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## Spatial heterogeneity of benthic community assemblages with an emphasis on reef algae at French Frigate Shoals, Northwestern Hawai'ian Islands

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**Abstract** Reefs in tropical atoll systems have historically been described on a geomorphic basis, and segregated into loosely defined fore-reef, back-reef, and lagoonal reef zones. However, recent oceanographic monitoring data have shown that physical factors within a single geomorphic zone can vary significantly, calling into question whether benthic communities within a single zone are biologically similar. To determine the amount of benthic variability that may occur in a geomorphic zone, percent cover of benthic organisms was determined at the species level for 28 sites in three geomorphic zones at French Frigate Shoals, Northwestern Hawai'ian Islands. Multivariate statistical analyses found most windward fore-reef and back-reef sites to be statistically similar, but considerable variation to exist among sites within calmer lagoonal areas. Surveys revealed macroalgae to dominate over scleractinian coral species at the majority of sites in this healthy, subtropical reef system, although select lagoonal areas were dominated by dense coral communities.

**Keywords** Coral reef · Ecozone · Geomorphic zone · PRIMER · Monitoring · Rapid ecological assessment

### Introduction

Most basic texts dealing with coral reef biology have historically divided tropical reef systems into simple zones based on the geomorphic characteristics (Dawes

1998; Lalli and Parsons 1997; Nybakken 1988; Sumich 1988). Ocean facing reefs are labeled as reef slopes or buttresses, sublittoral, and fore-reef zones, while lagoon facing reefs inside the reef crest are alternatively called reef flats, littoral zones, or back-reefs. Reefs within the lagoon are sometimes termed moat reefs, lagoon reefs, or patch reefs. Although significant variation may exist within each geomorphic zone, these areas are commonly used by reef biologists to circumscribe distinct habitat types because each experiences broadly similar environmental conditions unique from the others (Morton and Challis 1969; Odum and Odum 1955; Womersley and Bailey 1969). Ocean facing reefs are typically dynamic environments, experiencing high wave and surge energy, as well as variable depth ranges, which effect light and temperature (Sumich 1988). Back reefs and lagoon reefs are more sheltered from high wave energy and experience higher irradiance because of shallow depths. However, while back reefs are continually flushed and sometimes experience high surge because of their proximity to the reef crest, lagoon reefs represent calmer environments with reduced water circulation and potentially higher water temperatures (CRED, unpublished data).

Because each geomorphic zone experiences differing environmental conditions, benthic communities within each zone were hypothesized to exhibit greater similarity than communities between zones. However, subtle variations in a suite of physical or biotic factors such as storm-generated disturbance, turbidity, and herbivory may structure well-defined geomorphic zones into smaller microcosms, each supporting unique benthic communities (Connell et al. 1997; Hixon and Brostoff 1996; Huston 1985; Littler and Littler 1984). For further understanding of the similarities and differences within and among geomorphic zones, an increased knowledge of how benthic community assemblages are organized in each zone is essential.

Several recent studies have attempted to model spatial differences in tropical reef systems. Many have relied on advances in satellite imagery and remote sensing to

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create maps of habitat types, however, the resolution of these studies has been limited to functional groups and they are unable to detect differences in species composition (Garza-Pérez et al. 2004; NOAA 2003). Models have also been created to predict benthic composition based on the presence of herbivores and abiotic conditions. For instance, the Relative Dominance Theory (RDT) (Littler and Littler 1984) is often used to explain the distribution of algal functional groups in reef settings based on the nutrient regimes and grazing pressure and has been supported in experimental field studies (McCook et al. 2001; Smith et al. 2001). It remains to be seen, however, how this theory relates to large-scale ecological data sets where additional parameters [i.e. chemically defended species (Gross 2003), sedimentation or sand scour by wave energy, or the effects of water motion on boundary layer dynamics] might be contributing to benthic community dynamics.

