CARBONATE SEDIMENTOLOGY OF A WINDWARD SHOREFACE: KAILUA BAY, OAHU, HAWAIIAN ISLANDS

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ABSTRACT

The diverse field of sedimentology offers a range of scales and processes for research in settings from the bottom of the sea to the heights of the Himalayas. Research may involve studies of the texture, composition, and mineralogy of rocks and unconsolidated sediments, the processes by which sediment is produced, transported, and deposited, and the investigation of ancient and modern environments. The research that follows in this dissertation is divided into three chapters which correspond to three research publications, all converging on a specific theme: carbonate sedimentology in oceanic island settings. Each paper employs a multidisciplinary approach to the study of coastal and shallow-marine environments of low latitudes, attempting to illustrate the important relationship between reef productivity and coastal dynamics.

The first paper, *Standing crop and sediment production of reef-dwelling foraminifera*, is a study of the population dynamics and sediment production potential of benthic foraminifera in the waters surrounding Oahu, Hawaii. The objectives of this study are to assess the population density of benthic foraminifera on fringing reef flats and slopes of Oahu, to estimate sediment production by the dominant genus *Amphistegina*, and to compare population status to data available from 1970s.

The second paper, *Age and composition of carbonate shoreface sediments*, utilizes sedimentological and geochemical techniques to understand sediment dynamics in a windward setting (Kailua Bay, Oahu). The purpose of this paper is to analyze the texture, composition, mineralogy, and radiocarbon age of calcareous sediments from diverse

subenvironments of the carbonate reef-dominated shoreface (from the shoreline to 4 km offshore).

The third paper is entitled *A budget of Holocene carbonate sediments, Kailua Bay, Oahu, Hawaii*. The purpose of this paper is to construct a quantitative, field-based budget describing the production, storage, and loss of calcareous sediment during the last 5000 years in carbonate reef-dominated Kailua Bay. The model's approach to assessing sediment supply on oceanic islands may also be applied to other systems to aid in interpreting coastal morphology and behavior.

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CHAPTER 1

STANDING CROP AND SEDIMENT PRODUCTION OF REEF-DWELLING FORAMINIFERA ON OAHU, HAWAII

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ABSTRACT

Most of Oahu'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 biogenically-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 10^5 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 continues for Oahu and neighboring islands to describe their roles in the sediment budget more completely.

INTRODUCTION

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 environmental 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 Oahu

The beaches of Oahu are of monumental economic, recreational, and cultural importance to the people and state of Hawaii. 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 Oahu. 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 Oahu 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 foraminifera 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 Oahu, 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 Oahu, Muller (1974) reported that a mean standing crop of 1.7×10^5 individuals per square meter produced 0.51 kg $CaCO_3$ $m^{-2}y^{-1}$, or 3.4×10^{-6} 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 Oahu's nearshore waters was needed for our studies of sediment dynamics. Incorporating new biodensity 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 Oahu; 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 Oahu: 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 Oahu'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 rotaliines *Amphistegina lessonii*, *Amphistegina lobifera*, and *Heterostegina depressa* and the miliolines *Peneroplis* spp., *Sorites marginalis*, and *Amphisorus hemprechii* (Figure 1-1). Note that we now recognize *A. hemprechii* as what Muller (1976, 1977) and Hallock (1981) called *Marginopora vertebralis*. In nearshore regions around Oahu, the consistently high density of these foraminifera, mostly *A. lessonii* and *A. lobifera*, occurs between 2 and 20 m water depth. 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 ~ 25–40 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 was rinsed over a 63-µm-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.

RESULTS

Hallock (1981) found that foraminiferal densities at sites around Oahu 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 (Table 1-1, Figure 1-1). 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 1-2. The highest rates (>0.6 $kgm^{-2}y^{-1}$) 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 $kgm^{-2}y^{-1}$. Maximum rates >1 $kgm^{-2}y^{-1}$ are exceptional, occurring at

only four sites where the standing crop of *Amphistegina* spp. exceeded 30 x 10^4 individuals per square meter (Figure 1-2).

Population densities and calculated production rates varied with habitat and local conditions. For example, densities at Punaluu (windward Oahu) 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 $kgm^{-2}y^{-1}$), because the foraminiferal community was dominated by two species of the milioline *Peneroplis*. We therefore additionally distinguish 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: Mokuleia and Pūpūkea. Mokuleia lies toward Kaena Point on the western end of Oahu'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 (~ 15 x 10^4 individuals per square meter) but below the island-wide 8-m average of 23 x 10^4 individuals per square meter. *Amphistegina* composed more than 80% of the total foraminiferal community.

