

Standing Crop and Sediment Production of Reef-Dwelling Foraminifera on O'ahu, Hawai'i¹

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ABSTRACT: Most of O'ahu's nearshore and beach sands are highly calcareous and of biogenic origin. The pale-colored constituent grains are the eroded remains of carbonate shells and skeletons produced by marine organisms living atop the island's fringing reefs and in the shallow waters near shore. Previous studies have shown that the tests of symbiont-bearing benthic foraminifera compose a substantial portion (up to one-fourth) of these organically produced sands. We sampled a variety of reef flat and slope habitats to obtain standing-crop data and production estimates for several sand-producing genera of reef-dwelling foraminifera. We found that modern communities of these shelled protists occur in dense numbers islandwide, reaching densities up to 10⁵ individuals per square meter of suitable substrate in the more productive habitats. Further research on the contribution of foraminifera to beach, nearshore, and offshore sands is planned for O'ahu and neighboring islands to describe their roles in the sediment budget more completely.

THE FORAMINIFERA ARE a highly diverse group of shelled protists that have been important producers of calcareous marine sediments for at least 320 million years. To a great extent, early studies of these protozoan microfossils arose through petroleum exploration; thus, foraminifera are among the best-known tools used in stratigraphic correlations and paleoenvironmental reconstructions (Matthews et al. 1980, Hallock and Glenn 1986).

The tests of benthic foraminifera are typically abundant constituents of shallow-water

carbonate sediments, and their assemblages in reefal deposits have been widely studied since the pioneering works of Cushman (1928). Previous research linked densities of living benthic foraminifera to sediment-production estimates (Myers 1943, Murray 1967), and in the last two decades, investigations of their cytology, life history strategy, and population biology have contributed to our knowledge of these ubiquitous protists (Lee and Anderson 1991). Their applications in science have progressed beyond classic "empty shell" derivations of micropaleontology and geochemistry, and living populations are now recognized for their importance in modern environmental assessments and in studies of sediment production and transport.

Although benthic and pelagic foraminifera are found in all marine environments from the Tropics to the poles, a number of low-latitude, shallow-water (i.e., depths within the euphotic zone) benthic foraminifera are particularly useful as sediment tracers (Coulbourn and Resig 1975, Li et al. 1995, Peebles et al. 1997), reef flat and slope markers (Hallock 1984), and sensitive envi-

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ronmental indicators (Hallock 1996, Murray 1973) owing to their habitat requirements. The cytoplasm of these "larger" reef-dwelling foraminifera is host to photosynthetic algal symbionts in a mutualistic relationship that is ecologically similar to that of zooxanthellae in scleractinian corals (Lee and Anderson 1991). It is well known that such symbiont-bearing organisms are characteristically efficient nutrient recyclers and generally require warm, clear, oligotrophic waters to flourish. Several genera of these larger foraminifera have nearly circumtropical distributions (e.g., *Amphistegina*, *Heterostegina*, *Peneroplis*) and thrive in reef, rubble, and sea grass habitats. These attributes coupled with the protists' small size, ease of collection, ability to be maintained in laboratory culture, and rapid response to environmental perturbation make them ideal for research purposes (Hallock 1996).

Environmental perturbations can induce a variety of community- and species-level responses in these symbiont-bearing foraminifera. Hallock et al. documented the inception (1993) and multiyear progression (1995) of stress-induced bleaching (symbiont loss) in *Amphistegina gibbosa* on coral reefs in the Florida Keys and other sites in the Caribbean. Research by Cockey et al. (1996) revealed a decadal-scale shift in foraminiferal dominance from larger, long-lived, symbiont-bearing taxa to small, fast-growing heterotrophic taxa, consistent with predictions of community response to gradually increasing nutrient flux. Other responses to perturbations and changing environmental conditions that have been documented in larger foraminifera include life-cycle modifications, dysfunctional reproduction, calcification damage, and variable test morphologies (Röttger and Hallock 1982, Hallock et al. 1986, Harney et al. 1998).

Shoreline Change on O'ahu

The beaches of O'ahu are of monumental economic, recreational, and cultural importance to the people and state of Hawai'i. Beach erosion, defined as the volumetric loss of sediment from the beach that occurs when

sand supply is decreased or when erosion is refocused away from coastal lands and onto the adjoining beach (Coyne et al. 1996), has become an immediate problem on O'ahu. Analysis of aerial photogrammetric data has revealed that seawall and revetment construction used to mitigate the impacts of coastal land erosion has caused the narrowing or complete loss of approximately 24% of the original length of sandy beaches on O'ahu in the last several decades (Fletcher et al. 1997). The importance of foraminifera as producers of carbonate sand has been well established, and we have initiated a modern investigation of their roles in the sediment budget of these high volcanic islands in the expectation that better sand management principles will improve resource conservation.

Reef deterioration (D'Elia et al. 1991, Ginsburg and Glynn 1994) and coastal land loss (Pilkey et al. 1989) are issues of both scientific and public concern on a global scale. In low latitudes, both domains are intrinsically related to studies of nearshore carbonate production, erosion, and sediment transport. This is particularly true in the Hawaiian Islands, where a continental source of sand for the beaches is absent and where extensive circuminsular reef and channel systems serve as both sites of carbonate sand production and conduits for its transport. Hawaiian littoral and beach sands are generally of two types: dark detrital grains derived from upland erosion, and pale-colored skeletal material produced by marine organisms. Although the relative proportions of lithic and biogenic components vary with local conditions (e.g., intensity of weathering and degree of reef development), most of the beaches in the Hawaiian Islands are highly calcareous (Moberly et al. 1965).