The relatively unpolluted state of the Northwestern Hawaiian Islands (NWHI) offers an ideal system in which to begin understanding relationships between textbook geomorphic zones and actual benthic communities (Maragos and Gulko 2002; Friedlander et al. 2004). In the subtropical NWHI, coral abundance is relatively low with fore-reef, back-reef zones, and lagoonal reef zones averaging around 8% live cover (Friedlander et al. 2004). Algae, particularly algal turfs and green algal genera such as *Microdictyon* are major space occupiers in many areas (PSV, personal observation). Although, complete documentation of all types of

benthic cover is necessary for understanding relationships among sites, differences in algal communities may be key in defining habitats and are the focus of this study. The goals of the research presented here were to: (1) determine percent cover of benthic organisms at the species level to understand biological community organization, (2) conduct multivariate analyses between sites using percent cover data to determine if benthic community assemblages within classic geomorphic reef zones are statistically similar, and (3) if geomorphic zones are not biologically distinct, establish a posteriori ecozones based on the natural groupings of benthic cover.

## Materials and methods

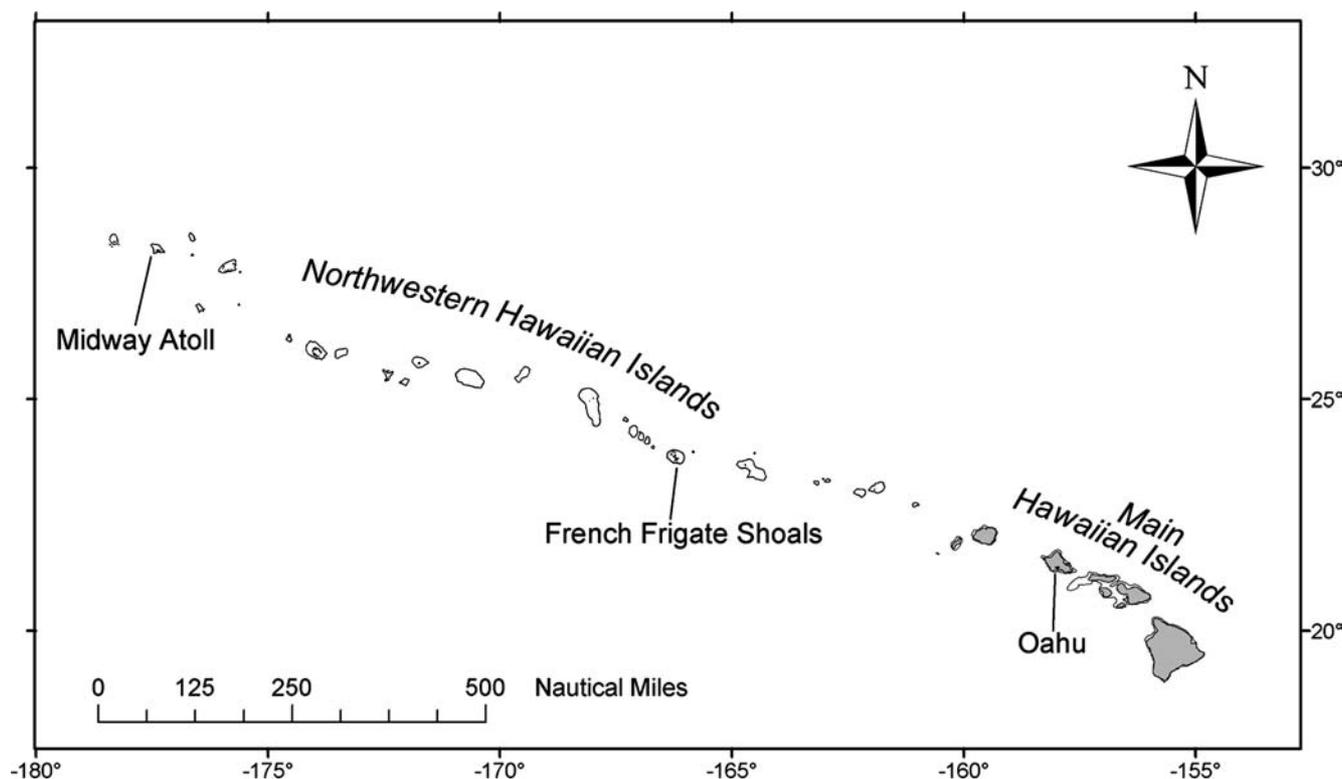
### Location and description

Centered at approximately 23°45' N latitude and 166°11' W longitude (Fig. 1), FFS represents a large, open atoll containing numerous low sand islets and two basalt pinnacles. The eastern side of the atoll system consists of an ocean-facing reef system with classic fore-reef, reef crest, and back-reef zones. Inner lagoonal areas are characterized by shallow sandy and hard bottom communities with numerous, sometimes extensive, patch and linear reefs separated by deep trenches.

