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CHARACTERIZATION OF CORAL COMMUNITIES AT WAKE ATOLL IN THE REMOTE CENTRAL PACIFIC OCEAN

JEAN C. KENYON[1], VICTOR BONITO[2], and CASEY B. WILKINSON[3]

ABSTRACT

Little published or unpublished information exists concerning the benthic community structure or coral fauna at Wake Atoll in the Central Pacific. Here, we apply multivariate statistical analyses to data acquired in 2005 from several complementary survey methods that operate at different scales of spatial and taxonomic resolution to characterize the coral communities in the fore-reef habitat, which is further stratified by geographic sector and depth zone. Both broad-scale towed-diver surveys and site-specific photoquadrat surveys revealed high dissimilarity in overall benthic composition between the northeast and southwest sectors. Coral cover in the northeast sector is more than 2.5 times greater than in the southwest sector; encrusting and massive growth forms dominate in the northeast sector while encrusting and digitate growth forms dominate in the southwest sector. Coral cover and colony abundances are less dominated by a few key genera in the northeast than in the southwest sector, though the genera *Montipora, Pocillopora*, and *Favia* are the most numerically abundant taxa in both sectors. Octocorals account for more than 25% of the total coral cover in the northeast sector but less than 5% of the total coral cover in the southwest sector. The deep northeast stratum showed among the highest diversity of growth forms as well as the highest total coral cover, octocoral cover, and coralline algal cover. We provide a list of 101 anthozoan and hydrozoan corals observed at Wake Atoll during survey activities since the year 1979. Five scleractinian species at Wake are on the IUCN Red List of Threatened Species™. The 80 taxa with well-established species names contain components from the Mariana Islands, northern Marshall Islands, and Hawaiian Islands, but show the closest resemblance to the Mariana Islands. Our spatially widespread surveys that generate independent metrics of benthic cover and coral abundance collectively provide the most comprehensive description of coral communities at Wake Atoll produced to date and also provide an important record by which to monitor the response of this community to changing ocean conditions.

INTRODUCTION

Wake Atoll (19°17′N, 166°37′E) is a small closed atoll in the central Pacific that is extremely isolated from other shallow coral reefs. It lies 2260 km northeast of Guam (13°25′N, 144°47′E) in the southern Mariana Islands, 1900 km southwest of Kure Atoll (28°25′N, 178°20′W), the nearest reef in the Hawaiian Archipelago, and 546 km northwest of Bok-ak (Taongi) (14°39′N, 168°58′E), the nearest reef in the Marshall Islands. The emergent land consists of three low-lying coral islets (Peale, Wake, and Wilkes; Figure 1) that border a shallow lagoon. A reef flat, over which most water exchange takes place between the open ocean and the lagoon, comprises the western side of the atoll (Lobel and Lobel, 2008). The atoll's longest axis extends ~ 8 km in a southeast-northwest direction, with prevailing winds arriving from the east-northeast.

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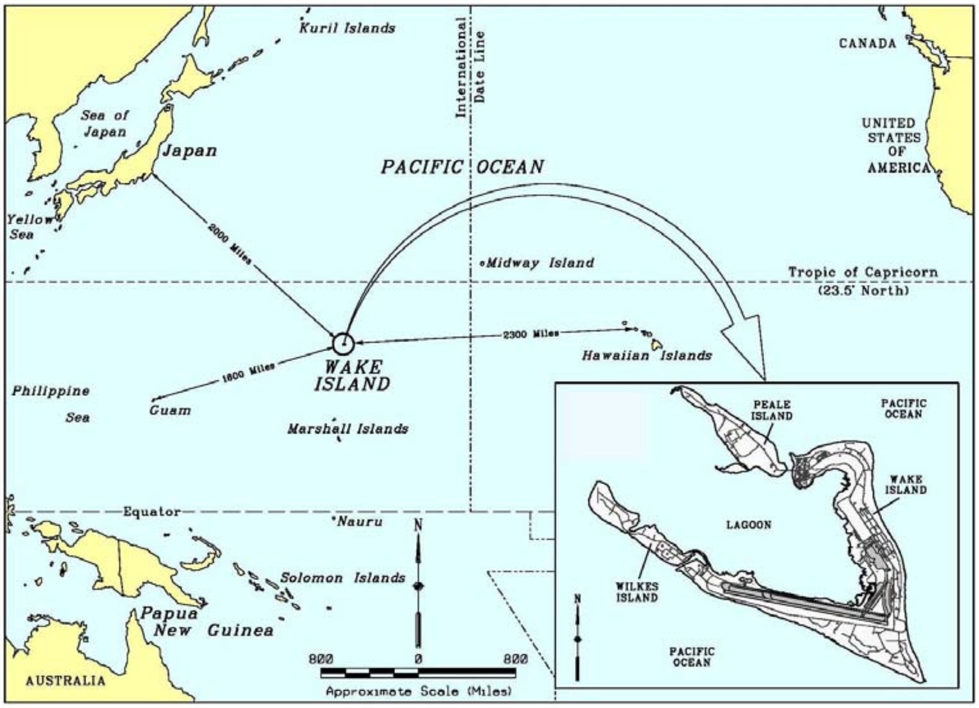

Figure 1. Location of Wake Atoll in the central Pacific

The first visitors to Wake Atoll were probably early navigators from the Marshall Islands who periodically visited the atoll to hunt sea turtles and birds. In 1568 the Spanish explorer Mendaña was the first European to report sighting the atoll (Bryan, 1959), which was later named for the British sea captain William Wake who documented its location in 1796 (Lobel and Lobel, 2008) The U.S. Exploring Expedition, which visited in December 1841 under the leadership of Lt. (later Commodore) Charles Wilkes, provided the first surveys, maps, and detailed descriptions of the atoll, noting that “the reef around this island is very small in extent” (Wilkes, 1844). Wake was formally claimed by the United States in 1898 during the Spanish American War. During the 1923 *Tanager* Expedition led by Honolulu’s Bernice P. Bishop Museum, the southwestern islet was named for Lt. Wilkes and the northwestern island for Titian Peale, a naturalist and artist who accompanied the U.S. Exploring Expedition. In 1934 the U.S. Navy was given responsibility for Wake and a military base was constructed in early 1941. Attacked and captured by the Japanese in December 1941, the atoll remained in Japanese possession until their surrender in 1945. Following World War II, Wake came under the administration of the U.S. Army Space and Missile Defense Command, serving as a support facility for testing intermediate-range target missiles. On January 6, 2009, President George W. Bush established the Pacific Remote Islands Marine National Monument, which includes the emergent and submerged lands and waters extending 50 nautical miles (nmi) from the mean low water line at Wake and 6 other U.S.-administered islands and atolls in the Pacific. The land areas at Wake remain under the jurisdiction of the U.S. Air Force, but the waters from 0 to 12 nmi are protected as a unit of the National Wildlife Refuge System. Fishery-related activities seaward from the 12-nmi refuge boundaries out to the 50-nmi monument boundary are managed by the National Oceanic and Atmospheric Administration (NOAA).

Knowledge of the shallow water coral fauna of Wake Atoll previously has been limited to observations contained in an unpublished list (J. Maragos, pers. comm.) and an interagency government report (USFWS, 1999). Although coral specimens were collected from Wake during the 1923 *Tanager* Expedition (Gregory, 1924; Olson, 1996), no publication treating their taxonomic analysis was ever produced as was done for other marine invertebrate groups (Edmondson et al., 1925). Maragos visited the atoll in May 1979 and compiled a list including 31 scleractinian and hydrozoan species from 14 genera based on qualitative snorkel surveys at five locations, two along the shallow south fore reef, two on the northern reef flat, and one in the channel between Peale and Wake Islands (Figure 2). In June 1998, M. Molina representing the U.S. Fish and Wildlife Service compiled a list including 41 species from 22 scleractinian and hydrozoan genera based on scuba surveys at six sites at a depth of ~10 m on the fore-reef slope along the southern exposure of the atoll (Figure 2). Together their records totaled 52 species from 25 genera. In October 2005, reef assessment and monitoring activities were initiated at Wake Atoll by the NOAA, Pacific Islands Fisheries Science Center's Coral Reef Ecosystem Division as part of a larger multidisciplinary effort to assess and monitor coral reef ecosystems in the U.S. Pacific Islands (Brainard et al., 2008). Broad-scale towed-diver surveys were initiated to provide a spatial assessment of the composition and condition of shallow-water benthic habitats coupled with site-specific surveys to assess species composition, abundance, percent cover, size distribution, and general health of salient benthic organisms including corals.