An important factor affecting land loss on sandy shores is the sediment budget, a quantitative estimate of sand sources and sinks. Benthic genera that host algal endosymbionts, particularly *Amphistegina* spp., contribute the bulk of the foraminiferal fraction in Holocene reef sediments in the Indo-Pacific, with production rates that rival those of reef-building corals and calcareous algae (Hallock 1981). Wells (1957) considered fora-

minifera third in importance as carbonate producers on modern coral reefs (after corals and calcareous algae), and Moberly and Chamberlain (1964) found that larger foraminifera dominated the calcareous component of beach sands on O'ahu, composing 27% of the total volume (80% of which was contributed by *Amphistegina* alone). However, because foraminifera are nearly three times more resistant to abrasion than the other major constituents of Hawaiian beach sands (Moberly 1968), their concentration on beaches is not directly indicative of their carbonate-production potential.

Carbonate Production

In studies of living populations of *Amphistegina* on O'ahu, Muller (1974) reported that a mean standing crop of 1.7×10^5 individuals per square meter produced $0.51 \text{ kg CaCO}_3 \text{ m}^{-2}\text{yr}^{-1}$, or $3.4 \times 10^{-6} \text{ kg CaCO}_3$ per average individual. A model based on this relationship was formulated (Muller 1976) and used in detailed studies (Muller 1977) to estimate mean annual carbonate production (P_A) per individual based on the equation:

$$P_A = S_A * 3.4 \times 10^{-6} \text{ kg CaCO}_3 \text{ yr}^{-1}$$

where S_A is the standing crop of *Amphistegina* (number of individuals per square meter of suitable substrate). Because foraminifera have been characterized as such important contributors to the littoral sand budget of the Hawaiian Islands, an analysis of the contemporary living populations in O'ahu's nearshore waters was needed for our studies of sediment dynamics. Incorporating new bio-density data into this simple model renders modern production estimates that are directly comparable with similar data from the 1970s. The objectives of this study were thus to sample benthic foraminiferal communities in a variety of habitats, depths, and coastal regimes around the island of O'ahu; to generate standing-crop and relative percentage data on the major sand-producing species; to calculate modern estimates of annual carbonate production by the genus *Amphistegina*; and to compare these results with prior data

in evaluating production changes that might have occurred.

MATERIALS AND METHODS

Moberly and Chamberlain (1964) used three general classes to describe the fringing reefs of O'ahu: the narrow, deep, irregular reefs of the north and west coasts; the wide, generally shallow fringing reefs of the windward coast; and the wide, very shallow reefs of south (protected) coasts. In choosing the nearshore sampling sites, we consulted published descriptions of previously sampled locations and bottom habitats (Muller 1977, Hallock 1981), as well as aerial photographs and nautical charts. Each of O'ahu's general reef types and coastal regimes was sampled at least twice.

The symbiont-bearing foraminifera identified by Muller and in this study are the rotalines *Amphistegina lessonii*, *Amphistegina lobifera*, and *Heterostegina depressa* and the miliolines *Peneroplis* spp., *Sorites marginalis*, and *Amphisorus hemprechii* (Figure 1). Note that we now recognize *A. hemprechii* as what Muller (1976, 1977) and Hallock (1981) called *Marginopora vertebralis*. In nearshore regions around O'ahu, the consistently high density of these foraminifera, mostly *A. lessonii* and *A. lobifera*, occurs between 2 and 20 m. Because the bulk of the production by these two species occurs in less than 10-m water depth (Muller 1977), sampling was confined to depths between 2 and 10 m for scientific and logistical purposes.

At each of 11 locations, divers collected four to six loose cobbles of benthic substrate, each with a surface area of $\sim 25\text{--}40 \text{ cm}^2$, into labeled plastic bags. Reef slope habitats were collected in 8–10-m water depth at every site, and in 5-m water depth at nine sites. The reef flat environment was sampled in 2-m water depth at four sites. The sealed bags containing rubble and seawater were frozen within hours of collection to preserve the color of living foraminifera for later identification. Once thawed, the individual cobbles were scrubbed to remove the attached sediment, algae, and foraminifera. The resultant slurry