### Data collection

Quantitative data of benthic cover was collected at 28 sites between 11 September and 4 October 2002 using a

**Fig. 1** Map of the Hawaiian archipelago showing location of French Frigate Shoals



modified version of the Preskitt Method (Preskitt et al. 2004). At each site, phycologists worked along two 25-m transect lines set in a single-file row, with each transect separated by 10 m. Twelve photos were taken at each site using a photoquadrat (0.18 m<sup>2</sup>) equipped with either a Sony DSC P-9 or an Olympus C-4040 digital still camera and an Ikelite substrobe DS-50: 6 at randomly selected points along the two transects (three per transect), and six at points 3 m perpendicular from each random point in the direction of shallower water. With the exception of some shallower back-reef and lagoonal sites, most transects were placed at a standard 10–15 m depth.

### Data analysis

PhotoGrid (<http://www.photogrid.netfirms.com>) was used to place 100 randomly stratified points on each digital photoquadrat image (300 dpi), and percent cover of individual algal and invertebrate species or substrate type was estimated by identifying items under each point. Highly epiphytized macroalgae or crustose coralline algae were recorded as both macroalgae and turf, leading to percent covers over 100% for most photoquadrats. Species presence and abundance data from each photoquadrat were treated as individual replicates within a site and a Bray–Curtis similarity matrix of quadrats created using PRIMER-E. Before analysis, a fourth-root transformation was performed on quantitative data to lessen the influence of prevalent species and increase the weight of rare species. Data were rigorously compared using a one-way analysis of similarity (ANOSIM; maximum permutations = 5000) to determine if differences in similarities occurred among all sites. Sites were also grouped into a priori geomorphic zones and rigorously compared through a two-way nested analysis of similarity (ANOSIM; sites nested within geomorphic zone; 5000 permutations) to determine if geomorphic zones were biologically distinct. Photoquadrats in the data matrix were then averaged by site, and a Bray–Curtis similarity matrix was generated to create cluster diagrams and multi-dimensional scaling

(MDS) ordinations (number of restarts = 30) visually comparing site relationships.

### Ecozone determination

In an effort to better understand the natural site groupings, a posteriori ecozones were initially interpreted as groups in which no pairwise ANOSIM *r*-statistic was greater than ~ 0.250 (Clarke and Warwick 2001). When these ecozones were compared to cluster diagrams and MDS ordinations, some groupings showed significant overlap with neighboring groups on the MDS ordination. Ecozones were reassessed through comparison to satellite maps, photographs from quadrats, and field notes. Overlapping groups on the MDS ordination that occurred in the same geographic area were combined as long as the majority of *r*-statistics for the group remained below 0.250. The final result was a set of ecozones defined by a combination of geomorphic and biological features. The average percent cover of organisms for each ecozone was determined by averaging site percent covers.

## Results

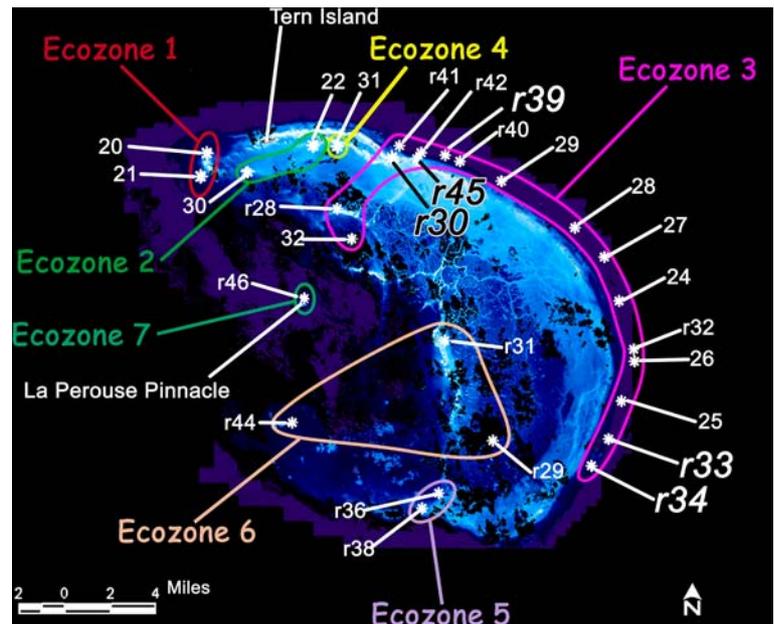
Benthic cover was determined for 336 photoquadrats from 28 sites representing three geomorphic zones at FFS: ten fore-reef, five back-reef, and 13 lagoonal sites. When pre-determined geomorphic zones were compared using a two-way nested ANOSIM, resultant *r*-statistics were negative (data not shown) and indicated that more variability existed within than between geomorphic zones. Individual pairwise *r*-values between sites within geomorphic zones from the one-way ANOSIM found the majority of sites within fore-reef zones to be statistically similar (*r*-values below 0.250; Table 1). However, the vast majority of sites within back-reef and lagoonal zones did not exhibit strong similarities in terms of benthic species composition or cover. When comparisons were made between sites from different geomorphic zones, the degree of variation exhibited by sites between