The main aims of the present study are to (1) describe the community structure of the shallow-water (< 29 m) corals in the fore-reef habitat at Wake Atoll, based on broad-scale and site-specific quantitative surveys conducted in 2005, and (2) provide a species list of anthozoan and hydrozoan corals, compiling records from the suite of surveys conducted from 1979 to 2005, and (3) assess species overlap of Wake corals with the Mariana, northern Marshall, and Hawaiian Islands. In describing community structure, we applied survey methods that operate at different scales of spatial and taxonomic resolution to generate independent metrics of community abundance. For each method and metric we applied statistical analyses developed for use with multivariate ecological data to determine spatial differences and their underlying taxonomic basis. Our study, which presents a detailed and spatially widespread multivariate analysis of the coral communities in the fore-reef habitat at Wake Atoll, serves as an important baseline from the early years of the twenty-first century, which can serve as an important and useful standard for future generations of scientists, managers, and other stakeholders.

MATERIALS AND METHODS

Benthic Surveys

Towed-diver surveys were conducted in 2005 (18–21 October) according to the methods of Kenyon et al. (2006a) in the fore-reef slope habitat (Figure 2). Modifications to these methods included the use of a digital still camera (Canon EOS-10D, EF 20-mm lens) in a customized housing with strobes to photograph the benthos automatically at 15-sec intervals. Site-specific belt-transect surveys to assess coral colony abundance and size class were conducted by a single diver (J. Kenyon) from 18 to 21 October 2005 according to the general methods described by Maragos et al. (2004) for Rapid Ecological Assessments. Twelve sites (11–18 m depth) were surveyed on the fore-reef slope and one (2–3 m depth) in the western lagoon (Figure 2). Two 25 x 1 m transect belts were surveyed at each site except for the lagoon site, where transects were widened to 25 x 2 m due to low colony density. Each coral whose colony center fell within a 0.5-m-wide strip on each side of the lines (1-m-wide for the lagoon site) was classified to genus and its maximum diameter binned into one of six size classes (Mundy, 1996): 0–5 cm, 5–10 cm, 10–20 cm, 20–40 cm, 40–80 cm, or 80–160 cm. To determine percent cover of benthic components, 12 (35 cm x 50 cm) photoquadrats were concurrently photographed with a Sony DSC P-9 digital still camera with spatial reference to the same two 25-m transect lines: three photoquadrats at randomly selected points along each transect and three at points 3 m perpendicular from each random point in the direction of shallower water (i.e., 6 photoquadrats per transect; Preskitt et al., 2004; Vroom et al., 2005). Locations of site-specific surveys were determined on the basis of (1) maximizing spatial coverage along the fore reef within the allotted number of survey days; (2) establishing depths that allowed three dives per day per diver; (3) working within constraints imposed by other ship-supported operations; and (4) sea conditions.

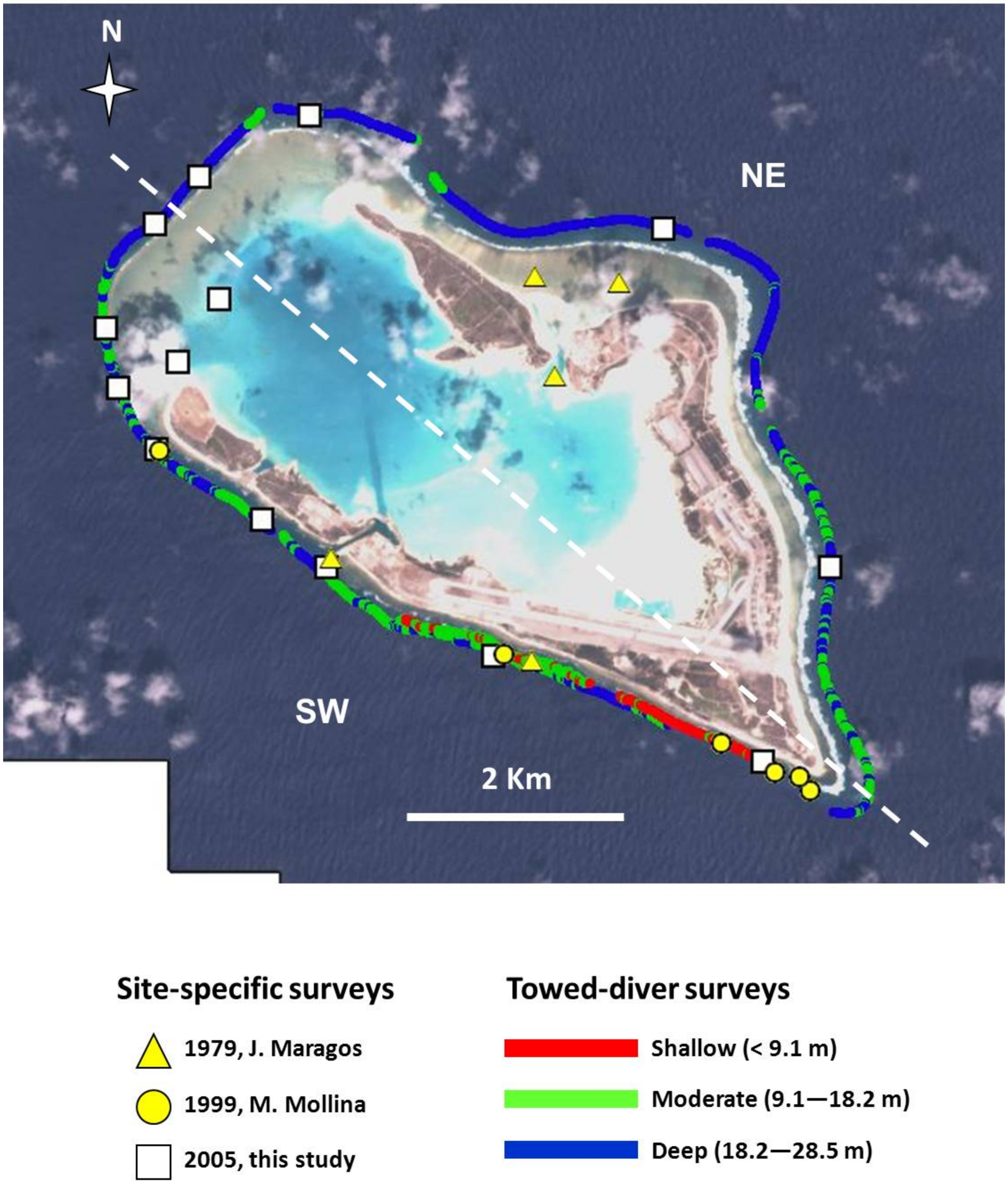

Figure 2. Location of towed-diver and site-specific surveys at Wake Atoll. Tow track lines are color coded according to the depth zone of the photographs sampled for image analysis.

Species lists of anthozoan and hydrozoan corals were compiled *in situ* by the lead authors in the vicinity of the transect lines at each site, and at an additional reef flat site north of Wilkes Island (Figure 2). Photographs were taken *in situ* for most species to assist in verifying taxonomic assignments and resolving uncertainties using Veron (2000) and Randall and Myers (1983), with revisions to the latter in Randall (2003). Samples were collected of 62 scleractinian, 1 hydrozoan, 4 alcyonarian, and 1 zoanthid taxa, which were examined with a dissecting microscope to additionally assist in identifications. Samples were tagged, numbered, linked to a photo library and data base with collection information, and deposited in the Florida Museum of Natural History coral collection curated by Gustav Paulay (catalog numbers 4073–4107 and 5900–5977). The resulting species list was integrated with lists previously compiled by J. Maragos (unpublished data, 1979) and by M. Molina (USFWS, 1999). To examine the geographic affinities of Wake corals, taxa with well-established species names were compared to lists from Hawai`i (Fenner, 2005), the Mariana Islands (Randall, 2003), and the northern Marshall Islands (Bok-ak, Pikaar, Tōke, Wōtte, Rondik, Ādkup, and Jemo; Maragos, 1994).

