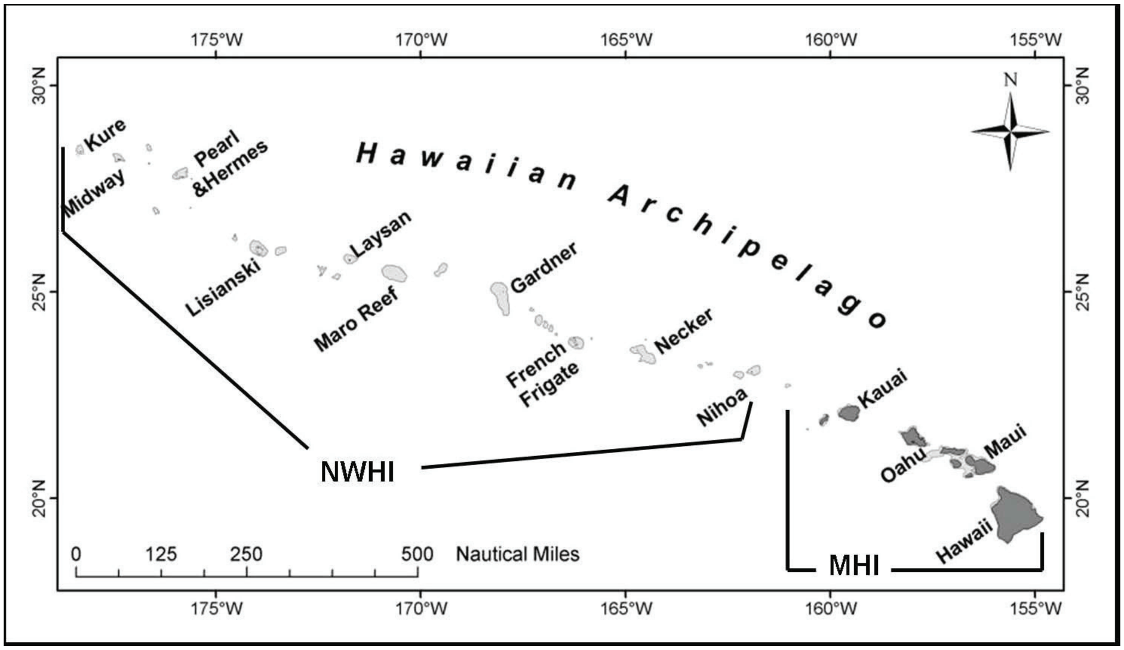

Figure 1. The Hawaiian Archipelago. NWHI = Northwestern Hawaiian Islands; MHI = main Hawaiian Islands. Lightly shaded areas represent 100-fathom isobaths.

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JEAN C. KENYON,[1] MATTHEW J. DUNLAP,[1] AND GRETA S. AEBY[2]

ABSTRACT

The distribution and abundance of scleractinian corals at Kure Atoll in the Northwestern Hawaiian Islands was determined by georeferenced towed-diver surveys that covered close to 27,000 m^2 of benthic habitat and site-specific surveys at 21 sites during 2000–2003. Three complementary methods (towed-diver surveys, video transects, and photoquadrats) were used to quantify percent cover of corals by genus or species in the fore-reef, back-reef, and lagoon habitats. Three genera, *Porites*, *Pocillopora,* and *Montipora*, accounted for more than 99% of the coral cover throughout the atoll, although their relative abundances vary considerably according to habitat and geographic sector within habitats. Fore-reef communities are dominated by massive and encrusting *Porites* and by *Pocillopora*, 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 provide the most detailed, spatially comprehensive description of coral communities at Kure Atoll produced to date and can serve as a solid baseline for determining the magnitude and direction of future changes. They are discussed within the context of factors known to affect community development on Hawaiian coral reefs including temperature, wave stress, coral bleaching and other diseases, marine debris, and crown-of-thorns seastars.

INTRODUCTION

As coral reefs worldwide are increasingly challenged by global phenomena such as climate change and ocean acidification (Hughes et al., 2003; Pandolfi et al., 2003; Kleypas et al., 2006), it becomes increasingly important to establish detailed quantitative baselines by which subsequent changes can be discerned. Pauly (1995) introduced the phrase "shifting baseline syndrome" in connection with fisheries, but the concept applies equally well to other marine ecosystem resources, including coral reefs (Birkeland,

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2004). In this view, each generation accepts as a baseline the conditions of its own experience and uses it to evaluate changes; in degrading systems, this results over time in a gradual accommodation to disappearing resources and inappropriate reference points for assessing losses. Detailed quantitative data, particularly those based on rigorous, repeatable analyses of durable photographic images that can be archived for inspection by other researchers, provide an invaluable benchmark for later comparisons. Technological advances over the past decade in digital imagery, data extraction software, global positioning system (GPS), geographic information system (GIS), and remote sensing have enabled the acquisition and analysis of descriptive data by which such benchmarks can be generated. Management agencies are in particular need of comprehensive, reliable documentation of the status of public resources for which they serve as stewards.

In 2006, Papahānaumokuākea Marine National Monument was established by U.S. Presidential Proclamation, opening a new era of management authority in the Northwestern Hawaiian Islands (NWHI) following nearly a century of various management regimes by Hawaii state and U.S. federal agencies. Kure Atoll (28^{o}25′N, 178^{o}20′W) is the northernmost atoll in the Hawaiian Archipelago (Fig. 1) and the world (Dana, 1971). Of the four atolls with perimeter reef in the Hawaiian Archipelago (French Frigate Shoals, Pearl and Hermes, Midway, and Kure) (Fig. 1), Kure is the second smallest, with an estimated shelf (< 20 m depth) area of 66.4 km^2 (Parrish and Boland, 2004). Like other coral reef systems in the NWHI, Kure has a checkered history of human interaction but has largely been spared from the anthropogenic activities implicated in the deterioration of many coral reefs worldwide (e.g., Done, 1992; Nyström et al., 2000). Nonetheless, the documentation of large quantities of destructive marine debris (Donohue et al., 2001; Donohue and Boland, 2003; Dameron et al., 2007) and two episodes of thermally induced coral bleaching over the past decade (Aeby et al., 2003; Kenyon et al., 2006a; Kenyon and Brainard, 2006) are indicative of the potential vulnerability of even remote locations to the consequences of modern human activities. Along with coralline algae, corals are major framework builders of modern Holocene reefs in Hawaii (Gross et al., 1969; Grigg, 1998) and their abundance and condition are often used as indicators of the health status of reefs (Pandolfi et al., 2005; Jokiel and Rodgers, 2007). Hence it is critical to establish a detailed, spatially comprehensive baseline of coral community structure at Kure Atoll that can be used by both present and future generations of stakeholders as a quantitative reference point from the early years of the 21st century.

Previous work on corals at Kure Atoll has been presented by Dana (1971), Grigg (1983), Maragos et al. (2004), and Siciliano (2006). This paper describes the community structure of the shallow-water (< 20 m) scleractinian corals at Kure Atoll, based on atoll-wide surveys conducted in 2000–2003. It differs from the work of previous authors in that it (a) uses three independent yet complementary methods of estimating live coral cover, (b) is more spatially inclusive, (c) provides density and size class data as well as percent cover data as metrics of community structure, and (d) is based on analysis of archived photographic imagery that is available for inspection and reanalysis. As such, it provides the most comprehensive portrait of extant coral communities at Kure Atoll produced to date and can serve to offset the “conceptual ratchet” (Birkeland, 2004) of a shifting baseline. These data are then discussed in the context of salient contemporary stressors known to affect the composition and condition of NWHI coral communities.

MATERIALS AND METHODS

Benthic Surveys

Towed-diver surveys were conducted in 2000 (2–3 October) and 2002 (23–24 September) according to the methods of Kenyon et al. (2006b). An additional survey was conducted in 2003 (4 August) to examine the south back reef, which had not been assessed on earlier surveys. On 2000 and 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 survey, 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 2000 and 2002 were sampled at 30-sec intervals (interframe distance ~ 22 m) and quantitatively analyzed for coral percent cover using the methods of Kenyon et al. (2006b). 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), 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 videographic imagery recorded during 2002 or 2003 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 GPS and ArcView GIS 3.3.

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 22–26 September 2002, according to the general methods described by Maragos et al. (2004) for 2002 Rapid Ecological Assessments. Three additional sites were surveyed with the same suite of methods on 4 August 2003. 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., 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. (2006c). The taxa that could be identified were *Pocillopora meandrina, P. damicornis, P. ligulata*, *Porites lobata, P. compressa, Montipora capitata,* and *Montipora* sp. 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 nondifferentially-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, and lagoon) and geographic sector (N, NE, E, etc.).