**Table 1** Comparison of pairwise *r*-statistics from one-way ANOSIM of sites at FFS

Sites compared	<i>r</i> -Values			
	Statistically similar		Statistically dissimilar	
	0.000–0.250	0.251–0.500	0.501–0.750	0.751–1.000
Fore-reef ( <i>n</i> = 45)	62%	33%	4%	0
Back-reef ( <i>n</i> = 10)	20%	60%	20%	0
Lagoonal reef ( <i>n</i> = 78)	21%	49%	22%	9%
Fore-reef to back-reef ( <i>n</i> = 50)	22%	64%	14%	0
Fore-reef to lagoonal reef ( <i>n</i> = 130)	19%	38%	34%	8%
Back-reef to lagoonal reef ( <i>n</i> = 65)	2%	38%	45%	15%

Sites from within and among geomorphic zones were compared and the number of comparisons that fell within each *r*-statistic range are presented as percentages. *N* number of pairwise comparisons in each group

**Fig. 2** Satellite image of French Frigate Shoals with quantitative sampling sites indicated. Lines surrounding sites indicate ecozones. Back-reef sites are distinguished from fore-reef sites by larger, italicized numbers

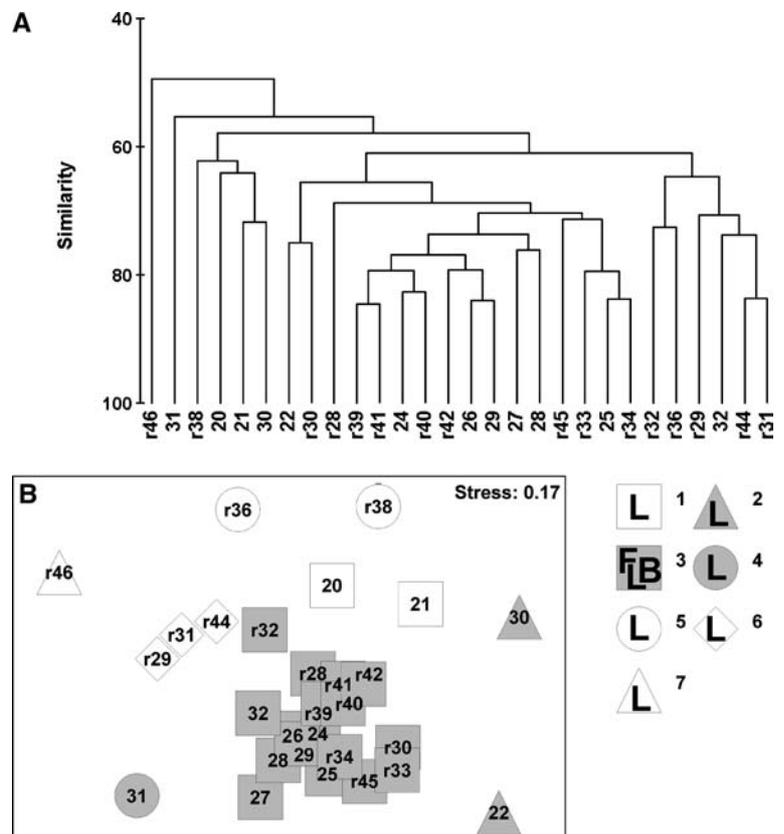


fore-reef and back-reef zones was equivalent to the amount of variation observed between sites within the back-reef zone alone (Table 1). High  $r$ -values ( $>0.750$ ) found several lagoonal reefs to differ significantly. The lowest  $r$ -values generally occurred between geographically close sites that exhibited similar environmental conditions (Fig. 2). Most  $p$ -statistic values were below 0.1, and only increased above 5.0 in cases where  $r$ -values

were below 0.1 (Global  $R=0.411$ , number of permuted statistics greater than or equal to Global  $R=0$ ). Cluster analysis and MDS ordination (Fig. 3) allowed for visual representation of relationships between sites.