Data Extraction and Analysis

Digital photographs from towed-diver surveys were sampled at 30-sec intervals and quantitatively analyzed for benthic percent cover by a single analyst (C. Wilkinson), using point-count software (Coral Point Count with Excel Extension; Kohler and Gill, 2006) and using 50 stratified random points per frame. Benthic classification categories included hard coral, soft coral, macroalgae, coralline red algae, noncoral macroinvertebrates, sand, rubble, and pavement. Hard corals were subclassified morphologically as branching, digitate, encrusting, massive, free-living (mushroom) and plate-like. Laser-projected dots used to calibrate image size did not appear on photographic imagery because of mechanical problems; consequently, scaling data from imagery recorded throughout the Northwestern Hawaiian Islands with the same methods (Kenyon et al., 2006b, 2007a, 2007b, 2008a, 2008b) were used to calculate average benthic area in captured frames. Survey distances were calculated using a global positioning system (GPS) and ArcView GIS 3.3. The depth of each captured frame was determined by matching the time stamp of the image with that of temperature/pressure data recorded by an SBE 39 recorder (Sea-Bird Electronics, Inc.) mounted on the habitat towboard. For statistical analysis, each frame was categorized in one of six strata defined *a priori* by the concatenation of two factors: sector (northeast or southwest, where a line between the southeast vertex of the island and the midpoint of the northwest-facing reef slope was used to separate northeast from southwest) and depth zone (shallow [< 9.1 m], moderate [9.1–18.2 m], or deep [18.2–28.5 m]). Thus, frames from towed-diver surveys that spanned more than one sector or depth zone were parsed into separate strata using the time stamp that linked GPS position and depth to recorded imagery. No frames were acquired from shallow depths in the northeast sector, resulting in data for only five of the six defined strata.

Photoquadrats were analyzed for benthic percent cover by a single analyst (J. Kenyon), using Coral Point Count with Excel Extensions (Kohler and Gill, 2006) and using 50 stratified random points per digital image. Anthozoans were identified to genus, while algae were categorized as *Halimeda*, other macroalgae, and coralline red algae. Additional benthic classification categories included noncoral macroinvertebrates, sand, rubble, and pavement. Site locations and tracks of towed-diver surveys georeferenced with nondifferentially corrected GPS units (Garmin® model 12) were mapped using ArcView GIS 3.3.

All statistical analyses were conducted using PRIMER-E®, version 6 (Clarke and Warwick, 2001; Clarke and Gorley, 2006). For towed-diver surveys, benthic percent cover data from each survey frame were treated as individual replicates within a stratum. Two separate matrices were created. One matrix included percent cover data of all benthic categories to examine differences in overall benthic composition among the strata. A second matrix included only coral data, standardized as percent of total coral cover, to examine differences in relative abundance of coral growth forms among the strata. Square-root transformations were performed on the data matrices to lessen the influence of prevalent benthic components and increase the weight of rare benthic components, and Bray-Curtis resemblance matrices were created from transformed data. To explore spatial distributional patterns, one-way analyses of similarity (ANOSIM; maximum permutations = 9999) were conducted on each matrix to determine if differences existed among the five sampled fore-reef strata. When ANOSIM detected global differences, R values from pairwise tests were examined to determine where major differences existed. SIMPER (similarity percentages routine) analyses using nontransformed data explored the contribution of individual benthic components or coral groups to the dissimilarities.

To visually depict the relationships of strata to each other based on benthic community structure, data were averaged by stratum, and a Bray-Curtis similarity matrix (with square-root transformations) was generated to create a cluster diagram (group average cluster mode) and nonmetric multidimensional scaling (nMDS) ordinations (number of restarts = 50).

Site-specific photoquadrat and coral belt-transect surveys were conducted within the moderate-depth zone at the 12 fore-reef sites and in shallow depths (2–3 m) at the single lagoon site. Percent cover data from each photoquadrat image were treated as individual replicates within sites. Treatment of photoquadrat percent cover data including all benthic categories was similar to that described for towed-diver survey percent cover data. From a matrix including only coral data, ranked cumulative abundance (*k*-dominance) curves were constructed from nonstandardized data, and ANOSIM was conducted on a matrix of distances generated by DOMDIS (dominance distance) between the dominance curves in the two fore-reef sectors. To explore the relative abundance of coral genera using the numbers of colonies rather than percent cover as a metric, *k*-dominance curves were constructed from nonstandardized colony count data, and ANOSIM was conducted on a separate matrix of distances generated by DOMDIS between the *k*-dominance curves in the two fore-reef sectors. SIMPER analysis on nontransformed data explored average similarities and dissimilarities among samples and the contribution of individual taxa to the dissimilarities. Neither photoquadrat nor colony count data from the lagoon patch reef were included in statistical analyses because the single site surveyed likely does not adequately represent the lagoon.

To examine differences in size-class structure among fore-reef sectors of the two most numerically abundant genera, *Pocillopora* and *Montipora*, the number of colonies of each genus was standardized and then cumulated at each site, and a resemblance matrix based on Euclidean distance was created for each genus. A one-way ANOSIM was conducted for each genus to determine if the size-class distributions differed between fore-reef sectors.

RESULTS

Towed-Diver Surveys

Survey Effort

The distance between frames sampled at 30-sec intervals from benthic tow imagery depends on the tow speed; the average interframe distance ranged from 16.5 m to 23.6 m (mean = 20.3 m, n = 12 tows). The average benthic area captured in laser-scaled frames from the Northwestern Hawaiian Islands and applied to the Wake tows was 0.583 m^2 (SE = 0.01 m^2, n = 6398 frames). Towed divers surveyed 22.5 km of benthic habitat (Table 1, Figure 2), from which 1038 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 (1038 frames x 0.583 m^2/frame = 605 m^2) samples a total survey area of 19,842 m^2 (Table 1).

Survey effort, assessed by the area analyzed in sampled frames, was greater on the southwest than the northeast fore-reef slope (323 m^2 and 283 m^2, respectively; Table 1). Of the three depth strata, survey effort was greatest at deep (18.2–28.5 m) depths. The shallow stratum (< 9.1 m) was only surveyed along the southeasterly portion of the southwest fore reef (Figure 2).

Spatial Analyses of Benthic Cover and Composition

Percent cover estimates of benthic components from analysis of towed-diver survey imagery exhibited 39% average similarity among all southwest fore-reef slope samples (n = 553) and 42% average similarity among all northeast fore-reef slope samples (n = 485) (Table 1), but average dissimilarity between the two fore-reef sectors was 68%. The northeast sector was dominated by coral (54% of cover) (Table 1), while the southwest sector was dominated by a combination of macroalgae and turf-covered pavement (29% and 23% of cover, respectively). Average similarity within the five strata ranged from 38% to 48%, with the lowest similarities found among shallow and deep southwest fore-reef samples and the highest among moderate-depth northeast fore-reef samples (Table 1). The highest coral cover (57%) as well as the highest coralline algal cover (8%) was found in the deep northeast stratum.

Table 1. Survey effort, coralline algal and coral cover, and average similarity of benthic composition in sampled frames from towed-diver surveys conducted on the fore-reef slope at Wake Atoll, 2005. Shallow: < 9.1 m; Moderate: 9.1–18.2 m; Deep: 18.2–28.5 m.