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 31 coral species at Kure Atoll based on qualitative Rapid Ecological Assessment surveys at 54 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 frames sampled at 30-sec intervals from benthic tow videos or still images depends on the tow speed; the average interframe distance ranged from 16.4 m to 27.5 m (mean = 22.3 m, *n* = 18 tows). The average benthic area captured in laser-scaled frames was 3556 cm^2 (SE = 77 cm^2, *n* = 1124 frames). Towed divers surveyed 39.1 km of benthic habitat (Table 1, Fig. 2), from which 1764 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 (1764 frames x 0.3356m^2/frame = 592 m^2) samples a total survey area of 26,923 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 and hardbottom lagoon habitats was emphasized in 2002 so as to document a novel coral bleaching event in progress that was most pronounced in these habitats.

Table 1. Coral cover determined from towed-diver surveys conducted at Kure 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 *Porites*	*Porites compressa*	*Pocillopora*	*Montipora*	Other coral
Fore reef	ALL	24.2	16663	10.5–16.4	9.7	57.1	0.1	41.0	1.1	0.7
	NW	2.2	1515		15.6	30.3	0.0	68.3	0.0	1.4
	N	2.8	1928		15.7	44.8	0.0	49.4	5.5	0.3
	NE	3.8	2617		11.3	65.4	0.0	32.5	1.2	0.9
	E	2.6	1790		10.4	90.4	1.2	7.6	0.0	0.9
	SE	2.0	1377		2.4	100.0	0.0	0.0	0.0	0.0
	S	5.7	3925		5.4	87.4	0.0	12.6	0.0	0.0
	SW	2.6	1790		7.2	49.3	0.0	50.7	0.0	0.0
	W	2.5	1721		16.0	28.3	0.0	70.6	0.0	1.2
Back reef	ALL	12.5	8607	0.7–1.4	10.8	11.2	0.6	27.0	60.8	0.4
	NW	2.3	1584		24.2	11.0	0.0	17.1	71.9	0.0
	N	2.5	1721		7.3	21.5	1.4	45.4	31.1	0.5
	NE	2.4	1653		5.8	15.5	5.2	79.3	0.0	0.0
	E	2.3	1584		3.2	23.1	0.0	76.9	0.0	0.0
	S	1.9	1308		2.8	48.2	0.0	44.6	0.0	7.2
	W	1.1	757		21.2	0.2	0.0	7.6	92.2	0.0
Lagoon	ALL	2.4	1653	1.2	18.6	1.8	84.3	9.4	3.0	1.5

[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 Fig. 3a.

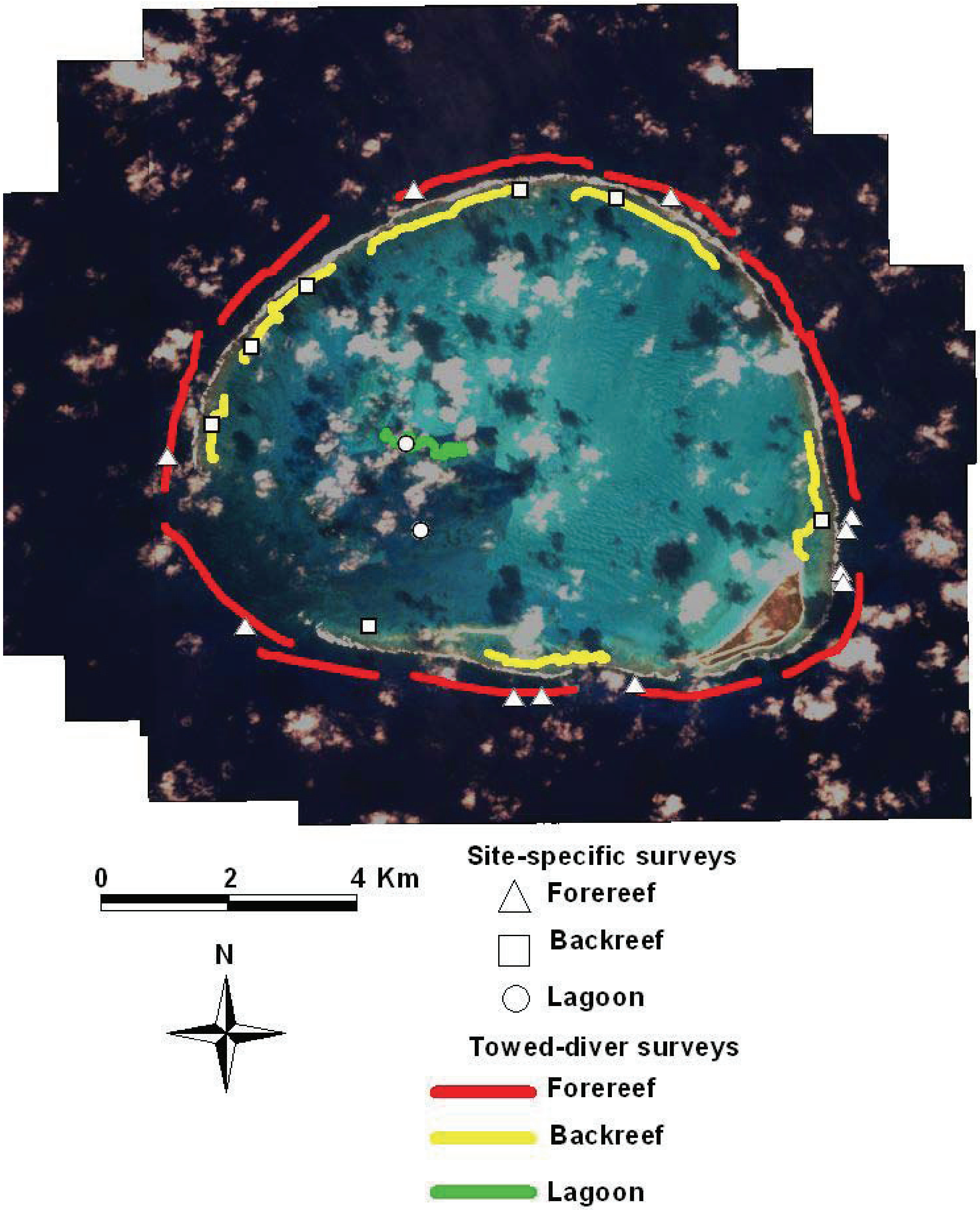

Figure 2. Location of towed-diver and site-specific surveys at Kure Atoll, NWHI, using IKONOS satellite imagery as a basemap. Irregular white and gray shapes overlying the lagoon are clouds and their shadows.

Average total coral cover across the atoll was low-to-moderate, ranging from 2.4% on the southeast fore reef to 24.2% on the northwest 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, $H = 40.02$, df = 2, $p < 0.001$). Moreover, a significant difference existed among habitats in the relative abundance of coral genera present (chi-square test, $X^2 = 366.45$, df = 6, $p < 0.001$). 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*) and by *Pocillopora*. *Montipora* dominated the back-reef habitat. Lagoon assemblages were dominated by *Porites compressa* (Table 1, Fig. 3a).

The average coral cover across 16,663 m^2 surveyed along the fore reef was 9.7% (Table 1). The differences among the eight fore-reef sectors in the average total percent coral cover were statistically significant (Kruskal-Wallis test, $H = 184.59$, df = 7, $p < 0.001$), and there were significant differences among sectors in the relative abundance of coral genera present (chi-square test, $X^2 = 231.60$, df = 7, $p < 0.001$). Total coral cover was highest along the arc of the fore reef proceeding counterclockwise from the north to the west sector, where *Pocillopora* dominated. Total coral cover was less in the southwest sector, where *Pocillopora* codominated with massive/encrusting *Porites*. Relatively lower coral cover was found along the arc of the fore reef proceeding counterclockwise from the south to the northeast sector, where massive/encrusting *Porites* accounted for nearly two-thirds or more of the coral cover. *Porites compressa*, *Montipora*, and other taxa contributed little to coral cover on the fore reef (Table 1, Fig. 3a).

The average coral cover across 8,607 m^2 surveyed along the back reef was 10.8% (Table 1). The differences among the six back reef sectors in the average total percent coral cover were statistically significant (Kruskal-Wallis test, $H = 160.97$, df = 5, $p < 0.001$), and there were significant differences among sectors in the relative abundance of coral genera present (chi-square test, $X^2 = 376.83$, df = 10, $p < 0.001$). Total coral cover was highest (> 21%) in the northwest and west back-reef sectors, where *Montipora* dominated. Total coral cover was lower (< 8%) in all other sectors, with varying patterns of dominance. *Pocillopora* dominated in the northeast and east sectors and codominated with massive/encrusting *Porites* in the south sector. No single genus clearly dominated on the north back reef. *Porites compressa* and other taxa contributed little to coral cover on the back reef (Table 1, Fig. 3a).

The average coral cover across 1,653 m^2 surveyed over hardbottom in the lagoon habitat was 18.6% (Table 1, Fig. 3a), where *Porites compressa* dominated (84.3% of total coral cover.)

