

Marine biological community baselines in unimpacted tropical ecosystems: spatial and temporal analysis of reefs at Howland and Baker Islands

Peter S. Vroom · Craig A. Musburger · Susan W. Cooper ·
James E. Maragos · Kimberly N. Page-Albins · Molly A. V. Timmers

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Abstract Howland and Baker Islands are two small, isolated reef and sand islets located near the equator in the central Pacific Ocean that are situated approximately 60 km apart. In 2004 and 2006, species-level monitoring at multiple sites, coupled with towed-diver surveys in 2002, 2004, and 2006 on both of these federally protected islands, revealed diverse fish, coral, macroinvertebrate, and algal assemblages. This study examines inter- and intra-island spatial and temporal differences in community composition among sites and presents baseline biological community parameters for two of the least impacted reef systems in the world. Despite similarities in species composition, permutational multivariate analysis of variance (PERMANOVA) and multidimensional scaling ordinations (nMDS) suggest biological communities at the two islands are distinct with Baker Island containing a greater percent cover of branched Acroporid corals and turf algae and Howland Island containing a greater percent cover of crustose coralline red algae and small, compact genera of coral. Both islands also contained considerable cover of non-invasive macroalgae. PERMANOVA further revealed benthic and fish species composition to differ between forereef and reef shelf sites from different sides of each island. When islands were considered as a whole, temporal changes were not noted between 2004 and 2006; however, temporal changes at select sites did occur, with coral cover decreasing significantly along the west side of Baker Island from 2004 to 2006.

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P. S. Vroom (✉) · C. A. Musburger · S. W. Cooper · K. N. Page-Albins · M. A. V. Timmers
Joint Institute for Marine and Atmospheric Research, University of Hawai'i, 1125 B Ala Moana Blvd,
Honolulu, Hawai'i 96814, USA
e-mail: Peter.Vroom@noaa.gov

C. A. Musburger
Department of Zoology, University of Hawai'i, Honolulu, Hawai'i, USA

J. E. Maragos
United States Fish and Wildlife Service, Pacific Remote Island NWR Complex, Honolulu, Hawai'i,
USA

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Abbreviations

BT	Belt transect
CPCe	Coral point count with Microsoft excel extensions
CRED	Coral reef ecosystem division
E	East
GPS	Global positioning system
nMDS	Nonmetric multidimensional scaling ordination
N	North
NW	Northwest
PERMANOVA	Permutational multivariate analysis of variance
REAs	Rapid ecological assessments
SIMPER	Similarity percentages
S	South
SE	Southeast
W	West

Introduction

As tropical reef ecosystems begin to change with increasing sea surface temperatures (Carpenter et al. 2008) and ocean acidification (Jokiel et al. 2008; Manzello et al. 2008), the importance of establishing solid baseline data of organismal biodiversity and abundance on our planet's few remaining "quasi-pristine" reefs becomes increasingly apparent (Knowlton and Jackson 2008). For example, recent documentation of healthy benthic and fish communities in the highly protected Northwestern Hawaiian Islands (Friedlander and DeMartini 2002; Vroom et al. 2005, 2006; Vroom and Timmers 2009) and U.S. Pacific Remote Island Areas (Vroom et al. 2006; Sandin et al. 2008) has fundamentally altered perceptions of the parameters useful for gauging reef health. Many scientists (Vroom et al. 2006; Bruno et al. 2009; Wismer et al. 2009) now realize that a high percent cover of macroalgae is NOT always indicative of decreased ecosystem health (Bruno et al. 2009; Vroom and Timmers 2009), and that macroalgae and corals often co-occur in relatively high abundance in healthy reef ecosystems (Vroom et al. 2006; Sandin et al. 2008). The all-encompassing paradigm that macroalgae are detrimental to reef systems (Hughes 1994; Steneck and Sala 2005) is too simplistic for the myriad types of reef systems that exist, and it is typically only in overfished or polluted environments that macroalgal phase shifts occur (Knowlton 1992; Hughes et al. 1999; Williams et al. 2001). Without baseline monitoring of minimally impacted environments such as presented in this study, incorrect assumptions regarding reef ecosystem function established through the study of degraded ecosystems will be perpetuated, thereby leading to detrimental management practices.

A recent analysis of over 1,500 reef sites from around the world suggests that no correlation between percent cover of coral and macroalgae (Bruno et al. 2009) exists in minimally impacted reef systems. Monitoring expeditions by the National Oceanic and Atmospheric Administration's (NOAA) Pacific Island Fisheries Science Center's (PIFSC) Coral Reef Ecosystem Division (CRED) at many of the most remote reefs in the Pacific

support this premise, and have documented percent cover of non-invasive macroalgae often equaling or exceeding percent cover of living coral (Vroom et al. 2005, 2006; Sandin et al. 2008; Vroom and Timmers 2009), without indication that either functional group has a competitive advantage over the other in naturally oligotrophic, top-predator dominated environments. The study of reef communities presented here documents species-level percent cover of all benthic organisms encountered coupled with abundance of associated fish communities at these remote Pacific islands for the first time to provide insight on community structure at healthy minimally impacted islands.