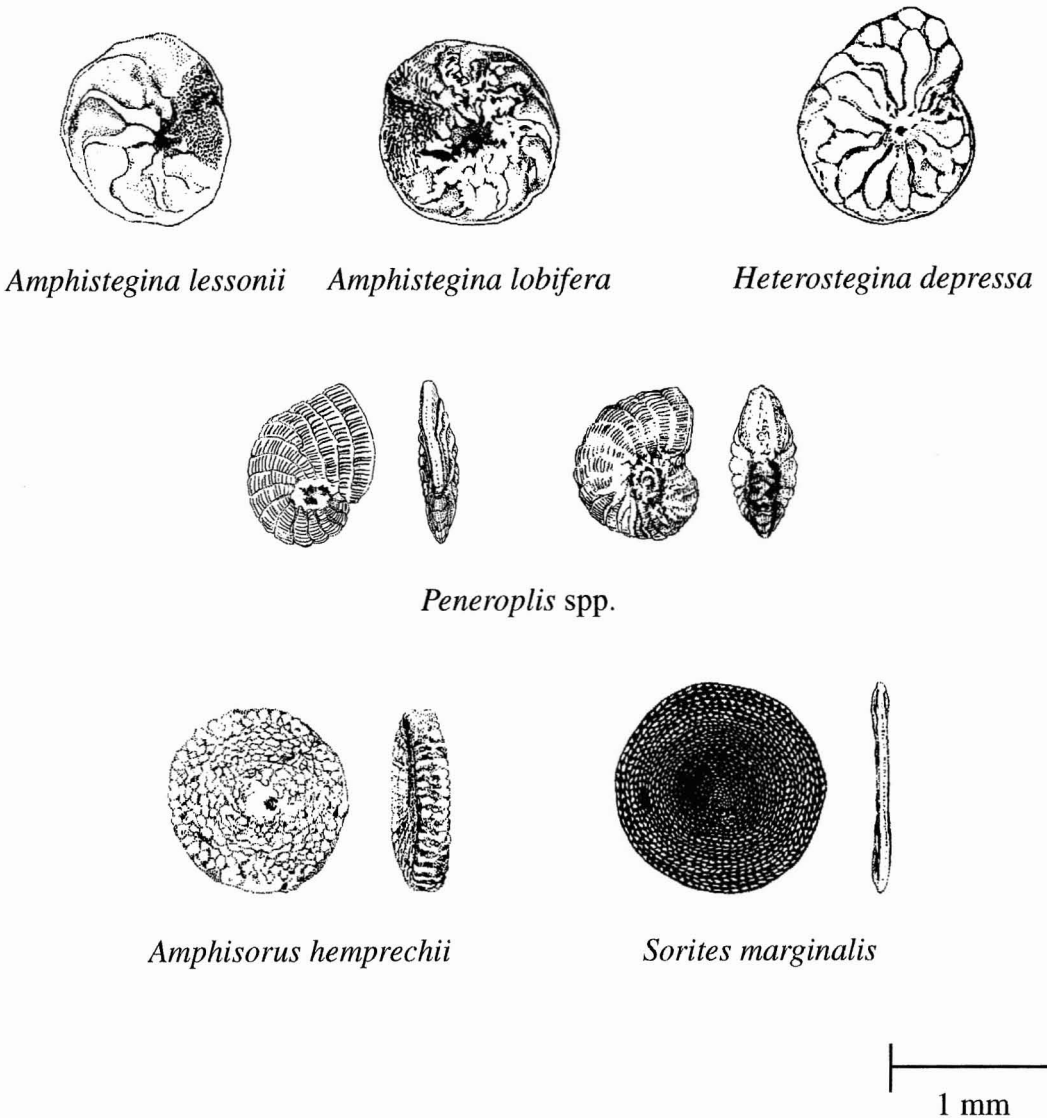


FIGURE 1. Symbiont-bearing benthic foraminifera identified in this study (after Hallock 1981).

was rinsed over a 63- μ m-mesh sieve, oven-dried, and reduced to manageable size by a random microsplitter. Foraminifera that were living at the time of collection retained the color imparted by their symbionts or protoplasmic pigments, and counts were made of the six species of larger foraminifera. The counts from the random splits were then extrapolated mathematically over the entire

sample. Substrate surface areas were obtained from digitized tracings of the rubble pieces, and the density of living foraminifera from each sample was then calculated for the area of substrate sampled. These methods of sample collection and processing are as described by Muller (1977) and have been widely used for more than two decades of foraminiferal research.

TABLE 1

STANDING CROP OF LIVING LARGER FORAMINIFERA ($\times 10^4$ INDIVIDUALS PER SQUARE METER) IN NEARSHORE REEF FLAT (2 m) AND REEF SLOPE (5 m, 8–10 m) HABITATS OF O'AHU, HAWAII

HABITAT	SITE	TOTAL	<i>A. lessonii</i>	<i>A. lobifera</i>	<i>Heterostegina</i>	<i>Amphisorus</i>	<i>Peneroplis</i>	<i>Sorites</i>
Reef flat (2 m)	Mālaekahana	6.4	1.5	4.1	0.13	0.13	0.51	0
	Punalu'u	22.8	11.0	7.7	1.3	0.59	2.3	0
	Kailua Bay	11.9	0.066	0.26	0.32	0.65	10.6	0
	Queen's Surf	0.19	0.015	0.030	0	0.044	0.10	0
	Average	10.3	3.1	3.0	0.43	0.35	3.4	0
Reef slope (5 m)	Kahe	36.3	22.4	7.5	1.2	0.69	4.4	0
	Mākaha	6.2	3.2	2.2	0.21	0.10	0.57	0
	Pūpūkea	9.9	6.0	3.3	0.07	0.20	0.27	0.068
	Mālaekahana	6.3	2.3	2.1	0.61	0.17	1.1	0
	Punalu'u	24.6	13.9	7.4	0.77	1.3	1.2	0
	Kailua Bay	3.2	1.7	0.66	0.11	0.12	0.58	0
	Sandy Beach	0.86	0.58	0.20	0.00	0.03	0.05	0
	Queen's Surf	1.3	0.34	0.52	0.06	0.06	0.34	0
	Magic Island	12.9	5.3	5.5	0.77	0.27	1.04	0.059
	Average	11.3	6.2	3.3	0.42	0.33	1.1	0.014
Reef slope (8–10 m)	Kahe	26.0	16.3	4.3	1.5	0.76	3.1	0.092
	Mākaha	48.1	20.5	17.8	2.1	0.87	6.9	0
	Mokulē'ia	14.8	8.8	3.4	1.4	0.24	0.83	0.12
	Pūpūkea	34.8	24.4	5.3	0.14	0.03	4.9	0
	Mālaekahana	31.3	21.8	5.9	1.0	0.92	1.6	0
	Punalu'u	10.4	7.2	2.2	0.18	0.36	0.54	0
	Kailua Bay	11.7	2.1	1.6	0.89	0.18	7.0	0
	Sandy Beach	19.8	10.3	8.4	0.29	0.36	0.43	0
	Queen's Surf	1.6	0.54	0.36	0.06	0.24	0.38	0
	Magic Island	22.4	13.4	7.0	1.1	0.22	0.53	0.10
	'Ewa	35.7	9.9	20.6	2.0	1.2	2.1	0
	Average	23.3	12.3	7.0	1.0	0.5	2.6	0.028

RESULTS

Hallock (1981) found that foraminiferal densities at sites around O'ahu were generally homogeneous and could thus be summarized as reef flat averages and reef slope averages. We found a similar result in our samples from June 1996 (Figure 1, Table 1). As expected, densities of the most important sand producers (symbiont-bearing rotaliines) were higher in reef slope (8–10 m) samples than in samples collected from shallower slopes and reef flat environments (<5 m). *Amphistegina* was the dominant constituent of the foraminiferal assemblages by several orders of magnitude in all but the shallowest of sites.