Site-specific Surveys: Video Transects

A total of 576 m^2 at 18 sites (32 m^2/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, $H = 23.31$, df = 2, $p < 0.001$). Average total coral cover was lowest on the back reef (8.1%) with progressively greater cover on the fore reef (8.7%) and lagoon (9.8%) (Table 2, Fig. 3b).

Eight scleractinian taxa were seen in Kure video transects (*Pocillopora meandrina*, *P. ligulata*, *P. damicornis*, *Porites lobata*, *P. compressa*, *Montipora capitata, Montipora* sp.*, Pavona duerdeni*). The differences among the three habitats in their relative abundance of coral taxa were statistically significant (chi-square test, $X^2 = 237.27$, df = 6, $p < 0.001$). The fore reef was dominated by pocilloporids (Table 2, Fig. 3b). Of the three distinguishable species of *Pocillopora* present in video transects, *P. meandrina* composed 92.1% of the total pocilloporid cover throughout the atoll. The back reef was dominated by *Porites lobata*, with lesser and roughly equal amounts of *Pocillopora* and *Montipora*. Similar to results from towed-diver surveys, the lagoon was dominated by *Porites compressa* (Table 2, Fig. 3b).

Site-specific Surveys: Photoquadrats

Video transects and photoquadrats were recorded concurrently at 18 sites with an additional 3 sites surveyed for percent cover by photoquadrats alone. Of the 18 sites where both methods were applied, the maximum difference in total coral cover calculated with the two methods was 9.5%; the average of the absolute values of the difference between video transect and photoquadrat total coral cover was 3.0%. The differences among the three habitats in their average total percent coral cover were statistically significant (Kruskal-Wallis test, $H = 8.22$, df = 2, $p = 0.016$). Average total coral cover was lowest on the fore reef (6.4%) with progressively greater cover on the back reef (6.8%) and lagoon (12.4%) (Table 2, Fig. 3c).

Ten scleractinian taxa were seen in Kure photoquadrats (Table 3). The differences among the three habitats in their relative abundance of coral taxa were statistically significant (chi-square test, $X^2 = 266.52$, df = 6, $p < 0.001$). The fore reef and back reef were dominated by *Porites lobata* (Table 2, Fig. 3b). Representation by *Pocillopora* was highest on the fore reef (42.8% of total), while representation by *Montipora* was highest on the back reef (14.4% of total). Of the three distinguishable species of *Pocillopora* present in photoquadrats, *P. meandrina* composed 80.8% of the total pocilloporid cover throughout the atoll using this method. Similar to results from towed-diver surveys and video transects, the lagoon was dominated by *Porites compressa* (Table 2, Fig. 3b).

Table 2. Coral cover determined from video transects and photoquadrats conducted at Kure Atoll, NWHI, in 2002 and 2003.

Habitat	# Sites surveyed	Average total % coral cover[a]	Range of transect depths (m)	Proportion of total coral cover[b]				
				Porites lobata	*Porites compressa*	*Pocillopora*	*Montipora*	Other coral
Video transects								
Fore reef	8	8.7	9.1–15.7	37.6	0.0	62.4	0.0	0.0
Back reef	7	8.1	1.5–3.3	50.4	0.0	26.0	23.6	0.0
Lagoon	3	9.8	0.6–6.7	7.1	70.5	14.4	8.0	0.0
Photoquadrats								
Fore reef	11	6.6	9.9–16.0	57.2	0.0	42.8	0.0	0.0
Back reef	7	6.8	0.6–3.9	58.6	0.0	25.6	14.4	1.4
Lagoon	3	12.4	0.6–8.5	0.0	85.2	9.4	5.4	0.0

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

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

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

A total of 4022 colonies were counted and classified by size class within belt transects covering 1500 m^2 at 23 sites. *Porites* was the most numerically abundant (i.e., highest density) taxon across the atoll system followed by *Pocillopora*, Faviidae, and *Montipora*. (**Fig. 4**, All Habitats). Only 38 colonies of *Pavona*, *Fungia* and *Psammocora* (< 1% of total) were not in these taxa. Relative densities of coral taxa followed a similar pattern within the fore-reef habitat as across the atoll system (Fig. 4); i.e., *Porites*, followed by *Pocillopora* and faviids, was the most numerically abundant taxon. In the back-reef and lagoon habitats, however, *Pocillopora* had the highest densities, followed by *Porites*. Highest overall colony density occurred on the fore reef (4.2 colonies m^{-2}) with lower and roughly equal colony densities in the bck-reef (1.5 colonies m^{-2}) and lagoon (1.6 colonies m^{-2}) habitats.

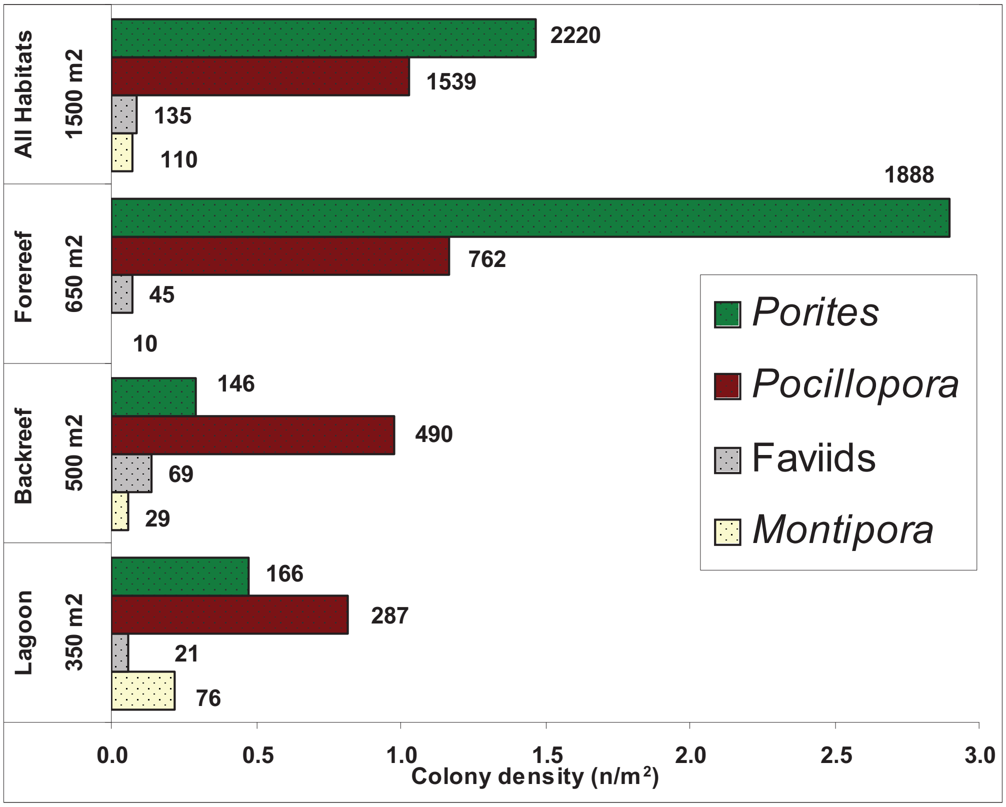

Figure 4. Colony density (no. m^{-2}) of four coral taxa at Kure Atoll, NWHI, in the lagoon, back reef, fore reef, and the three habitats combined. Number of colonies (n) were determined from belt transect surveys; area (m^2) surveyed in each habitat is shown next to habitat label. Values to the right of bars are the number of colonies of each taxon.

Coral communities at Kure Atoll are primarily composed of small colonies; nearly three-quarters (72.5%) of all colonies being < 20 cm maximum diameter. Although most taxa had distinctive size-class distributions in different habitats (Figs. 5, 6), only *Porites* in the back-reef habitat had more than 50% of colonies measuring > 20 cm maximum diameter (Fig. 6a).