Howland and Baker Islands are small, geographically isolated reef systems associated with the Phoenix Island group (Fig. 1). Both are no-take National Wildlife Refuges, protected by the U.S. Fish and Wildlife Service since 1973, and have recently become a part of the Pacific Remote Islands Marine National Monument. The islands lie approximately 60 km apart, and are unpopulated low sand islets covered by meager scrub that support dense seabird populations, insects, and land-dwelling crabs. CRED began quantitative, interdisciplinary, ecosystem-based monitoring of Howland and Baker Islands in 2000 in order to establish baseline biological data. Thus far, these efforts have documented marine communities containing percent cover of live corals ranging from 24.7 to 55.6% (Vroom et al. 2006; Sandin et al. 2008) and percent cover of macroalgae ranging from 19.7 to 21.8% (Vroom et al. 2006). Here we report the first quantitative species-level data for coral, algal, macroinvertebrate, and fish populations.

The ultimate goals of this study were to (1) gain understanding of benthic species composition and percent cover, and fish biodiversity and abundance, on two of the least impacted (Wilkinson 2004; Waddell and Clarke 2008) reef systems in the Pacific Ocean, (2) determine if each of these geographically proximate islands harbor similar biological communities, and (3) investigate whether temporal changes to biological communities may already be occurring.

Methods

Study areas

Howland and Baker Islands are characterized by narrow bands of reef located within meters of the coast on most shores, forming steeply sloping forereefs that drop to extreme depths. Both islands also contain shallow forereef terraces that support dense thickets of scleractinian coral species (Fig. 1). The islands are comparable in size (1.70 and 1.58 km² for Howland and Baker Islands, respectively) but differ in shape. The long axis and reefs of Howland Island are oriented north (N) to south (S), with the submerged N and S ends of the island consisting of small rounded promontories characterized by strong prevailing rip currents (Fig. 1). In contrast, Baker Island's long axis is oriented west (W) to east (E) with substantial reef cover along all four coasts (N, S, E, NW) (Fig. 1).

Both islands were intermittently mined for guano in the mid-1800s (Miller 1936) and experienced population pulses immediately prior to and during WWII (McClellan 1936; Black 1937a, b, c, 1938a, b, 1939; Kalama 1937). Baker Island was occupied for several months by thousands of U.S. troops, and was used as an air base for the military assault on Tarawa Island in 1943. After winning the battle, the troops abandoned Baker Island and dumped unwanted military material onto the reefs off the western landing. Since this brief human habitation that included several bombings (Bederman 1942), both reef ecosystems have been free from direct human impact for more than 60 years.

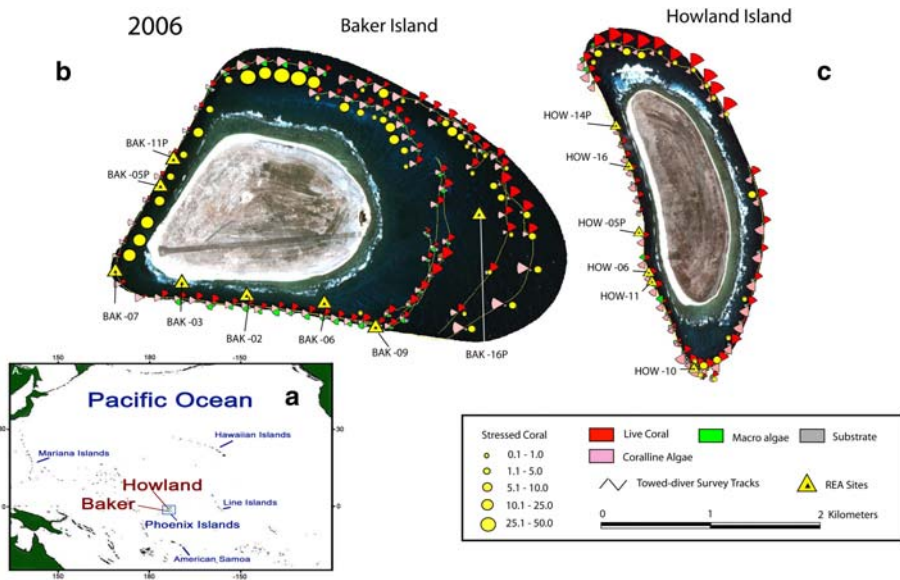


Fig. 1 2006 towed-diver and REA data. **a** Location of Howland and Baker Islands in the Pacific Ocean, **b** IKONOS satellite image of Baker Island, **c** IKONOS satellite image of Howland Island. Rapid Ecological Assessment (REA) study sites (Appendix S1) are depicted by *yellow triangles*. Towed-diver survey tracks show benthic functional group data summarized as pie-charts in 5-min intervals. Unlike 2002 and 2004 towed-diver data (Appendices S2, S3), pie slices do not add up to 100% cover due to usage of a binning classification method rather than exact estimation of percent cover (see “Methods”). Graduated slices are graphed based upon the proportionality of each benthic functional group in relationship to each other at towed-diver midpoints. The size of the pie is the median value of the numerically binned data. For example, the southern-most towed-diver observation in the northeast sector (adjacent to the letter “c”) depicts coral populations (*red*) binned as 10 (median value 87.5%), crustose coralline red algal populations (*pink*) binned as 3 (median value 15%), rubble (*gray*) binned as 2 (median value 3%) and both macroalgal populations (*green*) and sand (*brown*) binned as 1 (median value 0.50%). Images are cropped at the 30 m depth contour for each island. Image does not reflect actual location or distance of islands to each other