Estimates of (nearshore) carbonate production by *Amphistegina* spp. were calculated using Muller's equation; average values are given in Table 2. The highest rates (>0.6 kg

$\text{m}^{-2}\text{yr}^{-1}$) generally occurred in the 8–10-m depth interval around the island. In other reef-associated environments such as back reefs and shallow flats, production values ranged from 0.05 to 0.60 $\text{kg m}^{-2}\text{yr}^{-1}$. Maximum rates >1 $\text{kg m}^{-2}\text{yr}^{-1}$ are exceptional, occurring at only four sites where the standing crop of *Amphistegina* spp. exceeded 30×10^4 individuals per square meter (Figure 2). Population densities and calculated production rates varied with habitat and local conditions. For example, densities at Punalu'u (windward O'ahu) were higher at 2-m and 5-m depth than at 8 m owing to the lack of suitable substrate in deeper waters. Similarly, production by *Amphistegina* in Kailua Bay was minimal at all depths (<0.2 $\text{kg m}^{-2}\text{yr}^{-1}$), because the foraminiferal community was dominated by two species of the milioline *Peneroplis*. We therefore additionally distin-

TABLE 2

ESTIMATES OF CARBONATE PRODUCTION BY SYMBIONT-BEARING BENTHIC FORAMINIFERA AND OTHER REEF-ASSOCIATED ORGANISMS

ORGANISM	ENVIRONMENT	PRODUCTION RATE (kg CaCO ₃ m ⁻² yr ⁻¹)	LOCATION	REFERENCE
Foraminifera				
Benthic spp.	Reef flat (<5 m)	0.1–2.76	Palau	Hallock (1981)
<i>Amphistegina</i>	Tide pool	0.500	Hawai'i	Muller (1974)
	Reef flat (<5 m)	0.037	Hawai'i	Hallock (1981)
	Reef slope (5–15 m)	0.101	Hawai'i	Hallock (1981)
<i>A. lessonii</i>	Reef flat (2 m)	0.107	Hawai'i	This study
	Reef slope (5 m)	0.211	Hawai'i	This study
	Reef slope (8–10 m)	0.418	Hawai'i	This study
<i>A. lobifera</i>	Reef flat (2 m)	0.103	Hawai'i	This study
	Reef slope (5 m)	0.111	Hawai'i	This study
	Reef slope (8–10 m)	0.238	Hawai'i	This study
Algae				
<i>Halimeda</i>	Shallow lagoon	0.05	Bermuda	Wefer (1980)
Calcareous	—	0.9	Bahamas	Neumann and Land (1975)
Coralline	Algal ridge	10	—	Chave et al. (1972)
	—	0.5–2.5	Hawai'i	Littler (1971)
Reef communities				
	Barrier reef	3	Hawai'i	Smith et al. (1970)
	Seaward edge	4	—	Smith and Kinsey (1976)
	Protected areas	0.8	—	Smith and Kinsey (1976)
	Māmala Bay	12	Hawai'i	Grigg (1995)
	Coral on lava flow	1.4	Hawai'i	Oostdam (1963)
	Coral-algal reef	2.6	Kān'eohe Bay	Webb (1979)
	Sand/rubble flat	0.3	Lizard Island	Kinsey (1979)

guish our results by coastline and describe the (summer) habitat regimes sampled.

North Shore

During summer, this coastline is relatively quiescent in contrast to the intense surf it receives in the winter months. Samples were collected from relatively deeper, more irregular fringing reefs at two sites: Mokulē'ia and Pūpūkea. Mokulē'ia lies toward Ka'ena Point on the western end of O'ahu's northern coastline. The benthic habitat at our 8-m site consisted of scoured carbonate substrate in a moderate-energy setting. Reef channels were absent, and accumulation of loose sediments atop the reef was possible only in small pockets within the substrate. Densities of living foraminifera were high on samples of unconsolidated rubble ($\sim 15 \times 10^4$ individuals per square meter) but below the island-wide 8-m average of 23×10^4 individuals per square meter. *Amphistegina* composed

more than 80% of the total foraminiferal community.

Samples were also collected at Pūpūkea along the stretch of O'ahu's famous North Shore between the popular beaches of Wai-mea and Sunset. Topographical hardgrounds dominated our sites in 5-m and 8-m water depth at the downdrift end of a long section of sand beach (Sunset Beach). Rubble and loose sand were more common at 8 m, and the foraminiferal population at that depth was among the most dense found in O'ahu's waters (35×10^4 individuals per square meter). Crevices cut in the topography at 5-m depth were the only source of loose substrate at this site, where little or no sediment accumulation was noted and population densities were below average.

Windward Coast

During the summer, the windward side of O'ahu is influenced by the northeast trade