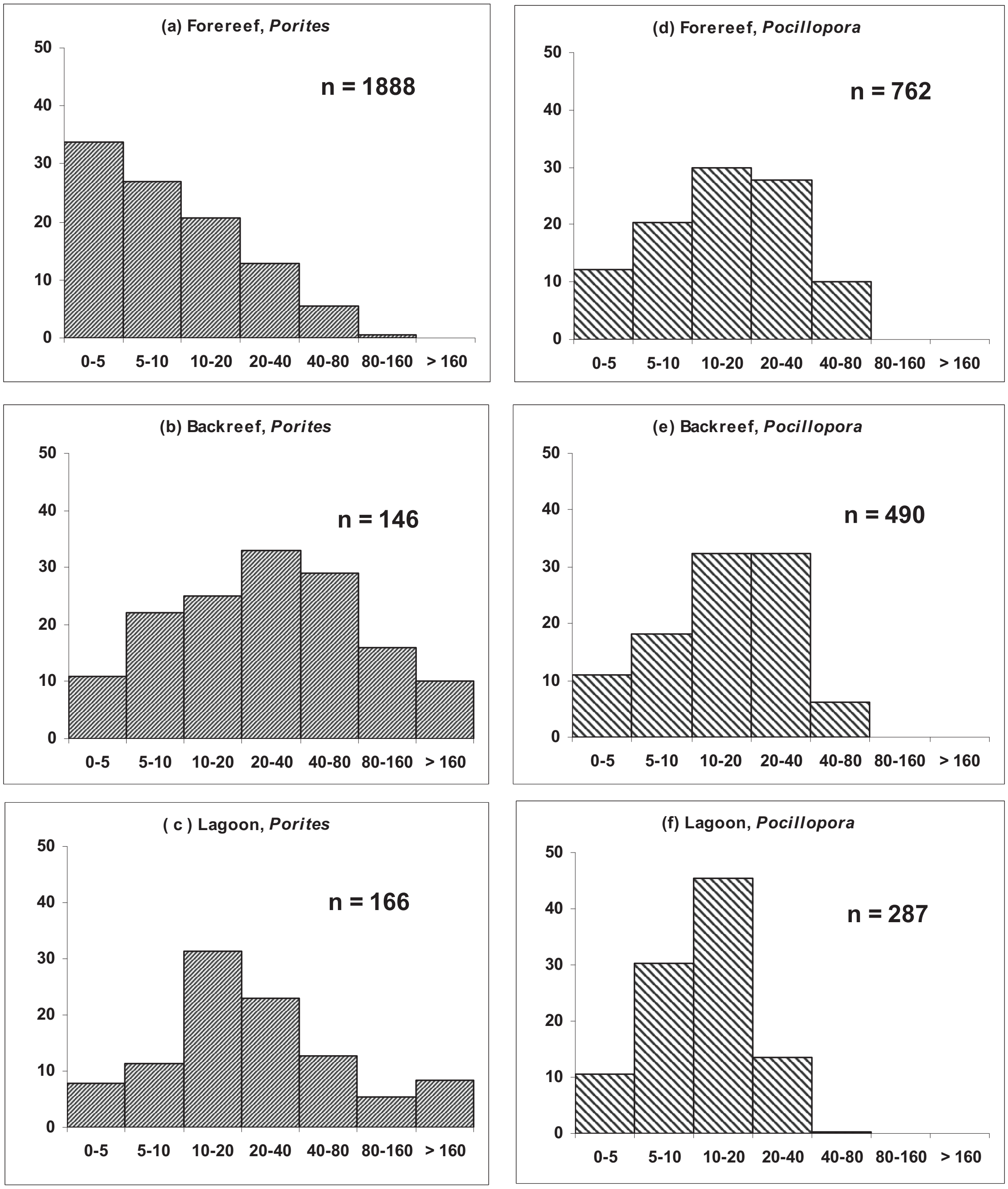

Figure 5. Size class (cm) distributions, by habitat, of scleractinian corals at Kure Atoll, NWHI. a–c *Porites*, d–f *Pocillopora*. Y-axis is percent of colonies enumerated in each taxon.

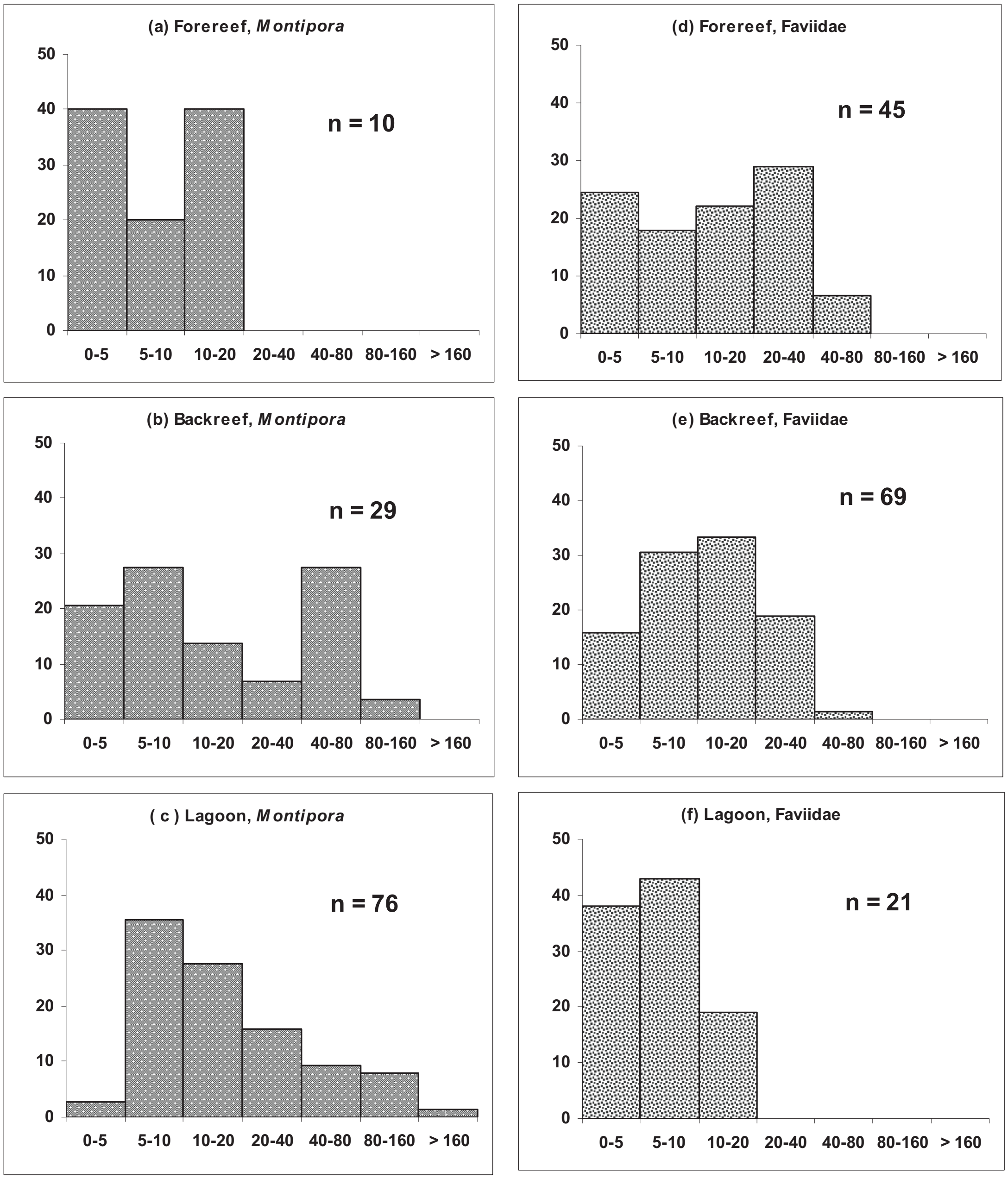

Figure 6. Size class (cm) distributions, by habitat, of scleractinian corals at Kure Atoll, NWHI. a–c *Montipora*, d–f Faviidae. Y-axis is percent of colonies enumerated in each taxon.

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).

Size class distributions of *Pocillopora* are similar on the fore reef and back reef (Figs. 5a,b), as are their colony densities (1.2 and 1.0 colonies m^{-2}, respectively, Fig. 4). Pocilloporids are more sparsely distributed (i.e., less dense) (Fig. 4) and smaller (Fig. 5c) in the lagoon habitat.

Montiporids are small (Fig. 6a) and rare (Figs. 3,4) on the fore reef. In both the back reef and lagoon habitat, a moderate proportion of the colonies were > 20 cm maximum diameter (37.9% and 34.2%, respectively)(Figs. 6b,c). While their density is highest in the lagoon (Fig. 4), their contribution to coral cover is greatest in the back-reef habitat (Fig. 3).

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 (Fig. 3).

DISCUSSION

Synopsis of Salient Results

The three survey methods used in the present study produced highly 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 coral cover was found in the lagoon habitat where estimates derived from towed-diver surveys (18.6%) were nearly twice as great as those derived from video transects (9.8%) (Tables 1,2). With regards to relative abundance, the chief discrepancy among the methods was found in the proportion of *Montipora* reported in the back-reef habitat from towed-diver surveys (60.8%) compared to estimates derived from video transects (23.6%) and photoquadrats (14.4%) (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 and relative abundance across large expanses of habitat than do site-specific surveys. Highest coral cover values derived from towed-diver surveys were found, in descending order, in the central lagoon, the northwest and west back reef, and the arc of fore reef proceeding counterclockwise from north to west. As assessed from atoll-wide towed-diver surveys, the fore reef was codominated by massive and encrusting forms of *Porites* and by *Pocillopora* while the back reef was dominated by *Montipora*, though dominance patterns varied by geographic sector. All three methods showed that lagoon patch reefs were dominated by *Porites compressa*.