Field data

Towed-diver surveys

Qualitative and quantitative data of benthic composition at the functional group level were collected from towed-diver surveys in 2002, 2004, and 2006 at Howland and Baker Islands (Fig. 1, Appendices S1–S3). Towed-diver surveys encompassed the entire perimeter of each island during each survey year with the exception of Baker Island in 2002. Towed-diver surveys involved towing two scuba divers 60 m behind a small boat at a constant speed (~1.5 knots) along approximately 2 km of habitat producing a 50-min survey (Kenyon et al. 2006). Positions were recorded every 30 s using a global positioning system (GPS) receiver on the small boat. Each 50-min survey was broken down into 5-min segments for in situ data collection. During 5-min segments in 2002 and 2004, the estimated benthic composition (live and stressed coral, crustose coralline red algae, macroalgae, and substrate) tabulated to a total cover of 100% (Appendices S2, S3). In 2006, with the exception of the stressed coral category, the benthic towed-divers binned their benthic composition estimates into predetermined numerical categories that correlated to a percent

range (1 = 0.1–1%, 2 = 1.1–5%, 3 = 5.1–10%, 4 = 10.1–20%, 5 = 20.1–30%, 6 = 30.1–40%, 7 = 40.1–50%, 8 = 50.1–62.5%, 9 = 62.6–75%, 10 = 75.1–100%). The stressed coral category was the percentage of the observed live coral percent cover that exhibited signs of stress (pale coloration, white color due to bleaching, disease, predation, or recent death) in the tow swath and not a percentage of the total benthic composition (Fig. 1).

REA surveys

Quantitative fish data were collected during Rapid Ecological Assessments (REAs) from reefs at 5 and 6 sites on Howland and Baker Islands, respectively, in January 2004 (Appendix S1), and at 6 and 8 sites, respectively, in January 2006 (Appendix S1). Every effort was made to survey sites along all sides of the islands, but weather and safety concerns restricted most Howland Island sites to the more protected W side. Study sites at Baker Island were located at reefs along W, E, and S sides of the island. Sites at which permanent transect pins were installed are indicated by a “P” after each site name (Appendix S1). At sites where permanent pins were not installed, divers relocated GPS coordinates and laid transect lines on pre-established headings. At each site, belt transects (BT) were conducted following the methodology of Friedlander and DeMartini (2002), where all fish were counted and identified to the lowest possible taxon along three 25-m transect lines set in a single file row and separated by 10-m. Most transects were placed at standard 10 to 15-m depths (Appendix S1). Fish surveyors were experienced with the fish fauna of these islands, and nearly all fish were identified to the species level.

Quantitative REA data of benthic communities were collected along the same transect lines as fish data (Appendix S1). At each site, phycologists worked along the first two 25-m transect lines after fish divers had completed their surveys. Twelve photos were taken at each site using a photoquadrat (0.18 m²) equipped with a Sony DSC P-9 digital still camera: 6 at randomly selected points along the 2 transects (3 per transect), and 6 at points 3 m perpendicular from each random point in the direction of shallower water (Preskitt et al. 2004; Vroom et al. 2005). Lists of all algal and coral species observed in the vicinity of each transect site were also compiled (Maragos et al. 2008; Miller et al. 2008; Tsuda et al. 2008).

Analyses

Towed-diver observer data were georeferenced to the recorded tracks through the application of a layback model in ArcView 3.3, which rectified the position of the diver (Kenyon et al. 2006) relative to the GPS location on the small boat. Through a custom-designed ArcView data analysis extension (Hoeke, CRED, unpublished), observer benthic composition estimates during each 5-min segment were graphically mapped on an Ikonos image for each island (Fig. 1, Appendices S2, S3). The benthic composition estimates were graphically presented by pie-charts that added to 100% cover for 2002 and 2004 (Appendices S2, S3). In 2006, the size of the pie-charts is relative to the number corresponding to the numerical bins with the exception of stressed coral (Fig. 1). Stressed coral is represented by graduated symbols since it was recorded as a percentage of the total live coral percent cover observed as stressed.

Benthic photoquadrats were analyzed using Coral Point Count with Microsoft Excel extensions (CPCe; Kohler and Gill 2006). One hundred stratified random points in a 10 by 10 grid were placed on each 300 dpi digital photoquadrat image, and percent cover of

benthic organisms or substrate type was estimated by identifying items under each point. Macroalgae, macroinvertebrates, and corals were identified to species, while turf algae, crustose coralline red algae, and cyanobacteria were lumped into functional groups. Data from each photoquadrat were treated as individual replicates within a site and a Bray–Curtis similarity matrix of quadrats was created using PRIMER-E[®], version 6 (Clarke and Warwick 2001; Clarke and Gorley 2006; Anderson et al. 2008). Similarly, fish abundance data from each transect were treated as individual replicates within a site and used to create a Bray–Curtis similarity matrix.

Prior to analysis, a fourth-root transformation of benthic and fish matrices was performed to lessen the influence of prevalent species and increase the weight of rare species. Three-way mixed model PERMANOVA (maximum permutations = 9,999) was used to test each data set, with site (nested within island), island, and year provided as factors. Non-Metric Multidimensional Scaling (nMDS) ordinations were used to visually depict relationships among sites within each sampling year. SIMPER analyses were conducted to examine the contribution to dissimilarity of individual species or functional groups.