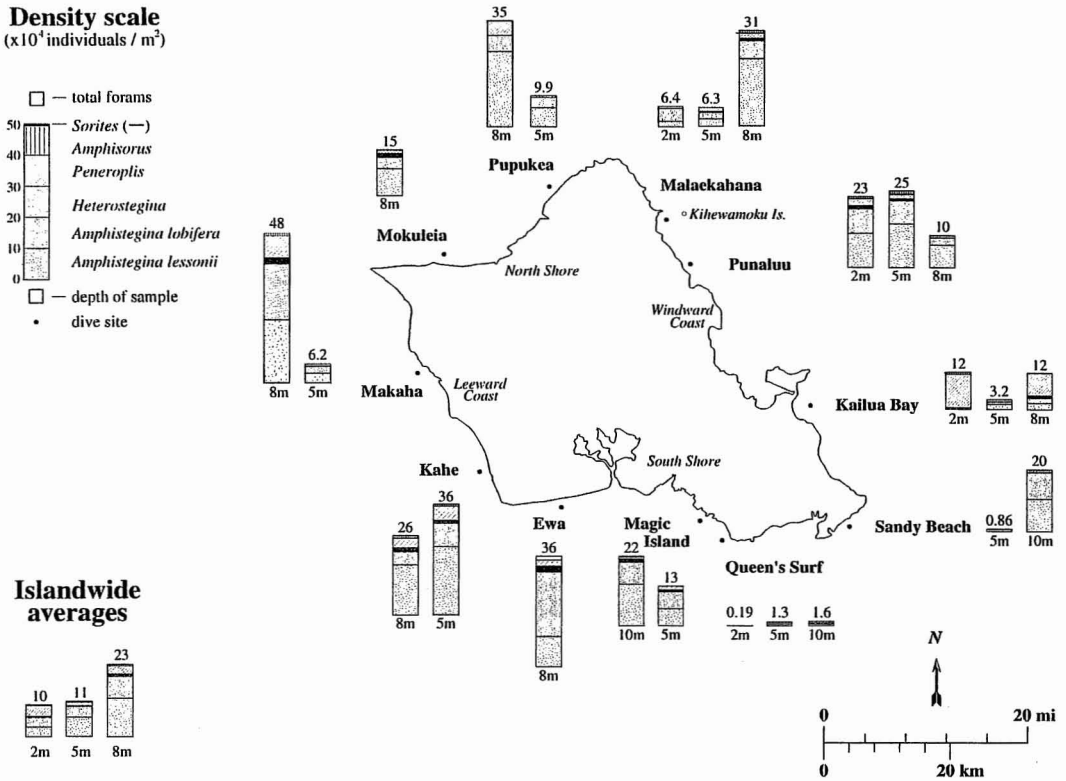


FIGURE 2. Sampling locations and population density data of six groups of symbiont-bearing benthic foraminifera collected from nearshore waters of O'ahu, Hawai'i.

winds that blow onshore nearly continuously at 10–25 knots. Wind-driven waves induce a choppy, confused sea surface, with waves of various heights (generally <2 m) and short periods (5–8 sec). Although wave energy is dissipated over the wide, fringing reefs of this coast, surge and currents can be quite strong during high wind conditions. The windward coast was sampled at three locations: Mālaekahana, Punalu'u, and Kailua Bay.

The northernmost site on the windward coast, Mālaekahana, was sampled at 2, 5, and 10 m during a low-tide shore dive along a transect directly toward small Kihewamoku Island. The extensive shallows of the Mālaekahana reef flat considerably dissipate the intense wave climate; thus pockets and small channels are common on shallow hardgrounds, acting as efficient traps for unconsolidated sediment and loose cobbles of sub-

strate. Samples from 2 m were collected inside the breaker line adjacent to such a channel. Water depths greater than 5 m were not reached until more than 1 km offshore where surge, longshore current, and breaking wave energies strengthened. At 5 m, benthic hardgrounds were the dominant habitat, and at 10 m sand and rubble were more common. All samples supported dense assemblages of foraminifera, particularly the deeper reef slope sample (31×10^4 individuals per square meter).

At Punalu'u, a freshwater lens resulting from stream runoff is often observed on the shallow flats, and extensive siltation of the substrate is common. Samples from 2 m were collected outside the extent of the lens and supported high standing crops of *Amphistegina*. Blankets of organic-rich sediments draped over old coral colonies between shore and 5-m water depth, where the water qual-

ity, suitable substrate, fish diversity, and visibility improved, and living corals and topographic features were common. At both of these shallower sites, living foraminiferal densities were more than double the island-wide average. Farther offshore at 8 m, water quality deteriorated severely, and the generally featureless bottom was dominated by pale, organic-rich sediments and little rubble. Densities of specimens living on what little rubble was found were less than half those found at 8-m sites elsewhere around O'ahu.

In Kailua Bay, the fringing reef is well developed and extensive. A wide submarine sand channel cuts across the reef and meanders a course through the bay, connecting nearshore zones to the deep (>40 m) sand field offshore. The channel represents an important source of and conduit for littoral sediments, but loose sand and rubble were rare in our sampling areas atop the fringing reef, trapped only in some small depressions of the substrate. *Halimeda*, an aragonitic calcareous green alga, proliferated inshore at the 2-m site, and unconsolidated sand and rubble were far more abundant. At these shallow sites, the miliolines *Peneroplis planatus* and *P. pertusus* composed a surprising 90% of the total foraminiferal community (12×10^4 individuals per square meter). The opaque nature of the miliolid test indicates that they dwell in shallow, brightly lit habitats. Islandwide, the greatest density of this genus was found in the 2-m-deep *Halimeda* beds in Kailua Bay. The 5-m and 8-m collection sites on the fringing reef were morphologically similar to one another and dominated by extensive, colorful encrustations of coralline algae and living coral but few loose cobbles of uncolonized substrate. Despite relatively low densities, *Amphistegina* represented 75% of the total foram community at 5 m. At 8-m water depth, however, the assemblage was dominated once again by *Peneroplis* (60%).

South Shore

During the summer months (April through September), the southern shores of O'ahu receive long-period swells of moderate

height (1–3 m) from storms generated in the South Pacific. Along this coast, there are regions of concentrated wave intensity and heavy surge. The southern shore was sampled at Sandy Beach, Queen's Surf, Magic Island, and 'Ewa's One'ula Beach Park.

Sandy Beach is a very energetic site with a powerful shorebreak. At 2-m water depth, firm substrate was completely absent. At 5 m, the few cobbles that were present supported a smaller (by two orders of magnitude) community of living foraminifera compared with other 5-m sites. The rarity of suitable habitat at these depths is due to the intense wave action that dominates the shoreface year-round. At 10-m depth, however, 0.7 km offshore and outside the heavy impact zone, extensive layers of volcanic tuff dominate the benthic substrate. Cobbles of this material support a thin veneer of sediment and high densities of living foraminifera (20×10^4 individuals per square meter). Remarkably, *Amphistegina* composed 95% of the population sampled at this depth.

Similar results reflecting the relationship between depth, wave energy, and foraminiferal densities were observed in samples collected from 2, 5, and 10 m off Queen's Surf in Waikīkī. At all depths, the nearshore environment is highly energetic in the summer. Breaking waves, heavy surge, and swift bottom currents scour the surface of what little hard substrate is present. As a result, the standing crop of foraminifera at these sampling depths was the lowest of all sites around O'ahu, by at least an order of magnitude.

Magic Island is semiprotected within the naturally embayed curve of O'ahu's southern coastline along Waikīkī, and the well-developed reef supports living coral and coralline algae in great numbers. During sampling, wave action was less intense at this site, and foraminiferal densities were found to be very high in both 5-m and 10-m samples (13 and 22×10^4 individuals per square meter, respectively). No samples were collected from 2-m water depth.