Comparison with Previous Surveys

Dana (1971), who conducted numerous nonquantitative snorkel surveys in all three habitats at Kure, reported 17 coral species. Grigg (1983) reported 13 species from southwest seaward reefs. Maragos et al. (2004) reported 31 species from 54 survey sites but provided no demographic data pertaining to their distribution across the atoll. In the present study, 10 species were distinguished in photoquadrats (Table 3); one additional species (*Pavona duerdeni*) was seen in a single video-transect frame. Of these 11 species, 8 are included among the top 11 species ranked with the use of occurrence and abundance indices developed by Maragos et al. (2004) (Table 3). Three of the four 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 Kure Atoll 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 lobata*	*Porites compressa*
2	*Pocillopora meandrina*	*Pocillopora ligulata*	*Porites lobata*
3	*Porites compressa*	*Pocillopora damicornis*	*Pocillopora meandrina*
4	*Montipora capitata*	*Pocillopora meandrina*	*Porites (Synarea) convexa*[a]
5	*Pocillopora ligulata*	*Leptastrea purpurea*	N.A.[b]
6	*Pocillopora damicornis*	*Porites compressa*	N.A.[b]
7	*Montipora flabellata*	*Cyphastrea ocellina*	N.A.[b]
8	*Leptastrea purpurea*	*Psammocora stellata*	N.A.[b]
9	*Psammocora stellata*	*Montipora capitata*	N.A.[b]
10	*Cyphastrea ocellina*	*Pocillopora cf. capitata*	N.A.[b]

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

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

The first scientific description of Kure coral communities (Dana, 1971) affords several interesting comparisons with the present study. Dana (1971) noted that Kure is located in the northeast trade wind belt, allowing each reef habitat a windward and leeward aspect. Dana (1971) observed that *Pocillopora meandrina* dominated on seaward (fore reef) windward reefs, an observation congruent with results from towed-diver surveys on northwest and north fore-reef exposures, but differing from the present results on northeast fore-reef exposures, where massive and encrusting forms of *Porites* dominated (Table 1). Similarly, Dana (1971) noted that *Porites lobata* dominated on seaward leeward reefs, an observation in agreement with results from towed-diver surveys on south and southeast fore-reef exposures, but differing from the heightened relative abundance of *Pocillopora meandrina* on southwest and west fore-reef exposures. Dana (1971) further reported that “the extreme leeward seaward reef has virtually no living coral,” an observation in agreement with our finding of relatively low coral cover (2.4–7.2%) along the southeast to southwest arc of fore reef. With regards to the back reef, Dana (1971) states that *Montipora verrucosa* (revised as *M. capitata*, Maragos, 1995) was particularly abundant in the northeast sector and that *Porites compressa*, another important species, formed large colonies up to 2 m diameter. In contrast, in imagery from towed-diver surveys *Montipora* was especially abundant on the north and northwest back reef but absent in the northeast (Table 1). *Porites compressa* was also rare in all back-reef zones (Tables 1,2, Fig. 3). Perhaps the greatest difference between observations by Dana (1971) and the present study is the absence of any mention of P. *compressa* on lagoon patch reefs by Dana (1971), whereas this species dominated the central lagoon patch reefs in the present study (Fig. 3).

Grigg (1983) reported a mean coral cover of 9% from two 50 m seaward transects off the southwest sector of Kure Atoll. This value is consistent with average fore-reef coral cover from all three methods in the present study (Tables 1, 2, Fig. 3) as well as a sector-specific value from towed-diver surveys (7.2%, Table 1), video transects (6.0%), and photoquadrats (6.0%). 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* from Maragos et al. (2004) but differs from the top ranking of *Porites compressa* by Grigg (1983) at southwest fore-reef sites (Table 3). *P. compressa* was rarely observed anywhere on the fore reef in the present study (Tables 1,2, Fig. 3).

Estimates of total coral cover by Siciliano (2006) in the three habitats at Kure were based in part on the coral size class data presented here and in part on visual estimates from an additional 43 sites surveyed in 2000 and 2001. In the mathematical conversion of size class data to percent cover estimates, Siciliano (2006) assumed a circular or elliptical shape for each enumerated colony and used the mean diameter of each of the seven size classes in diameter-to-area computations. The resulting coral cover estimates in all three habitats (fore reef 16.2%, back reef 27.0%, lagoon patch/reticulate reefs 27.1%) are higher than the highest values reported from any of the three methods used in the present study. Siciliano's (2006) estimates are likely high compared to those in the present study that are based on data extracted from photographic imagery because many coral colonies experience partial mortality that results in uneven contours and dead areas within colony boundaries, attributes that were not factored into diameter-to-area conversions.

Community Structure and Wave Exposure

Wave exposure is a major determinant controlling the development of Hawaiian coral reefs (Dollar, 1982; Storlazzi et al., 2005; Jokiel, 2006). Moberly and Chamberlain (1972) described four types of ocean swell, varying in their magnitude and frequency, which affect reef development in Hawaii: North Pacific winter swell, northeast trade wind waves, Southern Ocean swell, and kona storm-generated waves. Of these, large waves generated by the North Pacific swell, which approach from the north or northwest, pose the most significant wave disturbance to Hawaiian reefs (Grigg, 1998; Friedlander et al., 2005). On Kure fore reefs directly exposed to open ocean swell, highest coral cover, dominated by *Pocillopora*, was found along the 8.8-km-long arc of reef extending counterclockwise from north to west (Table 1, Fig. 2). Grigg (1998) showed that, at wave-exposed stations on Oahu in the main Hawaiian Islands, Holocene accretion is represented by only a thin veneer of living corals resting on an antecedent Pleistocene limestone foundation, and suggested that the present-day barrier reefs at Kure and other atolls in the Northwestern Hawaiian Islands may also be thin, transient veneers of Holocene growth limited to the thickness of single colonies growing on Pleistocene foundations. *Pocillopora* is a pioneer genus known to quickly colonize available habitat (Grigg and Maragos, 1974) such as that produced by wave-induced scour and abrasion, and has the highest growth rate of reef-building genera at Kure (1.69 cm year^{-1}; Siciliano, 2006). Hawaiian pocilloporid species rarely exceed 40 cm in diameter (Polachek, 1978; Bailey-Brock et al., 1994; Chess et al., 1997; Kenyon et al., 2006c). The similarity of the *Pocillopora* size-class distribution on the fore reef to that in the more protected back-reef habitat (Figs. 5a,b) underscores the suitability of its dense skeletal structure (Houck, 1978) and branched colony morphology, which acts as a baffle to high-energy water motion, to surviving in high-energy exposures (Dollar, 1982).

Northeast trade wind-generated swell, long period southerly swell from the southern ocean during the austral winter, and kona storm-generated swell from the southeast through the southwest quadrants are characterized by low to moderate waves (Grigg, 1998; Coral Reef Ecosystem Division, unpubl. data). The fore reef at Kure along exposures impacted by these wave regimes is dominated by massive and encrusting forms of *Porites* (Table 1). While capable of constructing colonies measuring meters in diameter (Dollar, 1982; Chess et al., 1997; Kenyon et al., 2006c), they rarely exceed 20 cm in diameter on these fore-reef sectors (Fig. 5a), most likely reflecting consistent exposure to heightened wave energy and long-period swell. Their high density (Fig. 4) and small size (Fig. 5a) in this habitat may either derive from high levels of recruitment or high levels of partial mortality resulting in genets being fissioned into numerous ramets (Karlson, 1991).

Though protected from the full force of open-ocean wave energy by an emergent rock ledge (Gross et al., 1969) and shallow surface reef (Dana, 1971), the back reef nonetheless experiences considerable surge as waves break and spill across the surface reef. Consistent with Grigg's (1998) finding of greater Holocene reef accretion at wave-sheltered than wave-exposed sites on Oahu, Siciliano (2006) calculated higher net calcification rates at Kure in the back-reef and lagoon habitats than the fore-reef habitat. The increased proportion of larger (> 20 cm diameter) *Porites* colonies on the back reef relative to the fore reef (Fig. 5a, b) is consistent with reduced disturbance from wave stress. Nearly 18% of *Porites* colonies attained unusually large (> 80 cm) sizes on the back reef (Fig. 5b); because *P. compressa* was rare on the back reef, these colonies correspond to species with massive and encrusting growth forms (e.g., *P. lobata*). Siciliano (2006) also noted that some individual heads of *P. lobata* and *P. evermanni* attained an extraordinary size in the back-reef and lagoon habitats.

Porites compressa is a very friable coral that is easily broken by even small wave forces (Grigg, 1998). It flourishes in the most wave-protected habitat, the lagoon (Fig. 3), where it forms large thickets by clonal propagation (Hunter, 1993) and displays a high growth rate (1.01 cm year^{-1}; Siciliano, 2006).