Results

Spatial analyses

REA surveys along transect lines at Howland and Baker Islands in 2004 and 2006 found 215 species of fish, 14 species of macroalgae and 24 species of coral to occur in conjunction with several invertebrate species (e.g. the “bubble tip anemone” *Entacmaea quadricolor* and the giant clam *Tridacna maxima*), and crustose coralline red algal, turf algal, and cyanobacterial functional groups. Combined algal functional groups (not including cyanobacteria) dominated between 57 and 92% of the substratum, while corals occupied 5 to 43% of the substratum (Fig. 1, Appendices S2–S5). Across both sampling years, macroalgal cover was greater than or equal to coral cover at 35% of the sites, while crustose coralline red algal cover was greater than coral cover at 87% of the sites.

Inter-island comparison

Despite sharing a large number of species, PERMANOVA demonstrated a significant main effect of island for both benthic and fish analyses (Table 3), and nMDS clearly separated sites from Howland and Baker Islands based on biological communities (Fig. 2). Although crustose coralline red algae, turf algae, and the staghorn coral *Acropora nobilis* were present at both islands (Table 1), SIMPER using benthic data revealed that differences in their percent covers contributed to 51.7 and 56.1% of observed differences between the islands in 2004 and 2006, respectively. Similarly, differences in the number of three schooling planktivores, *Pseudoanthias bartlettorum*, *Lepidozygus tapeinosoma*, and *Luzonichthys whitleyi* (Table 2) accounted for 78.0 and 64.9% of fish community differences between the two islands in 2004 and 2006.

At Baker Island, species of Acroporid corals covered a much greater area than at Howland Island (Table 1), and cumulatively accounted for 24.0% (2004) and 15.5% (2006) of inter-island differences. For example, *Acropora digitifera* covered 3.5 to 5.1 times more area at REA sites sampled at Baker Island than at Howland Island and *A. nobilis* covered 23.1 to 25.2 times more area (Table 1). As for fish community differences, the zooplanktivores *Chromis vanderbilti* and *Chromis acares* were 4.4 to 10.5 times

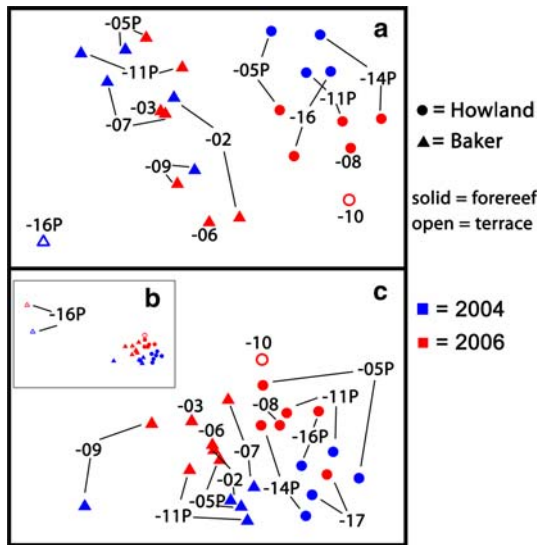


Fig. 2 Non-metric multidimensional scaling (nMDS) ordinations revealing relationships of sites at Howland and Baker Islands in both sampling years based on biological community structure. Both benthic and fish community data revealed sites at Howland Island (*circles*) to form a cluster distinct from sites at Baker Island (*triangles*). Similarly sites located on reef terraces (*open shapes*) were remote from forereef sites (*solid shapes*). **a** nMDS depicting site relationships based on benthic percent cover data (2D stress = 0.16), **b** nMDS depicting the remote relationship of BAK-16P to other surveyed sites based on fish count data (2D stress = 0.09), **c** site relationships (excluding BAK-16P) based on fish count data (2D stress = 0.09)

and 1.2 to 3.3 times more prevalent at Baker Island than Howland Island (Table 2), while the herbivore *Ctenochaetus marginatus* was 1.5 to 2.3 times more common (Table 2).

Conversely, at Howland Island, species of Pocilloporid corals covered a greater area than at Baker Island, with *Pocillipora eydouxi* and *P. meandrina* being 6.6 to 30.5 and 2.6 to 5.8 times more common, respectively (Table 1). The encrusting coral *Montipora aequituberculata* covered 180.2 times more area at surveyed sites at Howland Island than at Baker Island in 2004, while *Pavona clavus* and *Porites lobata* were 11.2 and 12.5 times more common at Howland Island than Baker Island in 2006. Counts of the zooplanktivores *Pseudoanthias bartlettorum*, *Lepidozygus tapeinosoma*, *Luzonichthys whiteleyi*, *Apogon apogonoides* *Thalassoma amblycephalum* and the mobile invertovores *Paracirrhites arcatus* and *Cirrhichthys oxycephalus* were noticeably higher at REA sites at Howland Island than at Baker Island (Table 2).

Intra-island comparisons

PERMANOVA showed significant main effects of site for both benthic and fish data sets, demonstrating that biological community composition differed spatially around each island (Table 3). This finding supports data collected by towed-diver surveys that revealed heterogeneity in functional group abundance around each island, with reef shelf sites often containing higher coral than more exposed forereef sites (Fig. 1, Appendices S2, S3) and ratios of functional groups differing depending on wave exposure. For instance, the S side of Baker Island exhibited higher concentrations of macroalgae than other locations (Appendices S2, S3).