Sector	Depth Zone	Distance surveyed (m)	Area surveyed[a] (m^2)	# Frames Analyzed	Area analyzed[a] (m^2)	Mean % coralline algal cover (SE)	Mean % total coral cover (SE)	Proportion of total coral cover							Average Similarity
								Branching	Digitate	Encrusting	Massive	Mushroom	Plate	Octocorals	
ALL	ALL	22500	19842	1038	605	6.0 (0.3)	36.0 (0.8)	2.5	19.0	40.2	18.8	0.0	0.9	18.6	36.2
SW	ALL	12685	11186	553	323	5.1 (0.4)	20.1 (0.7)	6.0	33.6	43.3	12.3	0.1	0.4	4.4	38.6
	Shallow			73	43	6.1 (1.4)	23.3 (2.1)	4.0	52.5	32.5	10.2	0.1	0.4	0.4	37.8
	Moderate			298	174	4.3 (0.5)	20.4 (1.0)	6.2	30.9	46.0	13.2	0.1	0.4	3.3	40.4
	Deep			182	106	6.0 (0.7)	18.5 (1.3)	6.4	29.3	43.5	11.9	0.1	0.4	8.4	37.8
NE	ALL	9815	8656	485	283	6.9 (0.4)	54.1 (1.1)	1.0	12.8	38.9	21.5	0.0	1.1	24.6	42.2
	Moderate			122	71	4.9 (0.6)	46.6 (1.9)	1.7	10.4	52.1	21.6	0.0	0.6	13.5	48.0
	Deep			363	212	7.6 (0.5)	56.5 (1.3)	0.8	13.5	35.3	21.5	0.0	1.2	27.6	41.3

[a] Area is based on average area of laser-scaled frames sampled at 30-sec intervals.

One-way ANOSIM of towed-diver survey data revealed percent cover of benthic components to be significantly different among the five strata (global $R = 0.171$, $p = 0.0001$). Of the 10 pairwise tests, the greatest differences were found between the deep northeast and each of the shallow and deep southwest fore-reef strata ($R = 0.32$ and 0.30, respectively) (Figure 3). SIMPER tests revealed that a large suite of benthic components contributed to the differences among the strata with turf-covered pavement, macroalgae, and sand making the largest contributions.

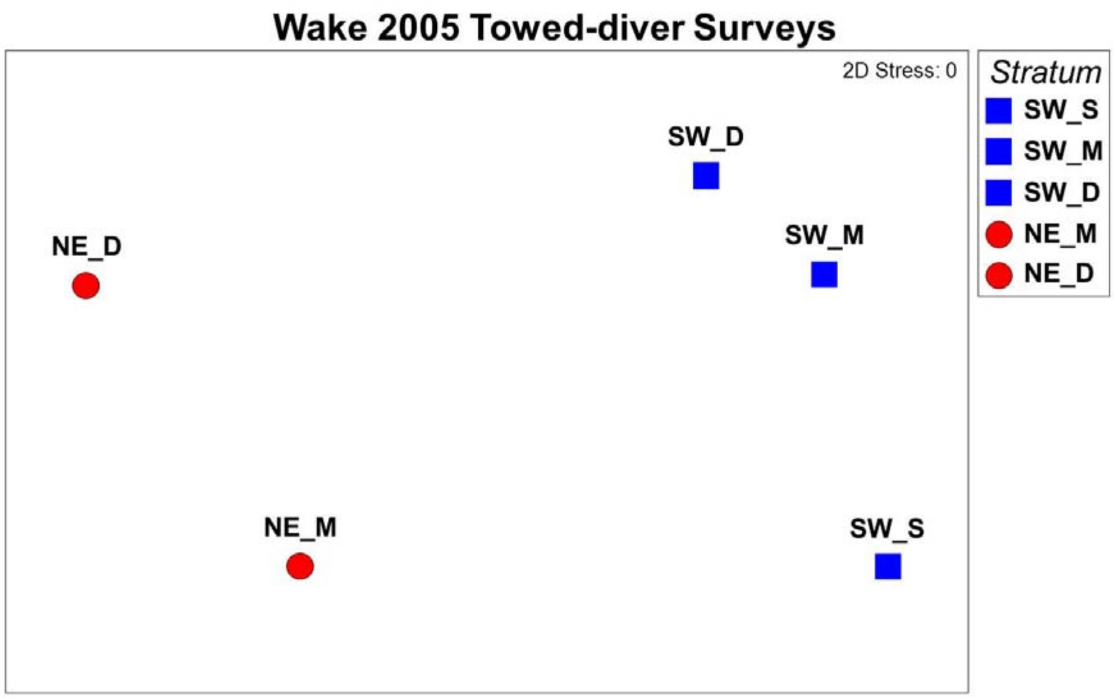

Figure 3. Nonmetric multidimensional scaling (nMDS) ordination depicting relationships of benthic communities based on percent cover data from towed-diver surveys. Each symbol represents the average of data derived from analysis of imagery captured at 30-sec intervals. Stratum key represents Sector_Depth, where SW = southwest and NE = northeast for sector; S = shallow, M = moderate, and D = deep for depth.

Spatial Analyses of Coral Cover and Composition

Mean total coral cover on the fore-reef slope was 36.0% (SE 0.8, $n = 1038$), with coral cover substantially higher in the northeast sector (mean 54.1%, SE 1.1, $n = 485$) than the southwest sector (mean 20.1%, SE 0.7, $n = 553$) (Table 1). Of the five surveyed strata, mean coral cover was highest (56.5%) on the deep northeast fore reef and lowest (18.5%) on the deep southwest fore reef. Average similarity of coral growth form relative abundance derived from analysis of towed-diver survey imagery ranged from 45% to 54%, with the lowest average similarities found among the deep southwest and deep northeast samples, and the highest among the shallow southwest samples.

Encrusting corals were the most abundant scleractinian growth form in all five fore reef strata except the shallow southwest, where digitate growth forms predominated (Table 1). Digitate corals were the next most abundant scleractinian growth form in the two other southwest strata (Figure 4), while corals with a massive growth form were the second most abundant scleractinian type in the northeast strata. Octocorals accounted for 25% of total coral cover in the northeast sector but were uncommon in the southwest sector. Branching, solitary mushroom, and plate-like coral growth forms were uncommon to rare in all five surveyed strata.