Community Development at High Latitudes

To redefine the environmental limits over which reefs exist today and to identify "marginal" reefs, i.e., those near or beyond "normal" environmental limits of reef distribution, Kleypas et al. (1999) assessed five environmental variables (temperature, salinity, light, carbonate saturation state, nutrients) considered to be first-order determinants of global reef distribution. With minimum weekly sea surface temperatures that fall to 17ºC (Coral Reef Ecosystem Division, unpubl. data), Kure conforms to a criterion by which reefs may be said to exist in a "marginal" environment. Despite Kure's status as the world's northernmost atoll (Dana, 1971), coral cover values in the three geomorphic habitats are comparable to those of more southerly atolls in the Northwestern Hawaiian Islands that have been quantified by methods and over time periods similar to those reported in the present study (Kenyon et al., 2006c, 2007). The range of coral cover values on the fore reef derived from the three methods at Kure (6.6–9.7%) is comparable to those at Pearl and Hermes (6.4–8.8%) and French Frigate Shoals (7.3–8.8%) (Fig.1). The range of values on the back reef at Kure (6.8–10.8%) shows somewhat lower coral cover than the ranges at Pearl and Hermes (10.1–15.1%) and French Frigate Shoals (9.7– 18.9%), as do the ranges of coral cover values in the lagoon habitat (9.8–18.6%, 14.4– 19.5%, 7.7–27.5% for Kure, Pearl and Hermes, and French Frigate Shoals, respectively.) Hence, in terms of coral cover, Kure appears to have somewhat more attenuated coral development than more southerly atolls in the Hawaiian Archipelago with similar histories of limited human disturbance, but not markedly so. Coral colony average densities are also higher in all three habitats at Kure than at Pearl and Hermes (Kenyon et al., 2007).

In measuring gross carbonate production by hermatypic corals on different islands along the Hawaiian Archipelago, Grigg (1982) calculated a minimum value at Kure, where he proposed that deposition by reef-building corals can no longer keep pace with subsidence rates and erosion, a latitudinal threshold termed the Darwin Point. Siciliano (2006) constructed a calcium carbonate budget for Kure Atoll which, in contrast to the assumptions and methods of Grigg (1982), was based on the growth rates of all the major coral genera in each of the three habitats, factored in the contribution of coralline algae to reef accretion, and subtracted rates of biological and mechanical erosion from gross accretion. Siciliano's (2006) atoll-wide estimate of gross carbonate framework production at Kure is an order of magnitude greater than the gross framework production estimated by Grigg (1982) (6.1 vs. 0.3 kg m^{-2} year^{-1}, respectively). An atoll-wide, average upward accretion rate of 2.14 mm year^{-1} was also an order of magnitude higher than that proposed by Grigg (1982) for Kure (0.2 mm year^{-1}). While Grigg (1982) argued that the amount of carbonate limestone contributed by corals at Kure was only 20% of that necessary to keep pace with recent (< 6000 years) changes in sea level, Siciliano's (2006) accretion rates imply that Kure has effectively kept pace with sea level rise during this period.

Health Status of Kure 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 ten reef systems in the Northwestern Hawaiian Islands, Kure ranked seventh, followed only by the three basalt islands Gardner Pinnacles, Nihoa, and Necker (Fig. 1). Like most reef systems in the NWHI, however, Kure outranked all eight islands in the populated main Hawaiian Islands. Additional factors such as coral bleaching, prevalence of coral disease, marine debris, and crown-of-thorns seastars are germane to assessing the overall health status of coral communities at Kure Atoll.

Despite winter seawater temperatures at Kure that are marginal for coral reef development (Kleypas et al., 1999), maximum summer sea surface temperatures (SST) are generally found at the three northernmost atolls (Fig. 1) (Brainard et al., 2004), and analyses of historical SST data sets show a warming trend in the Hawaiian Archipelago that is most pronounced at the northern end of the chain (Jokiel and Brown, 2004; Barton and Casey, 2005). Prolonged periods of elevated summertime SST resulted in mass coral bleaching in the NWHI in 2002 and 2004 (Aeby et al., 2003; Kenyon et al., 2006a; Kenyon and Brainard, 2006; Hoeke et al., 2006). Incidence of coral bleaching in 2002 was greatest at the three northernmost atolls, including Kure, where the highest incidences were documented on the back reef (64% of coral cover), followed by the lagoon and fore reef (37% and 14% of coral cover, respectively). These spatial patterns corresponded closely to the relative abundance of coral taxa in the three habitats, as *Montipora*, followed by *Pocillopora*, showed the greatest differential susceptibility to bleaching whereas massive and encrusting forms of *Porites* were highly resistant to bleaching (Kenyon et al., 2006a). Bleaching was milder at Kure in 2004, with a somewhat higher incidence on lagoon patch reefs than the back reef (16% and 14% of colonies, respectively) and little bleaching on the fore reef (2% of colonies) (Kenyon and Brainard, 2006). *Montipora*, followed by *Pocillopora*, again showed the highest differential susceptibility to bleaching. The shallow (< 2 m) crest of a large, central patch reef system at Kure (Fig. 2), dominated by *Montipora* and *Pocillopora*, was heavily bleached in 2002. Comparison of total coral cover from towed-diver surveys conducted in 2004 along track lines comparable to those reported in the present study show little change on the fore reef or back reef, but a reduction by nearly half (18.6% to 9.5%) in the central patch reef system (J. Kenyon, unpubl. data). As of 2007, bleaching of this magnitude has not been further observed in the NWHI, though annual surveys have been conducted during the late summer when SSTs reach their peak.

Numerous studies in the past decade conclude that coral diseases are contributing to the observed world-wide degradation of coral reefs (e.g., Pandolfi et al., 2005; Richardson and Voss, 2005; Santavy et al., 2005), and their incidence is increased by elevated temperatures with associated bleaching (Harvell et al., 1999; Kuta and Richardson, 2002; Rosenberg and Ben-Haim, 2002). Three disease states affecting *Porites* have been documented at Kure Atoll (Aeby, 2006) with two diseases recently reported affecting *Montipora* (G. Aeby, unpubl. data). As elsewhere in the NWHI, coral disease is widespread on the reefs of Kure but occurs at levels indicative of a healthy ecosystem. Disease surveys in 2004 showed that mean disease prevalence (proportion of all colonies affected) at Kure was 5.6 ± 3.1% (SE), which is comparable to the average prevalence of disease found among all islands within the NWHI (5.1 ± 1.1%, n = 64) (G. Aeby, unpubl. data). However, Kure was found to have higher levels of *Porites* disease as compared to the other islands within the NWHI (23.5 ± 11.7 % vs. 7.9 ± 3.1%). This was surprising as the abundance of *Porites* in the coral communities at Kure is among the lowest in the NWHI. However, *Porites* trematodiasis was the most prevalent disease found on *Porites* at Kure. This disease is caused by the larval stage of a digenetic trematode that requires three different hosts (mollusc, coral, fish) for completion of its life cycle (Aeby, 1998). As such, presence of this disease on reefs may be reflective of a healthy ecosystem with abundant multiple hosts available for maintenance of the parasite's life cycle.

Marine debris, particularly derelict fishing gear, is a persistent stressor to corals and other marine fauna throughout the NWHI (Donohue et al., 2001; Boland and Donohue, 2003). Abandoned nets physically damage corals through abrasion and breakage, repeating their cycle of damage when entangled colonies are detached from the benthos by the influence of wind-driven wave action. Shallow (< 10 m) reefs along trade-wind exposures are particularly impacted by marine debris (Donohue et al., 2001) as it is driven by prevailing winds from areas of high accumulation just north of the North Pacific Transition Zone Chlorophyll Front (TZCF) within the North Pacific Subtropical Convergence Zone (STCZ) (Pichel et al., 2007). The TZCF migrates throughout the year, such that marine debris is concentrated during winter when surface convergence in the STCZ is strongest and the TZCF reaches its southernmost position just north of Kure (Pichel et al., 2007). Resurvey in 2001 of small areas (< 1.3 km^2) frequently used by endangered Hawaiian monk seals (*Monachus schauinslandi*) at Kure, Pearl and Hermes, and Lisianski/Neva Shoal (Fig. 1) that were cleaned of marine debris in 2000 indicated the highest accumulation rate (number of items km^{-2} year^{-1}) occurred at Kure (Boland and Donohue, 2003). 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 2000 to 2007 have removed 526 metric tons of fishing debris which includes 50.3 metric tons from Kure (R. Brainard, unpubl. data). Weight analysis of debris removed in 2005 from shallow areas (< 4.5 m) that were cleaned of marine debris in 2004 at Pearl and Hermes and Kure 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). Because the area occupied by reef is relatively limited in the lagoon at Kure, however (4.17 km^2; Siciliano, 2006), debris tends to accumulate primarily on the back reef, particularly along the arc extending counterclockwise from southeast to west (Dameron et al., 2006). Further development of an economic way to remove derelict nets at sea based on knowledge of convergence dynamics (Pichel et al., 2007), coupled with on-going atoll-based removal efforts, may assist in reducing net-inflicted damage to coral communities.