Table 1 Average percent cover (SE) of the 20 most dominant benthic organisms along transect lines at surveyed sites by island

	Howland Island			Baker Island		
	2004		2006	2004		2006
	Mean	SE	Mean	Mean	SE	Mean
Macroalgae						
<i>Dicryota friabilis</i>	–		–	1.11 (0.51)		0.15 (0.15)
<i>Halimeda fragilis</i>	2.04 (0.43)		2.93 (0.86)	3.15 (2.25)		4.93 (2.05)
<i>Halimeda heteromorpha</i>	–		–	0.39 (0.39)		2.01 (1.73)
<i>Lobophora variegata</i>	18.85 (4.06)		0.17 (0.17)	14.24 (4.14)		3.40 (1.44)
<i>Peysommelia inamoena</i>	0.25 (0.25)		–	0.24 (0.24)		2.62 (1.58)
<i>Wrangelia anastomosans</i>	0.56 (0.35)		6.25 (2.23)	–		–
Turf algae	3.23 (1.02)		23.04 (3.72)	8.89 (2.99)		29.35 (7.22)
CCA	49.13 (2.26)		44.04 (4.45)	36.83 (7.32)		37.51 (4.30)
Cyanobacteria	0.71 (0.25)		–	4.18 (2.29)		0.31 (0.16)
Corals	0.35 (0.24)		0.15 (0.12)	1.24 (0.67)		0.76 (0.45)
<i>Acropora digitifera</i>	–		–	0.39 (0.39)		0.85 (0.85)
<i>Acropora hyacinthus</i>	–		–	27.06 (4.71)		14.62 (3.09)
<i>Acropora nobilis</i>	1.17 (1.01)		0.58 (0.40)	–		–
<i>Favia mathaii</i>	0.40 (0.40)		0.60 (0.38)	0.58 (0.58)		–
<i>Hydnophora microonos</i>	0.54 (0.36)		2.00 (1.27)	0.18 (0.15)		–
<i>Montipora aequituberculata</i>	10.75 (3.17)		3.99 (2.89)	0.06 (0.06)		–
<i>Pavona clavus</i>	2.44 (1.85)		5.61 (3.36)	–		0.50 (0.33)
<i>Pocillopora eydouxi</i>	2.44 (0.82)		3.97 (0.75)	0.08 (0.08)		0.60 (0.43)
<i>Pocillopora meandrina</i>	1.23 (0.51)		1.74 (0.75)	0.47 (0.47)		0.30 (0.17)
<i>Porites lobata</i>	2.98 (1.85)		0.50 (0.27)	–		0.04 (0.04)
Non-coral invertebrates	–		1.43 (1.43)	1.43 (0.93)		0.56 (0.37)

Table 2 Counts (SE) of the 17 most prevalent fish species along transect lines at surveyed sites by island

Trophic Guild	Species	Trophic level	Howland Island		Baker Island	
			2004	2006	2004	2006
Zooplanktivores	<i>Apogon apogonoides</i>	3.5	37.60 (16.33)	1.22 (1.31)	–	–
	<i>Chromis acaras</i>	3	65.07 (28.70)	77.78 (18.65)	215.22 (86.62)	90.17 (31.21)
	<i>Chromis margaritifer</i>	3	16.27 (4.06)	26.44 (6.40)	27.56 (13.24)	27.75 (9.14)
	<i>Chromis vanderbilti</i>	3.2	11.33 (2.14)	8.11 (5.64)	188.78 (138.70)	36.00 (17.12)
	<i>Lepidozygus tapeinosoma</i>	3.4	2,213.33 (592.02)	241.67 (59.99)	1,021.11 (351.68)	160.08 (76.19)
	<i>Luzonichthys whiteleyi</i>		1,046.67 (326.02)	484.94 (95.26)	605.56 (268.11)	410.42 (206.05)
	<i>Pseudanthias bartlettorum</i>		2,576 (503.05)	923.33 (126.98)	1,555.56 (462.17)	645.08 (197.69)
	<i>Thalassoma amblycephalum</i>	3.1	23.33 (11.46)	77.11 (24.12)	17.56 (14.93)	47.50 (9.28)
Herbivores	<i>Acanthurus nigricans</i>	2	6.60 (2.06)	9.39 (4.42)	20.83 (2.52)	13.67 (2.43)
	<i>Centropyge loricula</i>	2.8	22.13 (2.66)	21.22 (2.86)	20.44 (5.12)	14.58 (4.43)
	<i>Ctenochaetus marginatus</i>		9.53 (2.74)	21.89 (4.97)	16.50 (3.34)	33.33 (9.25)
	<i>Ctenochaetus sp</i>		20.80 (3.49)	12.00 (3.53)	32.78 (8.36)	24.75 (6.35)
Cor	<i>Plectroglyphidodon dickii</i>	3.4	18.00 (4.20)	23.56 (3.37)	42.22 (10.42)	45.75 (19.00)
	<i>Plectroglyphidodon johnstonianus</i>	3.3	23.60 (4.45)	23.44 (3.59)	24.00 (4.39)	11.75 (3.69)
MI	<i>Cirrhitichthys oxycephalus</i>	3.8	24.53 (3.85)	10.78 (1.51)	2.78 (1.20)	2.92 (0.90)
	<i>Paracirrhites arcatus</i>	3.6	34.40 (4.22)	38.33 (2.35)	11.67 (3.27)	10.17 (4.37)
Pk	<i>Myripristis berndti</i>	3.7	5.20 (3.36)	7.94 (2.36)	6.28 (2.26)	44.33 (12.01)