Seven distinct a posteriori ecozones were interpreted based on a combination of ANOSIM  $r$ -values (Table 1), MDS and cluster diagrams (Fig. 3), and geographic position (Fig. 2). All 10 fore-reef and all five back-reef

**Fig. 3** Relationship of sites at FFS based on benthic species cover. **a** Cluster analysis showing relationship of individual sites. **b** MDS ordination showing relationship of individual sites. Ecozones 1–7 are indicated by shapes. Ecozones containing *M. setchellianum* are shaded; ecozones lacking *M. setchellianum* are white



**Table 2** Middle portion of table presents percent cover of major benthic categories for ecozones found at FFS, standard deviations in parentheses

	Ecozone 1	Ecozone 2	Ecozone 3	Ecozone 4	Ecozone 5	Ecozone 6	Ecozone 7
<b>Environment type</b>	Lagoonal reefs (n = 2)	Lagoonal reefs (n = 2)	Fore-, back-, and lagoonal reefs (n = 17)	Lagoonal reef (n = 1)	Lagoonal reefs (n = 2)	Lagoonal reefs (n=3)	Lagoonal reef (n=1)
<b>Depth range</b>	9.5-12.5 m	1.83-7.3 m	1.83-13.7 m	2.4-6.4 m	12.2-24.1 m	3.3-19.5 m	6 m
<b>Scleractinian Coral</b>	24.46 (11.14)	9.04 (12.79)	6.45 (6.38)	35.80	57.04 (10.31)	9.72 (0.61)	21.83
<b>Algae</b>	65.21 (0.06)	54.18 (18.99)	109.39 (14.68)	63.75	51.17 (12.02)	102.25 (8.30)	112.00
<i>Turf</i>	50.67 (6.01)	33.32 (4.22)	78.07 (8.06)	37.92	32.75 (8.72)	79.89 (2.14)	57.33
<i>Coralline</i>	9.33 (6.84)	2.76 (1.64)	15.45 (10.53)	20.5	18.25 (3.54)	19.28 (8.30)	49.00
<i>Fleshy Macroalgae</i>	5.21 (0.77)	18.10 (16.40)	15.87 (9.23)	5.33	0.17 (0.24)	3.08 (0.44)	5.67
<b>Sand</b>	8.58 (11.55)	46.88 (5.83)	3.68 (2.80)	0.25	1.00 (0.12)	1.92 (1.46)	0.08
<b>Other</b>	1.75 (0.47)	1.63 (1.24)	1.61 (0.77)	7.50	1.88 (2.06)	1.97 (1.78)	1.67
<b># Scleractinian Coral Species</b>	4.5 (4-5)	0.5 (0-1)	4.2 (1-8)	3	4.5 (3-6)	5 (2-7)	8
<b># Macroalgal Species</b>	4	6 (5-7)	6.6 (4-10)	9	3.5 (2-5)	6.3 (5-8)	8
<b># Non-Scleractinian Coral Invertebrate Species</b>	1	0.5 (0-1)	1 (0-2)	1	1	1 (0-2)	1

Major differences between ecozones are attributable to abundance of scleractinian coral, turf algae, coralline algae, and macroalgae. Pattern bars next to percent cover represent high (black), medium (striped), and low (grey) abundance. Scleractinian coral: high > 50%, medium 11–49%, low < 10%; turf algae: high > 75%, medium 51–74%, low < 50%; coralline algae: high > 25%, medium 11–24%, low < 10%; macroalgae: high > 15%, medium 7–14%, low