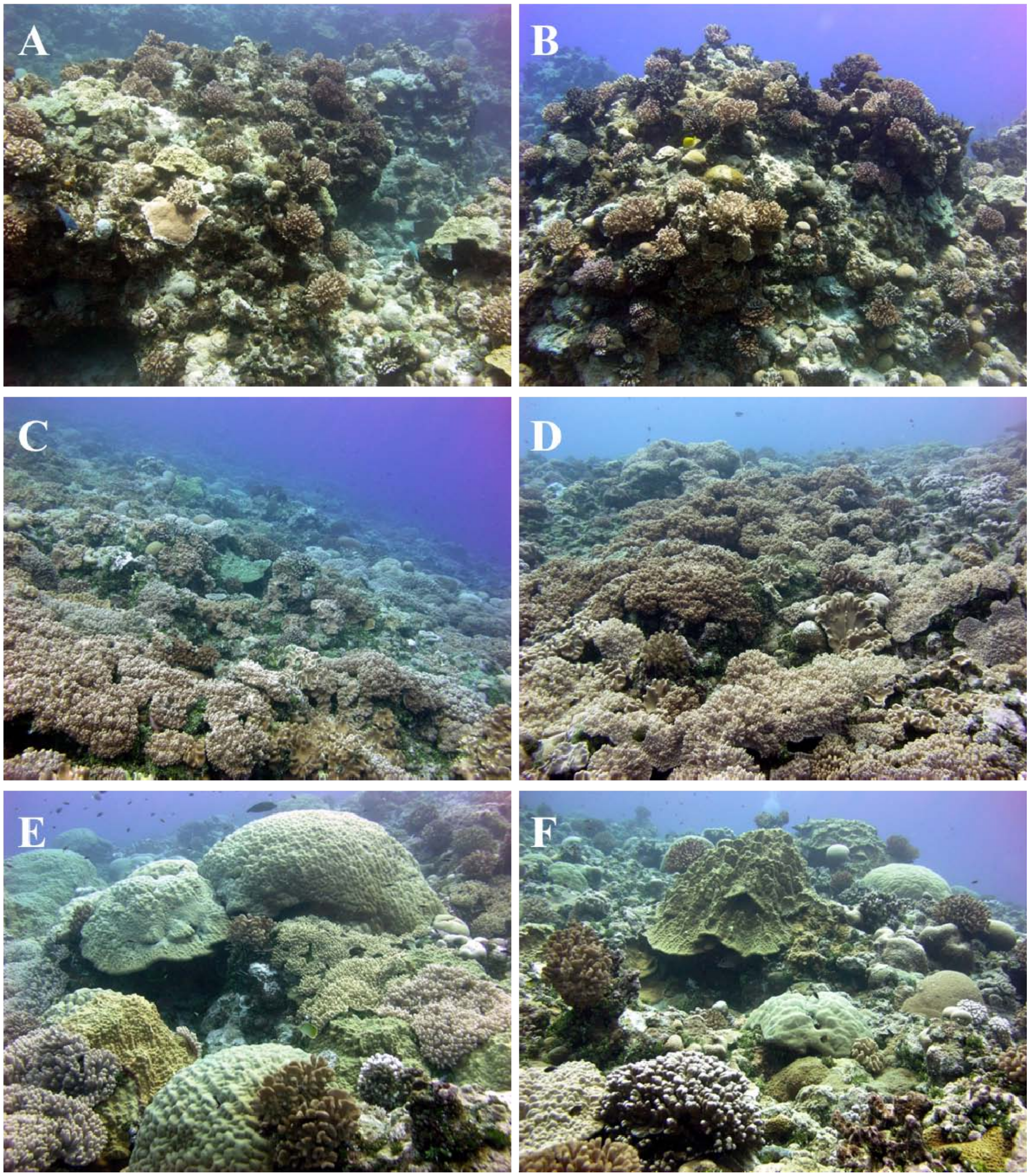

Figure 4. Benthic communities in two fore-reef sectors at Wake Atoll. (a, b) Southwest sector, showing abundance of coral with digitate growth form; (c, d) Northeast sector, showing abundance of octocorals;(e, f) Northeast sector, showing abundance of coral with massive growth form. All photos acquired by the lead author as a roving diver at moderate depths.

Species Inventory of Corals and Other Anthozoans

A total of 82 species of stony, soft, and hydrozoan corals and 1 other anthozoan were recorded during surveys conducted in 2005 (Table 2). When combined with species lists by Maragos (unpublished, 1979) and Molina (USFWS, 1999), a total of 101 species of stony, soft, and hydrozoan corals and 1 other anthozoan are now reported from Wake Atoll. Within the class Anthozoa, three taxonomic orders are represented. Within the stony coral order Scleractinia, 10 families containing 27 genera and 95 species are represented.

Of the 80 scleractinian and hydrozoan taxa whose identity were well established, 66 (82.5%) have been reported from the Mariana Islands, 58 (72.5%) from the northern Marshall Islands, and 19 (23.8%) from the Hawaiian Islands.

Site-Specific Surveys: Photoquadrats

Spatial Analyses of Benthic Cover and Composition

All fore-reef surveys were conducted in the moderate depth zone. Percent cover estimates of benthic components from analysis of photoquadrat imagery exhibited 35% average similarity among all southwest fore-reef samples (n = 84) and 33% average similarity among all northeast fore-reef samples (n = 60), but average dissimilarity between southwest and northeast fore-reef samples was 72%. Scleractinian and octocoral cover were greatest on the northeast fore reef, while macroalgae and pavement covered with turf algae dominated the southwest fore reef. Sand dominated the single, shallow (2–3 m) site surveyed in the lagoon (Table 3).

One-way ANOSIM revealed percent cover of benthic components to be significantly different between the two fore-reef sectors (global R = 0.186, p = 0.0001). SIMPER tests indicated that a large suite of benthic components contributed to the differences between the two fore-reef sectors with turf-covered pavement and sand making the strongest contributions.

Spatial Analyses of Coral Cover and Composition

Mean total coral cover ranged from 10.2% at the single site surveyed in the lagoon to 47.2% on the northeast fore reef (Table 4**).** Estimates of coral relative abundance derived from analysis of photoquadrat imagery exhibited 27% average similarity among all southwest fore-reef samples and 20% average similarity among all northeast fore-reef samples, but average dissimilarity between southwest and northeast fore-reef samples was 80%.

Twelve scleractinian, two alcyonacean (the octocorals *Lobophytum* and *Sinularia*), and one hydrozoan coral genera were scored in photoquadrats (Table 4). Cumulative ranked abundance (k-dominance) curves (Figure 5a) demonstrated lower dominance (greater equitability) of coral genera in the northeast relative to the southwest fore reef. ANOSIM revealed a significant difference between the k-dominance curves in the two fore-reef sectors (global R = 0.288, p = 0.044). SIMPER revealed that *Montipora*, *Pocillopora,* and *Favia* together accounted for ~50% of the average dissimilarity between the two fore-reef sectors.

Montipora was the most highly ranked coral genus in both fore-reef sectors, and was the only coral genus seen in photoquadrat imagery at the single site surveyed in the lagoon (Table 4). *Pocillopora* and *Porites* were the next most abundant coral genera on the southwest fore reef, while *Porites* and the octocoral *Sinularia* were the next most abundant on the northeast fore reef. All other genera individually accounted for <10% of the total coral cover in both fore-reef sectors.

Site-Specific Surveys: Coral Belt Transects

Coral Colony Relative Abundance

A total of 3578 colonies belonging to 19 scleractinian and 3 alcyonacean (the octocorals *Sarcophyton*, *Sinularia,* and *Lobophytum*) genera were recorded in belt-transects (Table 5). Average similarity of samples within the southwest fore-reef sector (77.2) was greater than the average similarity within the northeast fore-reef sector (69.0; Table 5).

Table 2. Scleractinian corals, octocorals, hydrozoan corals, and other Anthozoa reported at Wake Atoll from 1979 to 2005 surveys. Species denoted "*sensu* Randall" identified according to characteristics described in Randall and Myers (1983). RL = IUCN Red List of Threatened Species[TM]

	Data Source			Records		Habitats Observed		
SCLERACTINIAN CORALS	Maragos 1979	Molina 1998	Kenyon & Bonito 2005	Sample	Photo	Fore reef	Reef flat	Lagoon
Acanthastrea echinata	X	X	X		x	x	x	x
A. hillae			X	x	x	x		
Acropora abrotanoides			X	x	x	x		
A. aculeus [RL]		X				x		
A. acuminata [RL]	X						x	x
A. cf. *cerealis*			X			x		
A. formosa	X						x	x
A. humilis			X	x	x	x		
A. hyacinthus			X	x		x		
A. lutkeni			X		x	x		
A. cf. *microclados*			X	x	x	x		
A. nasuta	X	X				x	x	x
A. ocellata sensu Randall			X			x		
A. palmerae [RL]			X			x		
A. cf. *striata*			X	x	x			x
A. surculosa			X	x	x	x		
A. valida	X	X	X	x	x	x	x	x
Acropora sp. A[1]			X	x	x	x	x	x
Acropora sp. B[2]			X	x	x	x		
Acropora sp. C[3]			X	x	x	x		x
Acropora sp. D[4]			X	x	x	x		
Astreopora myriophthalma		X	X	x	x	x	x	
A. randalli			X		x	x		
Cyphastrea chalcidicum			X	x	x	x	x	x
C. microphthalma		X	X	x	x	x		
C. serailia	X	X	X		x	x	x	x
Echinopora lamellosa		X	X	x	x	x		
Favia favus		X	X		x	x		
F. helianthoides			X	x	x	x		
F. matthai			X	x	x	x	x	x
F. pallida	X	X	X	x	x	x	x	
F. speciosa	X						x	
F. stelligera	X	X	X	x	x	x	x	
Favia sp.			X		x	x		
Favites abdita	X	X				x	x	x
F. complanata			X			x		
F. flexuosa	X	X				x	x	
F. halicora	X	X		x		x	x	
Fungia scutaria		X	X	x	x	x		
Goniastrea edwardsi			X	x	x	x		x
G. favulus		X	X	x	x	x		
G. pectinata	X	X	X	x	x	x	x	