Cor corallivore, MI mobile invertivore, Pk planktivore

Trophic levels numbers are defined as follows: primary producers = 1, herbivores = 2, predators = 3, top predators = 3+. Trophic guild and level data from Kulbicki et al. (2005) and <http://www.fishbase.org>

Table 3 Results of PERMANOVA for benthic and fish analyses

	Source	df	SS	MS	Pseudo-F	P (perm)	Unique perms
Benthic percent cover	Is	1	43317	43317	6.5663	0.0001	9,932
	Ye	1	53424	53424	23.795	0.0003	9,936
	Si(Is)	12	89772	7481	8.8994	0.0001	9,795
	Is × Ye	1	5640.4	5640.4	2.5122	0.0697	9,958
	Si(Is) × Ye	7	15716	2245.2	2.6709	0.0001	9,867
	Res	253	2.1268E5	840.61			
	Total	275	4.3604E5				
Fish biodiversity	Is	1	6738.1	6738.1	3.3792	0.0006	9,888
	Ye	1	4079.1	4079.1	4.6387	0.0025	9,933
	Si(Is)	13	28586	2198.9	4.8053	0.0001	9,796
	Is × Ye	1	1218.6	1218.6	1.3857	0.2096	9,932
	Si(Is) × Ye	8	7034.8	879.35	1.9217	0.0001	9,740
	Res	50	22880	457.59			
	Total	74	72688				

Baker Island

Benthic species composition differed between forereef sites located on the two coasts surveyed at Baker Island (Fig. 2). Although temporal changes were observed in this region (see “Temporal comparison”), towed-diver (Fig. 1, Appendices S2, S3) and REA surveys along the steeply sloping west side of the island (BAK-05P, -11P) found benthic communities that contained relatively low coral cover and a substratum dominated by up to 55.1% cover of turf algae, up to 25.3% cover of the brown alga *Lobophora variegata*, and up to 38.8% cover of crustose coralline red algae (Appendix S4). Much of this algal cover overgrew dead skeletons of the coral *Acropora nobilis*. Live *A. nobilis* covered up to 26.9% of the substrate in 2004, but only 7.1% of the substrate in 2006 (Appendix S4). Western sites were also the only areas at Baker Island observed to contain up to 5.2% cover of the “bubble tip anemone” *Entacmaea quadricolor*.

Southern reef slopes (BAK-02, -03, -07, -09) were covered by 1.5 to 2.0 times more crustose coralline red algae than western sites, and were the only surveyed areas of the island to harbor the green macroalgae *Halimeda heteromorpha* and *H. micronesica* (Fig. 1, Appendices S2–S4). These southern sites also contained 23.4 to 36.4 times more *H. fragilis* than western sites across both sampling years (Appendix S4). The staghorn coral *Acropora nobilis* covered up to 39.3% of the substratum in 2004, although become somewhat overgrown by turf algae in 2006 (see “Temporal comparison”). The red alga *Peyssonnelia inamoena* and the corals *Fungia scutaria*, *Montipora caliculata*, and *Pocillopora eydouxi* were only recorded from photoquadrats surveyed in these southern areas (Fig. 1, Appendices S2–S4). No major differences in biodiversity or species counts of the most prevalent fish species observed were noticed between western and southern shores.

BAK-16P, the only eastern reef shelf site surveyed, differed from all other areas surveyed (Fig. 2) and contained an essentially monotypic thicket of the scleractinian coral *Acropora nobilis* that superficially appeared to cover 100% of the substrate. However, closer examination revealed that only tips of coral skeletons contained live polyps, while a

dense crustose coralline red algal community (up to 56.9% cover) cemented together the lower branches (Fig. 1, Appendices S2–S4). None of the small schooling zooplanktivores *Pseudoanthias bartlettorum*, *Lepidozygus tapeinosoma*, or *Luzonichthys whiteleyi* that were prevalent on western and southern reef slopes were observed on the eastern reef shelf.

Howland Island

At Howland Island, all survey sites except HOW-10 (2006) occurred within 1,500 m of each other on the steeply sloping forereef located off the west shore of the island (Fig. 1, Appendices S2, S3). Benthic communities at these western sites were dominated by crustose coralline red algae (29.7–56.9%) and exhibited coral cover ranging from 6.4 to 38.3%, macroalgal cover ranging from 0.2 to 30.3%, and turf algal cover ranging from 0.4 to 32.7% (Fig. 1, Appendices S2–S4). The most dominant macroalgae included the brown alga *Lobophora variegata* with up to 26.0% cover in 2004, the red alga *Wrangelia anastomosans* with up to 14.2% cover in 2006, and the green alga *Halimeda fragilis* with a similar percent cover (~5.8%) in both years (Appendix S4). The green algae *Avrainvillea lacerata* and *Caulerpa serrulata*, the red alga *Peyssonnelia inamoena*, and species in the red algal genus *Laurencia* typically exhibited percent covers of <3%. The most dominant corals included *Montipora aequituberculata* and *Porites lobata* with percent covers up to 17.6 and 8.3%, respectively (Fig. 1, Appendices S2–S4). With few exceptions, the corals *Acropora digitifera*, *A. globiceps*, *A. nasuta*, *A. nobilis*, *A. subulata*, *Favia matthaii*, *F. stelligera*, *Fungia scutaria*, *Gardineroseris planulata*, *Hydnophora microconos*, *Leptrastrea transversa*, *M. caliculata*, *Pavona clavus*, *Pocillopora eydouxi*, *P. meandrina*, *Psammocora haimeana*, *P. nierstraszi* all exhibited percent covers <3.0%. Cyanobacteria were uncommon, and never covered more than 1.5% of the substratum.