The crown-of-thorns seastar *Acanthaster planci* is a selective corallivore that has caused widespread damage on numerous reefs throughout the Indo-Pacific during population outbreaks (e.g., Chesher, 1969; Endean, 1973; Lourey et al., 2000). In Hawaii, a series of outbreaks were documented off the south coast of Molokai in the main Hawaiian Islands in the 1970s (Branham et al., 1971) and a localized outbreak occurred off the north coast of Oahu in 2005 (J. Kenyon and G. Aeby, unpubl. data). *Pocillopora* and *Montipora* have been documented as preferred prey in the main Hawaiian Islands even when other coral taxa were more abundant (Branham et al., 1971; Chess et al., 1997; J. Kenyon and G. Aeby, unpubl. data), though Keenan et al. (2004) reported that *A. planci* commonly fed on *Porites* on lagoon reefs at Pearl and Hermes Atoll (Fig. 1), where this genus dominates coral cover (Kenyon et al., 2007). Extensive surveys by towed divers conducted annually throughout the NWHI from 2000 to 2006 revealed low background densities ranging from 0 to 2.8 x 10^{-4} seastars m^{-2} (M. Timmers, unpubl. data). Seastar densities at Kure during this period ranged from 2 x 10^{-5} to 1.4 x 10^{-4} starfish m^{-2}. As far as is known, Hawaiian reefs appear to have been spared the widespread damage from *A. planci* infestations documented in other Indo-Pacific areas (e.g., Chesher, 1969; Endean 1973; Lourey et al., 2000). However, as reefs respond to ocean conditions associated with global climate change, the problems facing these reefs may also change. Though the high abundance of preferred prey *Pocillopora* and *Montipora* on the Kure back reef suggests potential vulnerability to *A. planci* should their populations become inflated, the relatively high wave surge across the back reef might serve to reduce aggregation in this habitat, as the species appears to prefer wave-sheltered environments (Moran, 1986; Chess et al., 1997).

Marine protected areas have emerged as an increasingly important way for managing reefs within the world's changing oceans, creating refugia for species that would otherwise be overexploited and potentially providing stock to damaged reefs through the movement of adults and larvae (Hoegh-Guldberg, 2006). At nearly 140,000 square miles, the Papahānaumokuākea Marine National Monument that includes Kure Atoll represents the second largest protected marine area in the world. Another management tool that is emerging in response to climate change is the identification of specific reef areas that are resistant and/or resilient to coral bleaching (West and Salm, 2003) as a result of localized cooling, shading, tolerant species, or other abetting factors (Marshall and Schuttenberg, 2006). Such areas may act as sources of replenishing propagules should corals on reefs linked by larval dispersal become damaged by episodes of bleaching or other sources of mortality. Fundamental to developing damage response plans is a sound knowledge of coral community structure on both fine and broad spatial scales, data such as summarized here for Kure Atoll. These insights can help focus monitoring regimes and provide researchers with a solid, rather than a sliding, baseline.

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REFERENCES

Aeby, G.S.

1998. A digenean metacercaria from the reef coral, *Porites compressa*, experimentally identified as *Podocotyloides stenometra. J. of Parasitol.* 84:1259 -1261

Aeby, G.S., J.C. Kenyon, J.E. Maragos, D.C. Potts

2003. First record of mass coral bleaching in the Northwestern Hawaiian Islands. *Coral Reefs* 22:256

Aeby, G.S.

2006. Baseline levels of coral disease in the Northwestern Hawaiian Islands. *Atoll Res. Bull.* 543:471-488.

Aeby, G.S., T. Work, S. Coles, and T. Lewis

2006. Coral disease across the Hawaiian Archipelago. Eos Trans. AGU, 87(36), Ocean Sciences Meeting Supplement, Abstract OS24L-03.

Bailey-Brock, J., R. Brock, and A. Kam.

1994. Coral growth on a sunken vessel serving as an artificial reef in Hawaii. *Bull Mar. Sci.* 55:1326.

Barton, A.D., and K.S. Casey

2005. Climatological context for large-scale coral bleaching observed since 1979. *Coral Reefs* 24(4):536-554.

Birkeland, C.

2004. Ratcheting down the coral reefs. *Bioscience* 54(11):1021-1027

Bohnsack, J.A.

2003. Shifting baselines, marine reserves, and Leopold's biotic ethic. *Proc. Gulf Caribb. Fish. Inst.* 54:783-784.

Boland, R.C., and M.J. Donohue

2003. Marine debris accumulation in the nearshore habitat of the endangered Hawaiian monk seal *Monachus schauinslandi* 1999-2001. *Mar. Poll. Bull*. 46:1385-1394. Brainard, R., R. Hoeke, R.A. Moffitt, K.B. Wong, J. Firing

2004. Spatial and temporal variability of key oceanographic processes influencing coral reef ecosystems on the Northwestern Hawaiian Islands. Abstract, NWHI 3rd Scientific Symposium, Honolulu, p. 18

Branham, J.M., S.A. Reed, and J.H. Bailey

1971. Coral-eating sea stars *Acanthaster planci* in Hawaii. *Science* 172:1155-1157.

Chesher, R.H.

1969. Destruction of Pacific corals by the sea star *Acanthaster planci.* Science 165:280-283

Chess, J.R., E.S. Hobson, and D.R. Howard

1997. Interactions between *Acanthaster planci* (Echinodermata, Asteroidea) and scleractinian corals at Kona, Hawaii. *Pac. Sci.* 51(2):121-133.

Dameron, O.J., M. Parke, M.A. Albins, and R. Brainard

2007. Marine debris accumulation in the Northwestern Hawaiian Islands: an examination of rates and processes. *Mar. Poll. Bull*. 46:1385-1394

Dana, T.F.

1971. On the reef corals of the world's most northern atoll (Kure: Hawaiian Archipelago). *Pac. Sci.* 1:80-87.

Done, T.J.
1992. Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia* 247:121-132.
Donohue, M.J., and R.C. Boland
2003. Marine debris accumulation in the nearshore marine habitat of the endangered Hawaiian monk seal, *Monachus schauinslandi* 1999-2001. *Mar. Poll. Bull.* 46:1385-1394
Donohue, M.J., R.C. Boland, C.M. Sramek, and G. A. Antonelis
2001. Derelict fishing gear in the Northwestern Hawaiian Islands: diving surveys and debris removal in 1999 confirm threat to coral reef ecosystem. *Mar. Poll. Bull.* 42(12):1301-1312.
Dollar, S.J.
1982. Wave stress and coral community structure in Hawaii. *Coral Reefs* 1(2): 71–81.
Endean, R.
1973. Populations explosions of *Acanthaster planci* and associated destruction of hermatypic corals in the Indo-West Pacific region. In *Biology and Geology of Coral Reefs*, III, ed. O.A. Jones and R. Endean, pp. 389-438. Academic Press
Friedlander A., G. Aeby, R. Brainard, A. Clark, E. deMartini, S. Godwin, J. Kenyon, R. Kosaki, J. Maragos, and P. Vroom.
2005. The State of Coral Reef Ecosystems of the Northwestern Hawaiian Islands. Pp. 270-311 in: Waddell, J. (ed.), The State of Coral Reef Ecosystems of the United States and Pacific Freely Associated States: 2005. NOAA Technical Memorandum NOS NCCOS 11. NOAA/NCCOS Center for Coastal Monitoring and Assessment's Biogeography Team. Silver Spring, MD. 522 pp.
Grigg, R.W.
1982. The Darwin Point: a threshold for atoll formation. *Coral Reefs* 1:29-34.
1983. Community structure, succession and development of coral reefs in Hawaii. *Mar. Ecol. Prog. Ser.* 11:1-14. 1998. Holocene coral reef accretion in Hawaii: a function of wave exposure and sea level history. *Coral Reefs* 17:263-272.
Grigg, R.W. and J.E. Maragos
1974. Recolonization of hermatypic corals on submerged lava flows in Hawaii. *Ecology* 55(2):387-395.
Gross, M.G., J.D. Milliman, J.I. Tracey Jr., and H.S. Ladd.
1969. Marine geology of Kure and Midway Atolls, Hawaii: a preliminary report. *Pac. Sci.* 23:17-25.
Harvell, C.D., K. Kim, J.M. Burkholder, R.R. Colwell, P.R. Epstein, D.J. Grimes, E.E. Hofmann, E.K. Lipp, A.D.M.E. Osterhaus, R.M. Overstreet, J.W. Porter, G.W. Smith, and G.R. Vasta
1999. Emerging marine diseases – climate links and anthropogenic factors. *Science* 285:1505-1510.
Hoeke, R., R. Brainard, R. Moffitt, and M. Merrifield
2006. The role of oceanographic conditions and reef morphology in the 2002 coral bleaching event in the Northwestern Hawaiian Islands. *Atoll Res. Bull.* 543:489-504.