Table 2. Continued	Data Source			Records		Habitats Observed		
SCLERACTINIAN CORALS	Maragos 1979	Molina 1998	Kenyon & Bonito 2005	Sample	Photo	Fore reef	Reef flat	Lagoon
G.retiformis	X	X				x	x	
Hydnophora exesa			X	x	x	x		
Leptastrea aequalis			X	x			x	
L. purpurea	X	X	X	x	x	x	x	
L. transversa			X	x	x	x		
Leptoria phrygia		X				x		
Leptoseris mycetoseroides		X	X	x	x	x		
Lobophyllia hemprichi	X					x		
Merulina ampliata		X	X	x	x	x		
Montastrea curta		X	X	x	x	x	x	
M. valenciennesi		X	X	x	x	x	x	x
Montipora danae		X				x		
M. foveolata	X	X	X	x	x	x		
M. grisea			X	x	x	x	x	x
M. hoffmeisteri	X	X	X		x	x	x	x
M. incrassata			X	x	x	x		
M. informis	X	X	X	x	x	x	x	
M. lobulata [RL]	X		X	x	x	x	x	x
M. marshallensis	X						x	
M. monasteriata		X	X			x		
M. tuberculosa			X	x	x	x		x
M. verrucosa		X				x		
Montipora sp. 2 *sensu* Randall			X	x	x	x		
Montipora sp. A[5]			X	x	x	x		x
Montipora sp. B[6]			X	x	x	x		
Montipora sp. C[7]			X		x	x		
Montipora sp. D[8]			X	x	x	x		x
Pavona duerdeni			X	x	x	x		
P. maldivensis			X	x	x	x		
P. varians		X	X	x	x	x	x	x
Pavona sp. 1 *sensu* Randall			X	x	x	x		
Platygyra daedalea		X	X	x	x	x	x	
P. lamellina			X		x	x		
P. sinensis		X		x		x		
Pocillopora damicornis	X		X	x	x		x	x
P. elegans [RL]			X		x	x		
P. eydouxi	X	X	X		x	x		
P. meandrina	X	X	X		x	x		
P. setchelli			X			x	x	
P. verrucosa	X	X	X	x	x	x	x	x
Porites lichen			X	x	x	x		
P. lobata	X		X	x	x	x	x	x
P. lutea	X	X	X		x	x	x	x
P. rus			X	x	x	x		
P. solida	X	X	X	x	x	x		

Table 2. Continued	Data Source			Records		Habitats Observed		
SCLERACTINIAN CORALS	Maragos 1979	Molina 1998	Kenyon & Bonito 2005	Sample	Photo	Fore reef	Reef flat	Lagoon
Psammocora profundacella			X	x	x	x		
Psammocora sp.	X		X	x	x	x	x	
Scapophyllia cylindrica			X	x	x	x		
Seriatopora hystrix	X						x	
Stylophora mordax			X	x	x	x		
Symphyllia radians		X				x		
S. recta		X	X	x	x	x		
Tubastrea sp.			X	x	x	x		
OCTOCORALLIA CORALS								
Lobophytum sp.			X	x	x	x		
Sarcophyton sp.			X	x	x	x	x	
Sinularia sp.			X	x	x	x		
Stereonephthya sp.			X	x	x	x		
HYDROZOAN CORALS								
Millepora exaesa		X				x		
M. platyphylla	X		X	x	x	x		
ZOANTHIDS								
Palythoa sp.			X	x	x	x		

[1]caespitose colonies; tubular incipient axial corallites are common; [2]thick-branched, with nariform radial corallites; [3]corymbose colonies with nariform radial corallites; [4]caespitose colonies with tubular radial corallites ; [5]encrusting colonies with coenosteal papillae; [6]encrusting colonies with prominent thecal papillae; [7]encrusting colonies with coenosteal papillae, often forming short ridges; [8]encrusting colonies with coenosteal papillae mostly forming short ridges

Table 3. Mean percent cover of benthic components, derived from photoquadrat imagery at Wake Atoll, 2005.

Category	Southwest Fore reef	Northeast Fore reef	Lagoon Patch
Scleractinian corals	16.6	39.4	10.2
Octocorals	0.1	7.8	0.0
Millepora	0.2	0.0	0.0
Halimeda	10.9	10.1	0.0
Other Macroalgae	14.7	9.7	11.3
Coralline Algae	0.4	5.5	0.0
Other Invertebrates	0.2	0.0	0.7
Pavement	26.6	25.3	12.0
Sand	22.0	2.0	59.8
Rubble	8.3	0.2	6.0
Average Similarity	34.6	32.7	44.0

Table 4. Relative abundance of coral genera, expressed as percent of mean total coral cover, derived from photoquadrat imagery at Wake Atoll, 2005.

Genus	Southwest Fore reef	Northeast Fore reef	Lagoon Patch
Acanthastrea	4.7	6.4	0.0
Astreopora	0.3	9.1	0.0
Cyphastrea	1.9	7.5	0.0
Favia	6.2	5.9	0.0
Favites	0.0	0.2	0.0
Goniastrea	2.4	2.3	0.0
Leptastrea	0.1	0.2	0.0
Lobophytum	0.0	5.5	0.0
Millepora	1.2	0.0	0.0
Montastrea	2.8	3.5	0.0
Montipora	39.1	27.6	100.0
Pavona	0.6	0.2	0.0
Pocillopora	27.4	3.3	0.0
Porites	12.8	17.2	0.0
Sinularia	0.6	11.2	0.0
Mean (SE) coral cover, %	16.9 (2.0)	47.2 (3.7)	10.2 (5.0)
Average Similarity	27.1	20.1	100.0

Cumulative ranked abundance (*k*-dominance) curves (Figure 5b) demonstrated lower dominance (greater equitability) of coral genera in the northeast relative to the southwest fore reef. Four scleractinian genera—*Pocillopora*, *Montipora*, *Favia*, and *Goniastrea*—accounted for >70% of all colonies enumerated in the southwest sector, while the four most abundant coral genera in the northeast sector (*Montipora*, *Favia*, *Pocillopora*, and *Acanthastrea*) accounted for only slightly more than half of all colonies enumerated in that sector (Table 5, Figure 5b). ANOSIM revealed a significant difference between the *k*-dominance curves in the two fore-reef sectors (global $R = 0.814$, $p = 0.001$). SIMPER revealed that *Pocillopora* and *Lobophytum* accounted for the greatest contributions to the dissimilarities between the two fore-reef sectors. All other genera individually accounted for < 10% of the total number of colonies in both fore-reef sectors.

At the single site surveyed in the lagoon, *Montipora* accounted for close to 80% of enumerated colonies.

Coral Size-class Distributions

All *Pocillopora* colonies had a maximum diameter < 40 cm (Figure 6a, b). Size-class distributions of *Pocillopora* did not vary significantly between the two fore-reef sectors (global $R = 0.184$, $p = 0.072$), with >75% of the colonies in each sector having a maximum diameter between 10 and 40 cm. Size-class distributions of *Montipora* did not vary significantly between the two fore-reef sectors (global $R = 0.123$, $p = 0.120$), with >15% of the colonies in each sector having a maximum diameter > 40 cm (Figure 6c, d).