HOW-10, the site located on the southern reef shelf differed from sites along the western forereef by containing 21.8% cover of the coral *Pavona clavus* (a cover 3.6 times higher than any other site; Fig. 2, Appendix S4). Similarly, *Pocillopora meandrina* exhibited a percent cover of 5.2%, which was 2.3 times higher than any western forereef sites. The green alga *Halimeda fragilis* was 2.5 to 33.8 times less common at this reef shelf site than on western forereefs, covering only 0.2% of the substrate (Appendix S4). In terms of fish abundances, HOW-10 differed from steep forereef sites by containing fewer individuals of the zooplanktivores *Lepidozygus tapeinosoma*, *Chromis acares*, and species of *Ctenochaetus*, and much higher abundances of the zooplanktivores *Chromis vanderbilti*, *Chromis margaritifer*, and *Thalassoma amblycephalum*, and the herbivore *Centropyge loricula* (Appendix S5).

Temporal comparison

Results from both benthic and fish PERMANOVA showed significant main effects of year (Table 3) indicating that community composition changed temporally. However, the lack of any significant island by time interaction (Table 3) coupled with a significant site by time interaction suggested that although some of the sites changed in community composition, biological composition at the islands as a whole remained static between 2004 and 2006 (Table 3).

SIMPER revealed that decreases in percent cover of *Acropora nobilis* (16.7% in 2004 to 8.1% in 2006), *Lobophora variegata* (16.1% in 2004 to 1.9% in 2006), and *Montipora aequituberculata* (4.3% in 2004 to 1.8% in 2006) combined with an increase in turf algae (6.6% in 2004 to 26.4% in 2006) accounted for 51.7% of observed temporal changes in

benthic communities (Table 1). Crustose coralline red algae, although only exhibiting a 1.2% decrease in cover overall, also contributed to 20.5% of temporal differences. A decrease in the number of three small, schooling planktivores, *Pseudoanthias bartlettorum*, *Lepidozygus tapeinosoma*, and *Luzonichthys whitleyi*, was responsible for 75.0% of the differences in fish abundances between 2004 and 2006 (Fig. 2; Table 2).

At Baker Island, benthic communities along west facing shores changed more dramatically than in other areas (Fig. 2), with a 2.7 to 9.5 times increase in turf algae accompanied by a 2.3 to 8.4 times decrease in the branched coral *Acropora nobilis* (Appendix S4). Abundances of the brown alga *Lobophora variegata* also showed a 2.3 to 3.6 times population decrease. Most south facing sites did not change as strikingly; however, BAK-07 did show a 4.3 times decrease in percent cover of Acroporid corals and a 4.4 times decrease in cover of *Lobophora variegata* while there was a 2.8 times increase in turf algae and CCA increased 1.9 times (Fig. 2, Appendix S4). In addition to decreases in the three schooling planktivores discussed above, a decrease in *Chromis acares* occurred at western sites (Appendix S5). However, biodiversity and abundance for most fish species did not change noticeably between sampling years.

At Howland Island, HOW-05P changed most markedly with abundances of *Lobophora variegata* and *Montipora aequituberculata* decreasing by 21.0 times and 219.8 times, respectively, while the red alga *Wrangelia anastomosans* and turf algae increased from 0 to 14.2% cover and 3.8 to 12.2% cover, respectively (Appendix S4). At HOW-11P and HOW-16, turf algal populations increased by 6.2 to 9.3 times and abundances of *Lobophora variegata* decreased from 21.3 and 26.0 to 0% cover at both sites. Benthic communities at most other locations surveyed in both 2004 and 2006 remained similar (Appendix S4). Except for a decrease in the three schooling planktivores discussed above, biodiversity and abundance for most fish species did not change noticeably between sampling years (Appendix S5).

Discussion

Ecosystem-wide analyses of biotic data from Howland and Baker Islands revealed an unexpected paradox: although the islands are geographically proximate, of comparable size, and geomorphically similar (Maragos et al. 2008; Miller et al. 2008), a comparison of benthic and fish communities between the two islands revealed them to be biologically distinct from each other. Generally, reef slope regions around Baker Island supported a much larger abundance of upright branched Acroporid corals (Table 1), while reef communities at Howland Island exhibited a higher abundance of smaller, more compact coral species and crustose coralline red algae (Table 1). Algal communities also differed with nearly twice as many algal species known from Baker Island as from Howland Island (Tsuda et al. 2008). The fish communities of Howland and Baker Islands documented during survey years were rich in carnivores and top predators, with the biomass of these types of fish similar to biomass estimates from the Northwest Hawaiian Islands and the US Line Islands (Brainard et al. 2005). However, although containing essentially the same mix of fish species at both islands, Howland Island contained much higher abundances of select zooplanktivores.

Howland and Baker Islands are grossly similar with no apparent boundaries preventing dispersal of organisms between them, so community differences are likely attributable to finer-scale geomorphology, physical forcing, or disturbance history. For example, water motion (Carpenter and Patterson 2007), substrate availability (Vermeij 2005; Becerro et al.