Hughes, T.P., A.H. Baird, D.R. Bellwood, M. Card, S.R. Connolly, C. Folke, R. Grosberg, O. Hoegh-Guldberg, J.B.C. Jackson, J. Kleypas, J.M. Lough, P. Marshall, M. Nyström, S.R. Palumbi, J.M. Pandolfi, B. Rosen, and J. Roughgarden
2003. Climate change, human impacts, and the resilience of coral reefs. *Science* 301: 929-933.
Hunter, C.L.
1993. Genotypic variation and clonal structure in coral populations with different disturbance histories. *Evolution* 47(4):1213-1228.
Jokiel, P.L.
2006. Impact of storm waves and storm floods on Hawaiian reefs. *Proc. Tenth Int. Coral Reef Symp., Okinawa* 390-398.
Jokiel, P.L., and E.K. Brown
2004. Global warming, regional trends and inshore environmental conditions influence coral bleaching in Hawaii. *Global Change Biology* 10:1627-1641.
Jokiel, P.L., and K.S. Rodgers
2007. Ranking coral ecosystem "health and value" for the islands of the Hawaiian Archipelago. *Pac. Cons. Bio.* 13(1):60-68.
Karlson, R.H.
1991. Fission and the dynamics of genets and ramets in clonal cnidarian populations *Hydrobiologia* 216/217:235-240.
Keenan, E.E., R.E. Brainard, and L.V. Basch
2004. *Acanthaster planci* distribution and predation at Pearl and Hermes Atoll. Abstract, Northwestern Hawaiian Islands Third Scientific Symposium, Honolulu, p. 65.
Kenyon, J.C., and R.E. Brainard
2006. Second recorded episode of mass coral bleaching in the Northwestern Hawaiian Islands. *Atoll Res. Bull.* 543:505-523.
Kenyon, J.C., R.E. Brainard, G.S. Aeby, J.Chojnacki, M.J. Dunlap, and C.B. Wilkinson
2006a. Mass coral bleaching on high latitude reefs in the Hawaiian Archipelago. *Proc. Tenth Int. Coral Reef Symp., Okinawa* 2:631-643
Kenyon, J.C., R.E. Brainard, R.K. Hoeke, F.A. Parrish, and C.B. Wilkinson
2006b. Towed-diver surveys, a method for mesoscale spatial assessment of benthic reef habitat: a case study at Midway Atoll in the Hawaiian Archipelago. *Coast. Manage.* 34(3):339-349.
Kenyon, J.C., P.S. Vroom, K.N. Page, M.J. Dunlap, C.B. Wilkinson, and G.S. Aeby
2006c. Community structure of hermatypic corals at French Frigate Shoals, Northwestern Hawaiian Islands: capacity for resistance and resilience to selective stressors. *Pac. Sci.* 60(2):151-173.
Kenyon, J.C., M.J. Dunlap, C.B. Wilkinson, K.N. Page, P.S. Vroom, G.S. Aeby
2007. Community structure of hermatypic corals at Pearl and Hermes Atoll, Northwestern Hawaiian Islands: unique conservation challenges in the Hawaiian Archipelago. *Atoll Res. Bull.* 549:1-23.
Kleypas, J.A., J.W. McManus, and L.A.B. Menez
1999. Environmental limits to coral reef development: where do we draw the line? *Am. Zool.* 39:146-159.

Kleypas, J.A., R.A. Feely, V.J. Fabry, C. Langdon, C.L. Sabine, and L.L. Robbins
2006. Impacts of ocean acidification on coral reefs and other marine calcifiers: a guide for future research. Report of a workshop held 18-20 April 2005, St. Petersburg, FL, sponsored by NSF, NOAA, and the U.S. Geological Survey, 88 pp.

Kohler, K.E., and S.M. Gill
2006. Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Computers & Geosciences* 32: 1259-1269.

Kuta, K.G., and L.L Richardson
2002. Ecological aspects of black band disease in corals: relationships between disease incidence and environmental factors. *Coral Reefs* 21:393-398.

Lourey, M.K., D.A.J. Ryan, and I.R. Miller
2000. Rates of decline and recovery of coral cover on reefs impacted by, recovering from and unaffected by crown-of-thorns starfish *Acanthaster planci*: a regional perspective on the Great Barrier Reef. Mar. Ecol. Prog. Ser. 196:179-186

Maragos, J.E.
1977. Order Scleractinia: Stony corals. In: Reef and shore fauna of Hawaii. Section 1: Protozoa through Ctenophora. B.P. Bishop Museum Special Publication 64(1): 158-241, D. Devaney and L. Eldredge (eds).
1995. Revised checklist of extant shallow-water stony coral species from Hawaii: (Cnidaria: Anthozoa: Scleractinia). *Bernice P. Bishop Museum Occasional Papers* 42:54-55.

Maragos, J.E., D.C. Potts, G.S. Aeby, D. Gulko, J.C. Kenyon, D. Siciliano, and D. Vanravenswaay
2004. 2000-2002 Rapid ecological assessment of corals on the shallow reefs of the Northwestern Hawaiian Islands. Part 1: Species and distribution. *Pac. Sci.* 58(2):211-230.

Marshall, P., and H. Schuttenberg
2006. A Reef Manager's Guide to Coral Bleaching. Great Barrier Reef Marine Park Authority, Townsville, 163pp. Moberly, R. and Chamberlain, T. 1972. Hawaiian beach systems. *Hawaii Inst. Geophys*. 64-2, 95pp.

Moran, P.J.
1986. The *Acanthaster* phenomenon. Oceanogr. Mar. Biol. Ann. Rev. 24:379-480

Nyström, M., C. Folke, and F. Moberg
2000. Coral reef disturbance and resilience in a human-dominated environment. *Trends Ecol. Evol.* 15(10):413-418

Pandolfi, J.M., J.B.C. Jackson, N. Baron, R.H. Bradbury, H.M. Guzman, T.P. Hughes, C.V. Kappel, F. Micheli, J.C. Ogden, H.P. Possingham, and E. Sala
2005. Are U.S. coral reefs on the slippery slope to slime? *Science* 307:1725-1726.

Parrish, F.A., and R.C. Boland
2004. Habitat and reef-fish assemblages of banks in the Northwestern Hawaiian Islands. *Mar. Biol.* 144:1065-1073.

Pauly, D.
1995. Anecdotes and the shifting baseline syndrome of fisheries. *Trends Ecol. Evol*. 10(10): 430.

Pichel, W.G., J.H. Churnside, T.S. Veenstra, D.G. Foley, K.S. Friedman, R.E. Brainard, J.B. Nicoll, Q.Zheng, and P. Clemente-Colón
2007. Marine debris collects within the North Pacific Subtropical Convergence Zone. *Mar. Pol. Bull.* 54:1207-1211 Polacheck, T. 1978. The population biology of four common Hawaiian corals. M.S. thesis, University of Hawai‘i at Mānoa, Honolulu.

Preskitt, L.B., P.S. Vroom, and C.M. Smith
2004. A rapid ecological assessment (REA) quantitative survey method for benthic algae using photo quadrats with SCUBA. *Pac. Sci.* 58(2):201-209.

Richardson, L.L., and J.D. Voss
2005. Changes in a coral population on reefs of the northern Florida Keys following a coral disease epizootic. *Mar. Ecol. Prog. Ser*. 297:147-156

Rosenberg, E., and Y. Ben-Haim
2002. Microbial diseases of corals and global warming. *Environ. Microbio.* 4: 381-326.

Santavy, D.H., J.K. Summers, V. D. Engle, and L.C. Harwell
2005. The condition of coral reefs in south Florida (2000) using coral disease and bleaching as indicators. *Environmental. Monitoring and Assessment* 100:129-152

Siciliano, D.
2006. Latitudinal limits to coral reef accretion: testing the Darwin Point hypothesis at Kure Atoll, northwestern Hawaiian Islands, using new evidence from high resolution remote sensing and in situ data. Ph.D. dissertation, University of California, Santa Cruz, 276 pp

Storlazzi, C.D., E.K. Brown, M.E. Field, K. Rodgers, and P.L. Jokiel
2005. A model for wave control on coral breakage and species distribution in the Hawaiian Islands. *Coral Reefs* 24:43-55.

West, J.M., and R.V. Salm
2003. Resistance and resilience to coral bleaching: implications for coral reef conservation and management. *Cons. Biol.* 17(4):956-967