< 6%. *N* number of quantitative sites used to determine calculations for each group. *Bottom portion* of table presents the average number of scleractinian coral, macroalgal, and non-scleractinian coral invertebrate species identified from each ecozone, with the ranges given in parentheses. Additional species may have occurred at each site, but were not present in sampled photoquadrats

sites, together with two northern-lagoonal sites, were placed together into one ecozone (Ecozone 3; Fig. 2). The remaining 11 lagoonal sites were split among six additional ecozones. Each ecozone was defined by a unique set of biological features or substrate type that distinctly set it apart from other ecozones (Table 2). For instance, sites in ecozone 2 contained 5.5–586.0 times more sand than other ecozones. Sites in ecozones 5 and 7 contained 1.6–8.8 times more scleractinian coral and 2.4–17.8 times more red coralline than other ecozones, respectively.

Overall, turf algal communities primarily composed of members of the Rhodophyte order Ceramiales were the most pervasive algae at all sites and covered up to 95% (site r45) of nonliving hard substrate (Table 2). Additionally, larger algae such as crustose corallines and some fleshy macroalgae (particularly *Microdictyon setchellianum* Howe) hosted robust turf/epiphyte communities. Turf algal communities were densest along the eastern back reef and southern lagoonal areas of the

atoll, with ecozones 3 and 6 exhibiting above 75% turf algal cover (Fig. 2, Table 2). Ecozones 2, 4, and 5, which exhibited the highest coral or sand cover at the atoll, had the lowest turf algal populations (< 40%).

Species of crustose coralline algae were major space occupiers at many sites, occupying more substrate than scleractinian corals in almost half the ecozones sampled (Table 2). Although most sites exhibited crustose coralline algal cover below 20%, crustose coralline algae occupied almost 50% of the benthos around La Pérouse Pinnacle (ecozone 7; Fig. 2). Ecozone 2, containing sites with expansive sandy areas, exhibited crustose coralline algal cover 3–18 times lower than sites from other ecozones.

With the exception of *M. setchellianum*, fleshy macroalgae were not typically abundant in most reef settings, and only 22 species were recorded during photoquadrat analyses. *M. setchellianum*, although completely absent on the southwest half of the atoll, covered up to 29% of the benthos (site 22) at back reef

and lagoonal sites on the northeast to east side of the atoll (Fig. 2, Table 2) and was a key organism used to define ecozones. The only other algal species to exhibit percent cover above 1% across several ecozones was *Halimeda velasquezii* Taylor, with up to 6% cover at site 20. *Asparagopsis taxiformis* (Delile) Trevisan de Saint-Léon (3.75% at r46), *Ganonema farinosum* (11.5% at r34), and *Laurencia majuscula* (Harvey) Lucas (4.17% at 30) were only locally abundant, showing high abundance at only one or two sites within an ecozone. All other fleshy macroalgae exhibited percent cover of below 1%.

### Ecozone descriptions

Ecozone 1 represented two lagoonal sites located near Shark Island in the northwest corner of the atoll (Fig. 2). These sites ranged in depth from 11.3 to 12.5 m and were exposed to high-energy northwestern swells. This zone was characterized by about 50% turf algal cover, 25% coral cover (mainly *Porites lobata* Dana and *Acropora cytherea* Dana), and 9% sand (Table 2). Macroalgal cover was low, although percent cover of *Halimeda* species was 3–130 times higher than in any other ecozone, with *H. velasquezii* being ten times more common than *H. discoidea* Decaisne.

Ecozone 2 represented two lagoonal sites with depths ranging from 3.0 to 7.9 m that were geographically distant from the reef crest (Fig. 2). Sand accumulation was between 5 and 586 times higher than in any other ecozone and was the factor that statistically linked sites in this area. Coral cover was relatively low (Table 2). Although statistically similar, sites were visually different. Site 22 was a shallow-reef zone (3 m) characterized by highly epiphytized beds of *M. setchellianum* and gregarious assemblages of *Liagora pinnata* Harvey, whereas site 30 consisted of patch reefs dominated by *A. cytherea* and separated by sand channels.

Ecozone 3, with depths from 1.8 to 6.8 m, represented a large geographic area that contained all windward fore-reef and back-reef sites along the north and east sides of the atoll and two lagoonal sites several kilometers away from the reef crest (Fig. 2). Sites were characterized by the highest turf algal cover and the densest beds of *M. setchellianum* recorded for the atoll (Table 2). Coral cover was among the lowest of the seven ecozones, and mid-levels of crustose coralline algae differentiated this ecozone from the low coralline algal cover found in ecozones 1 and 2 and the higher cover found in ecozones 4 through 7 (Table 2).