2006), wave energy (Fabricius 1997; Becerro et al. 2006; Smith et al. 2008), habitat complexity (Chabanet et al. 1997; Ault and Johnson 1998; Bergman et al. 2000; Ferreira et al. 2001), and herbivore grazing (Adjeroud et al. 2007; Box and Mumby 2007) have been shown to affect both pre- and post- settlement success and growth of benthic organisms. Benthic communities may then play a subsequent role in determining the faunal composition of fishes (Floeter et al. 2007). Furthermore, shallow reef terraces at Baker Island are almost twice the size as shallow reef terraces at Howland Island (4.37 vs. 2.61 km²), possibly allowing for greater habitat diversity that in turn might explain why a larger number of benthic species have been documented at Baker Island than Howland Island (Maragos et al. 2008; Miller et al. 2008; Tsuda et al. 2008). Finally, if disturbance rates occurred differentially among these reef communities, it is possible that reef assemblages at each island are at different successional stages. For example, studies examining the effects of mass coral bleaching in healthy reef ecosystems have documented the replacement of bleached corals primarily by turf algal (rather than macroalgal) communities (Adjeroud et al. 2002; McClanahan et al. 2002; Arthur et al. 2005).

Intra-island site comparisons

Oceanographic and weather conditions limited most quantitative surveys at Howland Island to the relatively calm W side (Fig. 1, Appendices S1–S3) where all sites contained comparable benthic covers (Appendix S4). HOW-10 was the only southern site sampled (2006 only), and was located on a forereef adjacent to a small shallow reef terrace on the S side of the island. SIMPER revealed differences in both fish and benthic communities between HOW-10 and all other Howland Island forereef sites.

At Baker Island, oceanographic conditions allowed for greater geographic coverage than at Howland Island, and subsequently greater benthic habitat diversity was recorded. As at Howland Island, benthic communities along the W sides of Baker Island (BAK-05P, -11P; Fig. 1, Appendices S1–S3) appeared relatively homogenous (Appendix S4), as did most S facing sites (BAK-02, -03, -06, 07, -09). This pattern is most likely due to slight to moderate differences in wave energy causing the percent cover of benthic organisms to differ slightly along different facing coastlines (Garcia-March et al. 2007; Scrosati and Heaven 2007). The dense *Acropora* thicket on the east coast (BAK-16P) was distinct from all other sites at Baker Island (Appendix S4), and likely exists because of reduced wave energy in this reef shelf area. BT fish analyses did not reveal distinctions between W and S facing forereef sites as observed in benthic analyses; however, fish abundances at BAK-16P were noticeably different and lacked the dense schools of zooplanktivores found in forereef regions.

Temporal comparisons

The similar patterns of benthic organisms recorded around Howland and Baker Islands from towed-diver surveys in 2002 and 2004 suggested that percent cover of benthic organisms on the reefs remained relatively stable despite months of anomalously high sea surface temperatures recorded in 2002 and 2003 (Brainard et al. 2005). However, the noticeable reduction of live branched Acroporid corals on the west side of Baker Island and the southeast shelf of Howland Island in 2006 (Appendix S3), and the prevalence of stressed or bleached corals noted around much of Baker Island and in reef shelf regions of Howland Island in 2006 (Fig. 1), indicated that some changes to the reef system had occurred. At Howland Island, rubble now exists where a thicket of staghorn coral once

stood, anecdotally suggesting that the coral community had been destroyed between 2004 and 2006. Although the source of coral death is unknown, possibilities included coral bleaching events, *Acanthaster* infestations, or severe storm and wave activity. Such wave activity may have been lacking at Baker Island where branched Acroporid coral skeletons remained intact but became overgrown by turf algal species. These corals did not appear bleached during 2004 towed-diver or REA surveys, and it remains unclear whether elevated sea surface temperatures experienced during 2002 and 2003 can be implicated in the death of these coral communities. At other sites at both Howland and Baker Islands, moderate to high temporal changes were observed in benthic communities as algal functional group or species composition changed.

Table 2 reveals that three species of anthias and damselfish exhibited the greatest difference in abundance numbers from 2004 to 2006. These species tend to form huge schools and mix together, making accurate counts difficult, so the margin of error in fish counts may be quite large. In 2006, many individuals of *Thalassoma amblycephalum* (a species that accounted for a relatively high percentage of differences observed between sampling years) that measured only 1–3 cm in length suggest that a recent recruitment event occurred prior to sampling, and may provide a clue as to differences in number of individuals counted between 2004 and 2006 of this species.

CRED visits Howland and Baker Islands for 2 and 3 days, respectively, every 2 years. Clearly, the data presented here represent only a snapshot of organismal biodiversity (Maragos et al. 2008; Miller et al. 2008; Tsuda et al. 2008) and abundance at these isolated reefs. Yet despite this limitation, multidisciplinary monitoring efforts provide a solid baseline of these reef systems and provide an unparalleled qualitative and quantitative understanding of the most common reef components encountered in these near-pristine reef systems. Both corals and macroalgae co-occur in high abundance, and both functional groups appear necessary for ecosystem function. As the effects of elevated sea surface temperatures and ocean acidification begin to occur, baseline studies of healthy reefs conducted now will become imperative for future informed management and conservation efforts to be successful. Additionally, understanding population parameters from isolated island reef systems provide a better global understanding of the types of organisms (and their abundance) necessary for healthy reef function (Bruno et al. 2009).

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