A similarly high density of living foraminifera was found in samples collected from the final site on O'ahu's southern shore.

In 8-m water depth offshore of One'ula Beach Park ('Ewa), the bottom was dominated by loose sand, occasional rubble, and various species of fleshy and calcareous algae. Surface and bottom currents here were moderate, but stabilizing beds of *Halimeda* and associated rubble supported a dense community of living foraminifera (36×10^4 individuals per square meter, among the highest values found). Firm substrate was absent at 5 m, and depths of 2 m were not visited.

Leeward Coast

The reefs of the leeward (Wai'anae) coast have been described as shallow, wide, and semiprotected (Moberly and Chamberlain 1964). Currents and wave energy are light to moderate in calm seas during the summer, but the degree of turbulence and intensity of shorebreak strengthen when large swells arrive from the north and west. Samples were collected from the Wai'anae reef in two locations: Kahe and Mākaha. During our sampling, the water clarity at both sites was exceptional, surge was minimal, and high wave energy was absent. At Kahe, reef slope samples were collected at 5-m and 10-m water depth where a sand field abuts the healthy fringing reef and forms narrow channels within it. Little unconsolidated substrate was present, but carbonate sediments were fairly abundant. Densities of living individuals were far above the islandwide averages at both depths (as high as 36×10^4 specimens per square meter).

A second leeward reef environment was visited offshore of the extensive beach southeast of Mākaha Point. Coral coverage was less extensive than at Kahe and unconsolidated substrate less common. Samples of reef rubble were collected from 8 m adjacent to a narrow sand channel leading shoreward, and they bore the densest of all foraminiferal communities sampled around the island (48×10^4 individuals per square meter). Farther shoreward along the channel, samples were collected in 5-m water depth from a similar (though slightly more energetic) habitat

where the density of living individuals was below average.

DISCUSSION

Foraminiferal Densities

The standing crop and relative abundance of living foraminiferal species vary substantially in modern warm, shallow, reef-associated environments depending on geographic region, energetic regime, water depth, benthic habitat, and water quality. In Hawai'i, very dense assemblages of symbiont-bearing foraminifera are typical of moderately energetic nearshore reef slope environments in 5–15-m water depth, where up to 10^6 individuals can be found per square meter of substrate (Muller 1974). Islandwide, samples collected at 2-, 5-, and 8-m water depth from reefal habitats in June 1996 reflect high densities of living, larger foraminifera (up to 10^5 individuals per square meter). Our counts of the living assemblages are considered minimum estimates, because we did not use staining methods (Peebles et al. 1997), nor did we identify or count juvenile specimens of very small size classes (e.g., <0.4 mm in diameter). Replicate samples were collected but not analyzed for variations.

We confirm that densities of symbiont-bearing foraminifera in O'ahu's nearshore waters are clearly dependent on the environmental factors described above, which must be considered in predicting and assessing the vitality of the foraminiferal community in a given area. For example, even if suitable substrate is abundant at an 8-m site on a reef slope in clear water (where one expects to find a dense assemblage), the standing crop of living foraminifera atop that substrate may be low because of the sweeping nature of local current and wave conditions. Analysis of replicate samples and seasonal collections could further quantify these observations, but it is clearly necessary to consider the overall nature of the sampling environment and the conditions to which it is subjected when assessing foraminiferal bio-

density, the health of the population, and the status of the reef itself.

Species Dominance

We found that the contribution of the two species of *Amphistegina* accounted for an average of ~80% of the modern foraminiferal assemblages in various reef slope (5–10 m) habitats islandwide and could be as high as 95% at some sites (e.g., Sandy Beach, 10 m). Overall, *Amphistegina* spp. are clearly the dominant benthic foraminifera in O'ahu's nearshore waters, and their biodensities meet or exceed the highest environmental index ranking described for healthy reef slopes (Hallock 1996). This genus, although "intermediate" in size (adults range from 1 to 3 mm in diameter), is one of the most prolific of all shallow-water foraminifera and is particularly important as a producer of sand-sized carbonate sediments in Hawai'i's nearshore waters.

Densities of the relatively smaller genus *Peneroplis* rival those of *Amphistegina* in shallow, well-lit reef flats (particularly in *Halimeda* beds in 2–5-m water depth) owing to the opaque nature of this miliolid's test. Islandwide, this genus contributes an average of ~40% to the foraminiferal communities sampled on reef flats (2 m) and generally <15% to those on reef slopes (5–10 m). In Kailua Bay, *Peneroplis* dominates the 2-m and 8-m samples, composing 90% and 60% of the total communities, respectively, although the standing crop of *Amphistegina* is still very high (on the order of 10^4). The other milioline genera identified in this study, *Amphisorus* and *Sorites*, are far less abundant islandwide. *Amphisorus* composes an average of ~8% of the foraminiferal assemblages sampled at 2-m depth around O'ahu. At reef slope depths (5–10-m samples), its contribution to the community falls below 3%. *Sorites*, a deeper-dwelling milioline genus expected to become more common in samples collected from depths >20 m (Hallock 1981), occurred in relatively minute numbers in nearshore reefal samples (<1% of the total assemblage) if at all.

Species interaction and dominance in the

foraminifera is influenced by factors other than shell type and habitat depth as discussed above. Benthic foraminiferal assemblages in the Pacific have previously been observed to shift from predominantly algal symbiont-bearing species to dominance by smaller species lacking symbionts in response to a limited anthropogenic nutrient source (Hirschfield et al. 1968). A community shift of this nature is an example of benthic succession along a nutrification gradient (Pearson and Rosenberg 1978) and is a predictable response in symbiont-bearing organisms that are efficient nutrient recyclers. We did not observe any indication of such an effect on the foraminiferal populations sampled in O'ahu's nearshore waters at depths <10 m.