Ecozone 4 consisted of a dense coral (*Porites compressa* Dana and *P. lobata*) patch reef arising in the middle of a sand plain within the lagoon. Despite almost 100% cover of coral skeleton, only the upper branches of *P. compressa* contained live tissue, a feature that resulted in benthic cover of living scleractinian corals being 36% (Table 2). Lower branches were

covered in dense algal turf (primarily *Dasya kristeniae* Abbott) and crustose coralline algae. Maximum depth was 6.4 m.

Ecozone 5 ranged in depth from 6.1 to 24.1 m and was comprised of two lagoonal sites located on the south side of the atoll (Fig. 2) that contained two to nine times more coral cover (*A. cytherea*, *P. lobata*, *P. compressa*, *Pocillopora meandrina* Dana) than any other ecozone (Table 2). Space not occupied by coral usually contained turf-covered crustose coralline algae. Macroalgae was scarce, covering less than 0.1% of the benthos.

Ecozone 6 contained disjunct sites located in the southern half of the atoll (Fig. 2) that ranged in depth from 3.4 to 19.5 m. Sites were characterized by high turf and coralline algal cover with low macroalgal and scleractinian coral abundance (Table 2). Unlike lagoonal zones of ecozone 2 in the northern half of the atoll (Fig. 2), *M. setchellianum* was completely absent.

Ecozone 7 consisted of one site located at the base of the two basalt pinnacles found at FFS (Fig. 2) and exhibited crustose coralline algal cover 2–18 times higher than any other ecozone. Scleractinian coral cover (*P. lobata*, *Acropora valida* Dana, *Pavona duerdeni* Vaughn) was over 20% (Table 2), although macroalgal cover was relatively low. Ecozone 7 exhibited the only luxuriant population of *A. taxiformis* found during our assessments. Depths ranged from 6.1 to 10.7 m.

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### Discussion

At the FFS, diversity and percent cover of dominant benthic organisms were similar among fore-reef and back-reef sites, allowing the labels given to these geomorphic zones to also adequately circumscribe biological zones (Figs. 2, 3, Tables 1, 2). Whereas, sites in fore-reef and back-reef areas often share similar physical characteristics, geological and oceanographic features within the lagoon zone (e.g. size and shape of patch reefs, location of islands and distance from the reef crest) lead to a spatially variable environmental regime (water flow, turbidity and temperature). This variability is exemplified by the biological heterogeneity found among lagoon sites (Table 1), and caused us to recognize that the single geomorphically defined lagoon zone does not adequately reflect the diversity of benthic communities present. Because numerous studies demonstrate that habitat heterogeneity plays an important role in maintaining species diversity (Levin 1974; Huston 1979; Diamond 1988), our results indicate the potential for the lagoon to support highly diverse habitat types and therefore be considered an important area for management.

Although fore-reef and back-reef sites on the windward side of FFS were less biologically heterogeneous than the lagoon, these areas are highly productive with overall algal cover (macroalgae + turf algae + coralline algae) 2–17 times higher than scleractinian coral cover in

nearly all ecozones. Such findings are in accordance with tropical reef studies from the Caribbean that found algae to often occupy a greater percentage of available substrate than corals or macroinvertebrates (Chiappone et al. 1997, 2001; Diaz-Pulido and Diaz 1997). Only ecozone 5, a relatively small area located in a lagoonal zone on the south side of the atoll, represented an area with comparable coral and algal cover (Table 2). These findings indicate that algae are a dominant component in these healthy subtropical reefs.