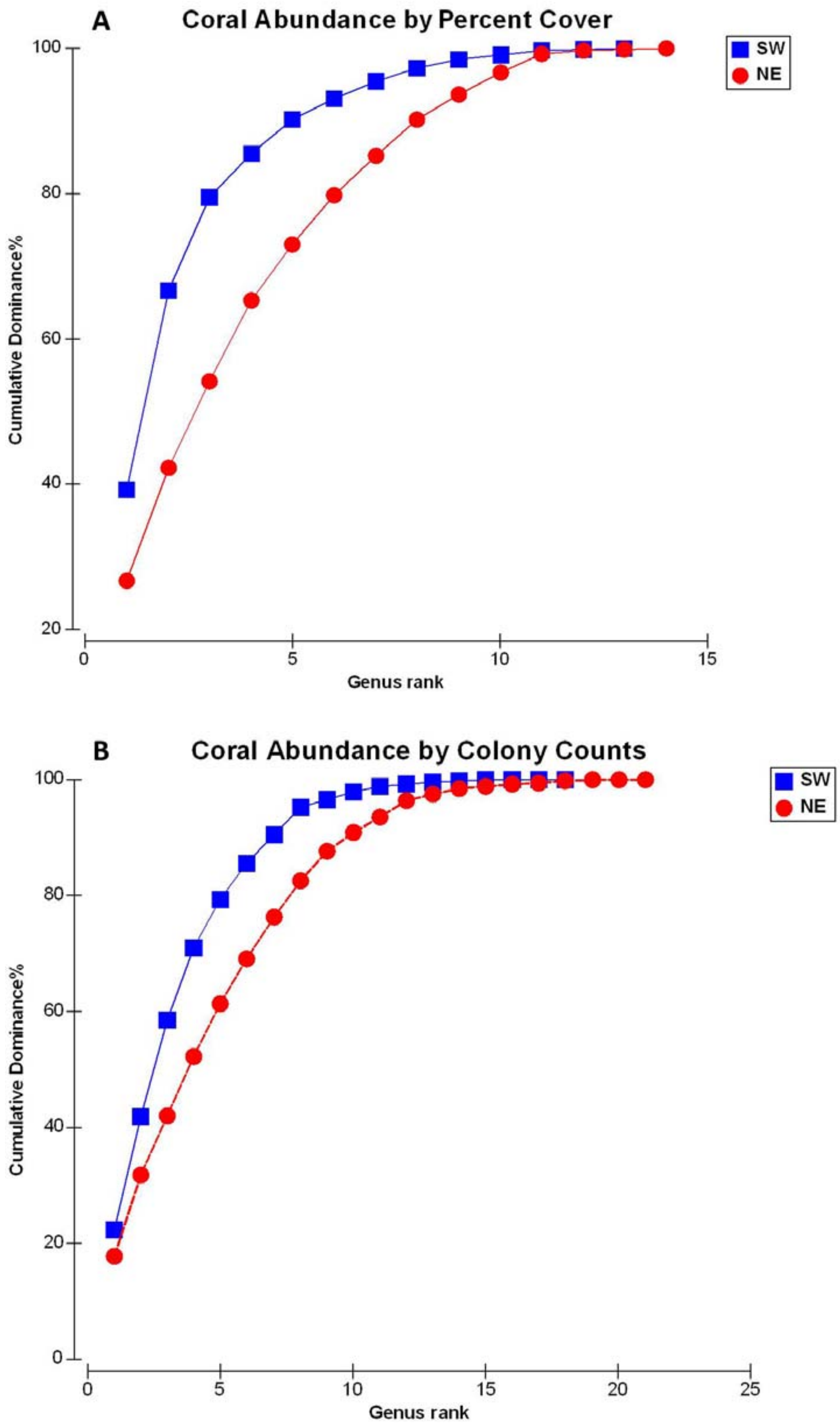

Figure 5. Cumulative ranked abundance curves (*k*-dominance curves) for corals in two fore-reef sectors at Wake Atoll. (a) Based on percent cover data from photoquadrats. (b) Based on colony counts in belt transects. SW = southwest, NE = northeast

Table 5. Relative abundance of coral genera, expressed as percent of total number of coral colonies, derived from belt-transect surveys at Wake Atoll, 2005.

Genus	Southwest Fore reef	Northeast Fore reef	Lagoon Patch
Acanthastrea	8.3	10.2	1.5
Acropora	0.1	0.3	3.0
Astreopora	1.3	3.2	0.0
Cyphastrea	4.9	2.8	6.1
Echinopora	0.4	0.5	0.0
Favia	16.7	13.9	4.5
Favites	0.0	0.1	0.0
Fungia	0.0	0.4	0.0
Goniastrea	12.4	7.2	0.0
Leptastrea	0.4	0.1	0.0
Lobophytum	0.0	9.0	0.0
Montastrea	4.8	6.2	4.5
Montipora	19.6	17.8	78.8
Pavona	1.2	0.8	0.0
Platygyra	0.1	1.1	0.0
Pocillopora	22.2	10.4	0.0
Porites	6.2	5.1	1.5
Psammocora	0.0	0.0	0.0
Sarcophtyton	0.0	2.8	0.0
Scapophyllia	0.0	0.1	0.0
Sinularia	1.0	7.9	0.0
Stylophora	0.0	0.3	0.0
Total colonies enumerated	2084	1428	66
Average Similarity	77.2	69.0	—

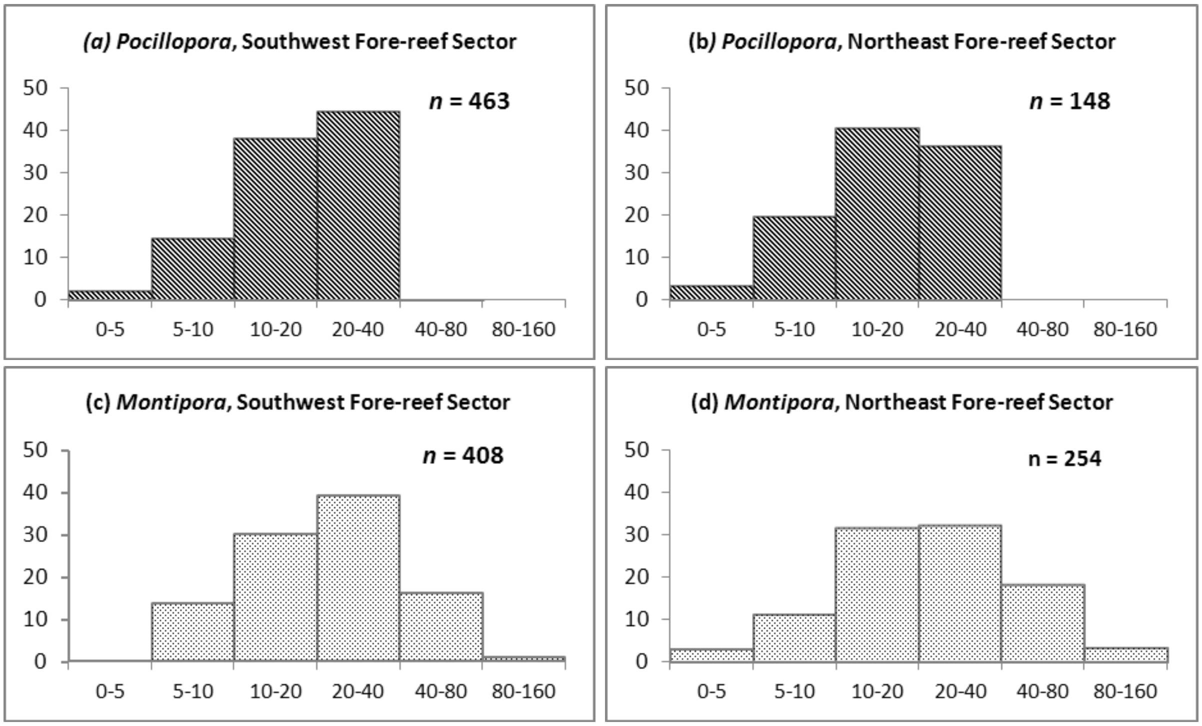

Figure 6. Size -class (cm) distributions of *Pocillopora* and *Montipora* in two fore-reef sectors at Wake Atoll. The x-axis is maximum diameter (cm); the y-axis is percent of *Pocillopora* (a-b) or *Montipora* (c-d) colonies enumerated in each sector.

DISCUSSION

Little published or unpublished information exists concerning the coral fauna at Wake Atoll. Here, we apply multivariate statistical analyses to data acquired in 2005 from several complementary survey methods that operate at different scales of spatial and taxonomic resolution to characterize the benthic fore-reef communities at Wake Atoll in relationship to strata defined by geographic sector and depth zone. Analysis of imagery recorded during broad-scale surveys conducted by towed divers provides a spatially extensive assessment of benthic communities at a relatively coarse level of taxonomic resolution, while site-specific surveys using photoquadrats and belt transects enable finer resolution of corals to the genus or species level. In the following discussion, the diverse metrics generated by these three methodologies are synthesized to provide a baseline description of fore-reef coral communities at Wake Atoll.