Carbonate Production

Rates of carbonate production by corals and coralline algae are reasonably well known (see Table 2), but estimates of carbonate production by foraminifera in tropical environments are primarily for single species and in most cases are severely data-limited (Hallock 1981). To link raw biodiversity data to sediment-production potential, details of population biology and reproductive strategy must be considered (Murray 1967, Muller 1974). The population parameters necessary to determine the carbonate productivity of a foraminiferal species include standing crop, growth and mortality rates, fecundity, and size-specific mass. Such information is available for *Amphistegina* (Hallock 1981, 1984, Muller 1974), as is the simple annual carbonate contribution model used in this and previous studies to convert standing-crop data (no. of specimens per square meter) to production values (kg CaCO₃ per square meter per year).

Estimates of annual carbonate production by symbiont-bearing benthic foraminifera and other reef-dwelling organisms are presented in Table 2, along with the production potential of various reef communities as a whole. This study's estimates are intended for use in a comparative manner and are limited to order-of-magnitude calculations. It has

been long established that larger, symbiont-bearing benthic foraminifera are important contributors to carbonate budgets of reefal habitats, and we have reaffirmed the importance of these protists to the nearshore environments and beaches of O'ahu.

Published accounts of benthic foraminiferal assemblages can be valuable resources in efforts to determine if biotic changes have occurred in coastal ecosystems (Cockey et al. 1996) and in estimates of carbonate sediment production. Ecologically sensitive populations of symbiont-bearing foraminifera (particularly *Amphistegina*, for which a great deal is known) are now also acknowledged as useful indicators of environmental quality.

These shallow-water protists play a particularly important role in the sand budgets of tropical volcanic islands and coral atolls. The bulk of O'ahu's littoral sands are calcareous and biogenic, produced offshore by the activity of reef-dwelling, carbonate-secreting organisms (e.g., coralline and calcareous algae, corals, foraminifera). Upon the death of these organisms, their skeletal fragments are broken down into carbonate sediments that are both stored in and transported over reefs of various size and character fringing O'ahu's shorelines—the primary source of the island's beach sands.

The universal importance of beaches to coastal economies and in shoreline protection and beautification is well described. O'ahu, the most populated island in the Hawaiian Chain, home of the capital Honolulu and 1 million residents, is visited by numerous foreign and American tourists each year. The average acre of beachfront land is worth more than \$2 million (Coyne et al. 1996). Recent evidence reveals alarming rates of beach erosion and shoreline retreat that not only threaten coastal landowners, but potentially the economy of the entire state. Shoreline armoring has resulted in the loss or narrowing of nearly a quarter of O'ahu's beaches in the last several decades (Fletcher et al. 1997). It is thus critical to Hawaiian coastal management efforts to continue to develop an understanding of sand production, flux, storage, and fate in the nearshore

region. This study has established that population densities of larger foraminifera in shallow, nearshore habitats around O'ahu remain very high. A modern analysis of the skeletal components of beach, littoral, and offshore sediments is needed to better understand the roles that foraminifera and other carbonate-producing organisms play in Hawaiian coastal systems and sediment budgets.

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LITERATURE CITED

- CHAVE, K. E., S. V. SMITH, and K. J. ROY. 1972. Carbonate production by coral reefs. *Mar. Geol.* 12:123–140.
- COCKEY, E. M., P. HALLOCK, and B. H. LIDZ. 1996. Decadal-scale changes in benthic foraminiferal assemblages off Key Largo, Florida. *Coral Reefs* 15:237–248.
- COULBOURN, W. T., and J. M. RESIG. 1975. On the use of benthic foraminifera as sediment tracers in a Hawaiian bay. *Pac. Sci.* 29:99–115.
- COYNE, M., R. MULLANE, C. FLETCHER, and B. RICHMOND. 1996. Losing Oahu: Erosion on the Hawaiian coast. *Geotimes* 41:23–26.
- CUSHMAN, J. A. 1928. foraminifera: Their classification and economic use. Vol. 1. Cushman Lab. Foraminiferal Res. Spec. Publ.
- D'ELIA, C. F., R. W. BUDDEMEIER, and S. V. SMITH. 1991. Workshop on coral bleaching, coral reef systems, and global change. Pages 1–49 in Report of proceedings. Maryland Sea Grant College Publ. No. UM-SG-TS-91-03, College Park, Maryland.
- FLETCHER, C. H., R. A. MULLANE, and B. M. RICHMOND. 1997. Beach loss along armored shorelines on Oahu, Hawaiian Islands. *J. Coastal Res.* 13:209–215.
- GINSBURG, R., and P. GLYNN. 1994. Summary of the colloquium and forum on global aspects of coral reefs: Health,