When macroalgae alone is considered, populations ranged between 0% (r38) and 36.3% (r34) although ecozone averages ranged between 0.17 and 23.53% (Table 2). These numbers are well below the persistent 25–57% macroalgal cover found in the anthropogenically impacted Florida Keys (Lirman and Biber 2000) and the annual fluctuation of 20–44% macroalgal cover reported for reefs in Colombia (Diaz-Pulido and Garzón-Ferreira 2002). At FFS, most lagoonal ecozones exhibited macroalgal cover below 6% (Table 2), similar to macroalgal densities reported for crest, terrace, and escarpment zones of reefs in Jamaica (Liddell and Ohlhorst 1987). The two ecozones (2 and 3) that exhibited macroalgal cover above 15% represented mostly windward fore-reef and back-reef sites located on the east-to-northeast side of the atoll (Fig. 2), yet contained over half the sites sampled and encompassed a geographically vast area along the eastern side of the atoll. In these areas, *M. setchellianum* (the most prevalent macroalga at these sites) exhibited up to 29% cover (sites 22 and r40). Past studies have shown *M. setchellianum* to form extensive algal meadows found at 30–40 m depths through the NWHI (Parrish and Boland 2004), and has been observed in groundtruthing photographs for single-beam sonar analyses at 40-m depths on the open, west side of FFS (J Miller, CRED). Clearly, undetermined physical oceanographic, ecological, or physiological processes exist that promote growth of this fleshy macroalga on more exposed zones of the atoll system and limit growth in lagoonal areas.

How are these distributional patterns of high macroalgal abundance explained? Fish surveys conducted simultaneously with algal sampling at the FFS demonstrated that fish populations were high across the entire atoll system, with herbivores most prevalent on the same fore-reef to back-reef zones that exhibited the highest macroalgal cover (DeMartini et al. 2002). Thus, higher macroalgal abundance cannot be explained by grazing pressure regimes, a conclusion also reached by Lirman and Biber (2000) when trying to understand macroalgal density in the Florida Keys. Instead, it is hypothesized that high algal growth may be promoted through one of three nutrient-linked processes that await further analysis: (1) increased water flow resulting from persistent wave energy on ocean-facing reef slopes or trade-wind generated vertical mixing may allow for increased uptake of ambient nutrients through the reduction of the algal boundary layers (Lobban and

Harrison 1997) in fore-reef and back-reef areas, (2) ocean currents or upwelling events (Leichter et al. 1996, 1998; Leichter and Miller 1999) may bring pulses of nutrient-rich water onto fore-reef zones of the atoll, or (3) algal morphologies may trap nutrients being leached from the substrate in north-to-east areas (due to proximity to emergent land) of the atoll system (Larned 1998).

The RDT (Littler and Littler 1984) helps explain distribution of algal functional groups in some locales at FFS. Lagoonal ecozones distant from the reef crest exhibited less water motion and lower fish densities than fore-reef and back-reef sites (DeMartini et al. 2002), conditions that reduce both nutrient uptake and grazing pressure. In agreement with the RDT, these areas exhibited among the densest turf algal communities and lowest coral and macroalgal cover found at FFS (ecozone 6). Similarly, lagoonal areas close to back-reef zones on the leeward side of the atoll that did not experience the same degree of water motion as windward reefs, but still maintained high fish densities (DeMartini et al. 2002), were dominated by corals (ecozone 5). All islands at FFS support dense seabird populations and are likely to exude a steady flow of guano into the marine ecosystem (Preskitt 2002). In agreement with the RDT, the only ecozone studied that would benefit from such a constant influx of nutrients (La Pérouse Pinnacle; ecozone 7) supported the highest crustose coralline algal community on the island. However, the RDT was not adequate for describing a combination of the highest macro-algal and turf-algal cover occurring simultaneously along north and east fore-reef zones of the atoll. Algae in these areas likely exhibit reduced boundary layers and higher nutrient uptake because of higher water motion or may receive elevated nutrient input from upwelling events.

In conclusion, we interpreted windward fore-reef and back-reef zones to fall into a single ecozone based on the statistical comparison of benthic species composition and geographic area, demonstrating that these geomorphic zones contain biologically similar areas. However, lagoonal reefs exhibited considerable diversity in biological assemblages and were split among several ecozones (Figs. 2, 3). Algae were found to be important components of this healthy, minimally impacted reef ecosystem, with over 50% algal cover at all sites examined (Table 2). Because of the presence of *M. setchellianum* on the windward sides of the atoll and its complete absence on leeward sides, it was hypothesized that mixing or upwelling events allow for increased nutrient uptake by macroalgal communities along the north and east reef slopes (Fig. 2), whereas less water motion in lagoonal zones did not promote substantial populations of fleshy macroalgae. This study documented detailed benthic community structure of reefs in the NWHI for the first time and suggests that algal distributional patterns are explained by a combination of oceanographic and physiological processes that await future experimentation.

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