Towed-diver surveys revealed broad differences between sectors and strata in overall benthic composition, mean coral and coralline algal cover, and dominant coral growth forms. While within-sector similarity of overall benthic composition was comparable for both the SW and NE sectors (39% and 42%, respectively), dissimilarity of benthic composition between the two sectors was high (68%) (Figure 3). Among the depth strata within the sectors, the greatest difference in overall benthic composition was found between the deep NE and two of the SW strata. In examining the coral component of overall benthic composition, mean coral cover in the NE sector was more than 2.5 times greater than in the SW sector (54.1% and 20.1%, respectively), with octocorals accounting for >25% of the total coral cover in the NE sector but < 5% in the SW sector. Encrusting and massive coral growth forms dominated in the NE sector, while encrusting and digitate coral growth forms dominated in the SW sector. Of the depth strata within the sectors, the greatest difference in coral growth form composition was found between the deep NE and the shallow SW strata, congruent with the major strata differences in overall benthic composition. Moreover, the deep NE stratum showed among the highest diversity of growth forms (i.e., lowest within-stratum similarity, 45%) while the shallow SW stratum showed the lowest diversity of growth forms (i.e., highest within-stratum similarity, 54%). The deep NE stratum was also distinguished by the highest total coral cover (56.5%), octocoral cover (27.6% of total coral cover), and coralline algal cover (8%).

Complementing the results from towed-diver surveys with regard to overall benthic composition, site-specific photoquadrats revealed comparable within-sector similarity for both the SW and NE sectors (35% and 33%, respectively), but high dissimilarity (72%) between the two sectors. Consistent with results from broad-scale towed-diver surveys, mean total coral cover derived from photoquadrats in the NE sector was more than 2.5 times greater than in the SW sector (47.2% and 16.9%, respectively), with good agreement in the magnitude of the independent estimates derived from towed-diver surveys and from photoquadrats. Octocorals accounted for 16.5% of the total coral cover in the NE sector but only 3.5% in the SW sectors; the discrepancy between octocoral relative abundance estimates from towed-diver surveys and photoquadrats in the NE sector (> 25% vs. 16.5%) likely reflects the small area sampled by the photoquadrats (8.4 m^2) relative to the extensive area sampled by towed-divers (283 m^2, Table 1).

Photoquadrat data revealed more taxonomically-detailed patterns characterizing the two fore-reef sectors at moderate depths. Congruent with variability between the NE and SW sector in the relative proportion of different coral growth forms (Table 1), there was high average dissimilarity (80%) between NE and SW sectors in the genus-level taxonomic composition of the coral cover. Equitability of the taxonomic composition of coral cover was significantly greater in the NE than the SW sector, though *Montipora* accounted for the highest contribution to mean total coral cover in both sectors. *Porites* was among the primary components of coral cover in both sectors, with octocorals and *Pocillopora* also dominating coral cover in the NE and SW sector, respectively.

In examining coral taxonomic composition using the number of colonies as a metric rather than percent cover, site-specific coral belt-transect data also revealed that equitability of the coral fauna was significantly greater in the NE than the SW sector, though three genera had the greatest relative abundances in both sectors: *Montipora*, *Pocillopora*, and *Favia*. Size class distributions of the most numerically abundant genera, *Montipora* and *Pocillopora*, were not significantly different between the two sectors, however.

Wake Atoll supports at least 102 species and 33 genera of corals and other cnidarians based on spatially limited surveys conducted between 1979 and 2005. These consist of 95 species in 27 genera of scleractinian stony corals; 2 species in a single genus of hydrozoan corals; 4 genera of soft octocorals; and 1 genus of zoanthid soft corals (Table 2). Scleractinian species richness at Wake is lower than in the northern Marshall Islands (168 species; Maragos, 1994) and Mariana Islands (377 species; Randall, 2003), but exceeds that in the Hawaiian Islands (65 species; Fenner, 2005). Zoogeographic analysis of the fish fauna (321 species) at Wake by Lobel and Lobel (2004) indicated the greatest species overlap occurred with the northern Mariana islands (87%) and the Marshall Islands (82%), and lower species overlap occurred with the southern Mariana Islands (66%) and Hawaiian Islands (40%). Zoogeographic analysis of the list of 80 coral species with well-established names presently reported from Wake Atoll also indicates greatest overlap with the Mariana (82.5%) and the northern Marshall Islands (72.5%) and lesser overlap with the Hawaiian Archipelago (23.8%). In comparison, marine benthic algae documented from Wake Atoll also contain components from the Marshall Islands and Hawaiian Islands, but show a closer resemblance to the Hawaiian Islands; of the 107 species of red, brown, and green algae recorded from Wake, 93.4% are represented in the Hawaiian marine flora whereas only 50.4% are reported from the Marshall Islands (Tsuda et al., 2010). The coral fauna at both Wake and the northern Marshall Islands remain poorly studied, however, relative to the Mariana Islands and the Hawaiian Islands. More spatially-extensive surveys and clarification of species that are currently only identified to the genus level are likely to modify the estimates of geographical overlap in this initial analysis. At Wake, greater search effort on the deeper fore reef, reef flat, and lagoon patch reefs will likely yield additional species.

Five coral species found at Wake are listed on the IUCN Red List of Threatened Species™ (*Acropora aculeus, A. acuminata, A. palmerae*, *Montipora lobulata*, and *Pocillopora elegans*; Table 2). All five species are categorized as Vulnerable, the lowest level of extinction risk in the Red List 3-tiered system of threatened species, based on the IUCN sub-criterion A4: an observed, estimated, inferred, projected or suspected population size reduction ≥ 30% over two generations in the past and one into the future, where the generation length was considered as 10 years except for *Pocillopora elegans* (5 years) (IUCN, 2001; Carpenter et al., 2008). While widely viewed as a useful index in estimating extinction risk, the IUCN Red List of Threatened Species™ carries no weight of law. In October 2009 the nongovernmental organization Center for Biological Diversity petitioned the NOAA to list 83 species of corals under the U.S. Endangered Species Act (ESA), including the five Wake species reported in this study. The ESA does have the weight of law. The National Marine Fisheries Service is currently leading the process to independently evaluate the extinction risk of these species, and if listed under the ESA, these corals would receive legal protection.

In conducting coral disease assessments at 40 different coral islands, banks, and atolls in the U.S. Pacific, Vargas-Ángel (2009) reported a mean prevalence of coral disease (proportion of colonies manifesting a disease state) of 3.9 at Wake. Though considered a low prevalence of disease, Wake ranked the ninth highest among the 40 locations. Skeletal growth anomalies were the most common affliction (mean prevalence 3.2), followed by tissue loss syndrome (0.3), bleaching (0.2), and pigmentation response (0.1). Although the absence of baseline information prior to the present study makes it impossible to know the degree to which Wake coral communities have been impacted by modern factors affecting reef dynamics (e.g., mass bleaching, crown-of-thorns seastar infestations, coastal point source pollution, sedimentation from dredging and construction, and marine invasive species), the fore-reef coral community appears overall in relatively good condition. Significant restrictions on fishing activities, including a ban on commercial fishing, the use of traps, most nets, automated spear guns, and a prohibition on the take of sharks, rays, bumphead parrotfishes (*Bolbometopon muricatum*) and napoleon wrasse (*Cheilinus undulatus*), reduce the threats from overfishing that have been identified as a medium or high threat to over 35% of the world's coral reefs (Waddell, 2005). Dominance of the reef fish community at Wake by secondary consumers (omnivores and benthic invertivores) (Williams et al., 2010) likely enhances coral health by maintaining grazers that help regulate algal and other epibenthic populations.

Corals and coral reefs are increasingly susceptible to the consequences of global climate change including increased mass coral bleaching and reduced accretion due to ocean acidification (Hoegh-Guldberg and Bruno, 2010). As the number of reports of degrading coral reefs increases in response to local and global stressors (e.g., Knowlton, 2001; Hughes et al., 2003; Pandolfi, 2005; Hoegh-Guldberg et al., 2007), it becomes increasingly urgent to establish detailed descriptive baselines by which the direction and pace of future changes can be determined. Our application of multivariate statistical analyses to survey data collected at different scales of spatial and taxonomic resolution has discerned spatial variation that provides a baseline for future surveys to detect future trajectories of change.

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