- hazards, and history. Pages i–viii in R. N. Ginsburg, compiler. Proceedings of the colloquium and forum on global aspects of coral reefs: Health, hazards, and history, 1993. Rosentiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida.
- GRIGG, R. W. 1995. Coral reefs in an urban embayment in Hawaii: A complex case history controlled by natural and anthropogenic stress. *Coral Reefs* 14:253–266.
- HALLOCK, P. 1981. Production of carbonate sediments by selected foraminifera on two Pacific coral reefs. *J. Sediment. Petrol.* 51:467–474.
- . 1984. Distribution of selected species of living algal symbiont-bearing foraminifera on two Pacific coral reefs. *J. Foraminiferal Res.* 14:250–261.
- . 1996. *Amphistegina* (foraminifera) densities as a practical, reliable, low-cost indicator of coral reef vitality. Pages 37–44 in M. P. Crosby, G. R. Gibson, and K. W. Potts, eds. A coral reef symposium on practical, reliable, low-cost monitoring methods for assessing the biota and habitat conditions on coral reefs. 26–27 January 1995. Office of Ocean and Coastal Resource Management, National Oceanic and Atmospheric Association, Silver Spring, Maryland.
- HALLOCK, P., and E. C. GLENN. 1986. Larger foraminifera: A tool for paleoenvironmental analysis of Cenozoic carbonate depositional facies. *Palaios* 1:44–64.
- HALLOCK, P., L. B. FORWARD, and H. J. HANSEN. 1986. Environmental influence on test shape in *Amphistegina*. *J. Foraminiferal Res.* 16:224–231.
- HALLOCK, P., H. K. TALGE, E. M. COCKEY, and R. G. MULLER. 1995. A new disease in reef-dwelling foraminifera: Implications for coastal sedimentation. *J. Foraminiferal Res.* 25:280–286.
- HALLOCK, P., H. K. TALGE, K. SMITH, and E. M. COCKEY. 1993. Bleaching in a reef-dwelling foraminifer, *Amphistegina gibbosa*. Pages 44–49 in Proceedings, 7th International Coral Reef Symposium, Guam, 21–26 June 1992, vol. 1.
- HARNEY, J. N., P. HALLOCK, H. K. TALGE, and D. E. WILLIAMS. 1998. Observations of a paratrimorphic life cycle in *Amphistegina gibbosa* populations from the Florida Keys. *J. Foraminiferal Res.* 28:141–147.
- HIRSCHFIELD, H. I., R. CHARMATZ, and L. HENSON. 1968. Foraminifera in samples taken from Eniwetok Atoll in 1956. *J. Protozool.* 15:497–502.
- KINSEY, D. W. 1979. Carbon turnover and accumulation by coral reefs. Ph.D. diss., University of Hawai'i, Honolulu.
- LEE, J. J., and O. R. ANDERSON. 1991. Symbiosis in foraminifera. Pages 157–220 in J. J. Lee and O. R. Anderson, eds. *Biology of foraminifera*. Academic Press, New York.
- LI, C., B. JONES, and P. BLANCHON. 1995. Lagoon-shelf sediment exchange by storms—evidence from foraminiferal assemblages, east coast of Grand Cayman, British West Indies. *J. Sediment. Res.* 67:17–25.
- LITTLER, M. M. 1971. Roles of Hawaiian crustose coralline algae (Rhodophyta) in reef biology. Ph.D. diss., University of Hawai'i, Honolulu.
- MATTHEWS, R. K., W. B. CURRY, K. C. LOHMANN, and M. A. SOMMER. 1980. Late Miocene palaeo-oceanography of the Atlantic: Oxygen-isotope data on planktonic and benthic foraminifera. *Nature (Lond.)* 283:555–557.
- MOBERLY, R., JR. 1968. Loss of Hawaiian littoral sand. *J. Sediment. Petrol.* 38:17–34.
- MOBERLY, R., JR., and T. CHAMBERLAIN. 1964. Hawaiian beach systems. *HIG Rep.* 64-2. Hawai'i Institute of Geophysics, University of Hawai'i, Honolulu.
- MOBERLY, R., JR., L. D. BAVER, and A. MORRISON. 1965. Source and variation of Hawaiian littoral sand. *J. Sediment. Petrol.* 35:589–598.
- MULLER, P. HALLOCK. 1974. Sediment production and population biology of the benthic foraminifer *Amphistegina madagascarensis*. *Limnol. Oceanogr.* 19:802–809.
- . 1976. Sediment production by shallow-water, benthic foraminifera at selected

- sites around Oahu, Hawaii. Marit. Sediments Spec. Publ. 1:263–265.
- . 1977. Some aspects of the ecology of several large, symbiont-bearing foraminifera and their contribution to warm, shallow-water biofacies. Ph.D. diss., University of Hawai'i, Honolulu.
- MURRAY, J. M. 1967. Production in benthic foraminiferids. *J. Nat. Hist.* 1:1–68.
- . 1973. Distribution and ecology of benthic foraminiferids. Crane, Russak, and Co., New York.
- MYERS, E. H. 1943. Life activities of foraminifera in relation to marine ecology. *Proc. Am. Philos. Soc.* 86:439–458.
- NEUMANN, A. C., and L. S. LAND. 1975. Lime mud deposition and calcareous algae in the bight of Abaco, Bahamas: A budget. *J. Sediment. Petrol.* 45:763–786.
- OOSTDAM, B. L. 1963. The thickness and rates of growth of corals on top of the historic lava flow near La Perouse Bay, Maui. Unpubl. rep. available from Hawai'i Institute of Geophysics, University of Hawai'i at Mānoa, Honolulu.
- PEARSON, T. H., and R. ROSENBERG. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr. Mar. Biol. Annu. Rev.* 16:229–311.
- PEEBLES, M. W., P. HALLOCK, and A. C. HINE. 1997. Benthic foraminiferal assemblages from current-swept carbonate platforms of the northern Nicaraguan Rise, Caribbean Sea. *J. Foraminiferal Res.* 27:42–50.
- PILKEY, O. H., R. A. MORTON, J. T. KELLEY, and S. PENLAND. 1989. Coastal land loss. 28th Int. Geol. Congr. AGU Short Course Vol. 2.
- RÖTTGER, R., and P. HALLOCK. 1982. Shape trends in *Heterostegina depressa* (Protozoa, Foraminiferida). *J. Foraminiferal Res.* 12:197–204.
- SMITH, S. V., and D. W. KINSEY. 1976. Calcium carbonate production, coral reef growth, and sea level change. *Science* (Washington, D.C.) 194:937–939.
- SMITH, S. V., K. J. ROY, K. E. CHAVE, J. E. MARAGOS, A. SOEGIARTO, G. KEY, M. J. GORDON, and D. KAM. 1970. Calcium carbonate production and deposition in a modern barrier reef complex. Pages 688–689 in *Abstr. Annu. Meet. Geol. Soc. Am., Milwaukee, Wisconsin*. 1970.
- WEBB, M. D. 1979. Pathways of CO₂, O₂, CO, and CH₄ in water flowing over a coral reef, Kaneohe Bay, Oahu, Hawaii. M.S. thesis, University of Hawai'i, Honolulu.
- WEFER, G. 1980. Carbonate production by algae *Halimeda*, *Penicillus*, and *Padina*. *Nature* (Lond.) 285:323–324.
- WELLS, J. W. 1957. Coral reefs. *Geol. Soc. Am. Mem.* 67:609–631.