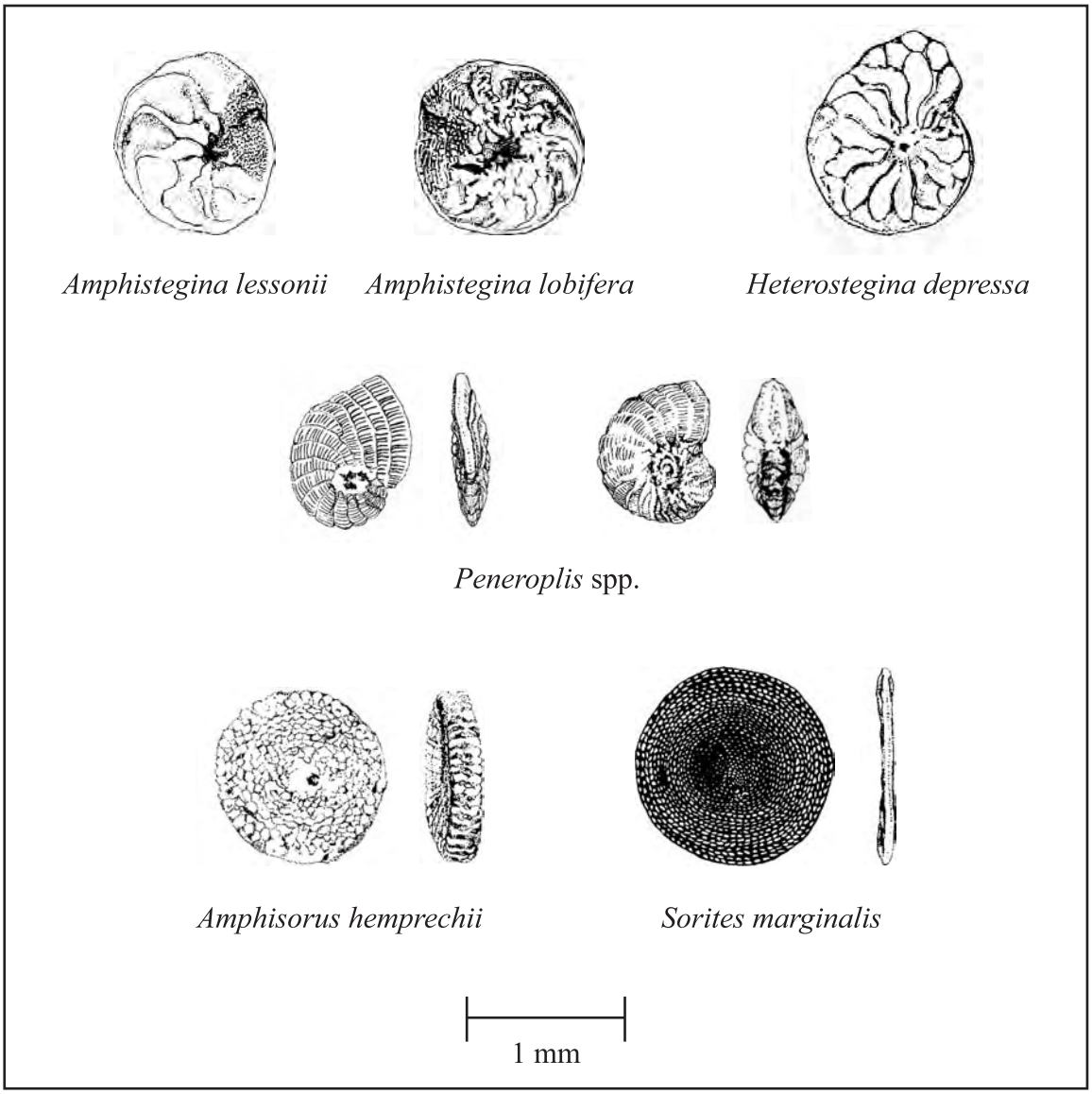

Figure 1-1. Symbiont-bearing benthic foraminifera identified in this study (after Hallock 1981).

Table 1-1. Standing crop of living larger foraminifera (x 10^4 individuals per square meter) in nearshore reef flat (2 m water depth) and reef slope (5 m, 8–10 m water depth) habitats of Oahu, Hawaii.

Habitat	**Site**	**Total**	*Amphistegina lessoni*	*Amphistegina lobifera*	*Heterostegina depressa*	*Amphisorus hemprechii*	*Peneroplis* spp.	*Sorites marginalis*
Reef flat (2 m)	Mālaekahana	6.4	1.5	4.1	0.13	0.13	0.51	0
	Punaluu	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
	Punaluu	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
	Mokuleia	14.8	8.8	3.4	1.4	0.24	0.83	0.12
Reef slope (8–10 m) (continued)	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
	Punaluu	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**

Table 1-2. Estimates of carbonate production by symbiont-bearing 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
Amphistegina	Tide pool	0. 50	Hawaii	Muller 1974
	Reef flat <5 m	0. 04	Hawaii	Hallock 1981
	Reef slope 5–15 m	0. 10	Hawaii	Hallock 1981
A. lessonii	Reef flat 2 m	0. 11	Hawaii	This study
	Reef slope 5 m	0. 21	Hawaii	This study
	Reef slope 8–10 m	0. 42	Hawaii	This study
A. lobifera	Reef flat 2 m	0. 10	Hawaii	This study
	Reef slope 5 m	0. 11	Hawaii	This study
	Reef slope 8–10 m	0. 24	Hawaii	This study
Algae				
Halimeda	Shallow lagoon	0. 05	Bermuda	Wefer 1980
Calcareous	--	0. 09	Bahamas	Neumann and Land 1975
Coralline	Algal ridge	10.	--	Chave et al. 1972
	--	0.5–2. 5	Hawaii	Littler 1971
Corals				
Reef communities	Barrier reef	3.	Hawaii	Smith et al. 1970
	Seaward edge	4.	--	Smith and Kinsey 1976
	Protected areas	0. 8	--	Smith and Kinsey 1976
	Mamala Bay	12.	Hawaii	Grigg 1995
	Coral on lava flow	1. 4	Hawaii	Oostdam 1963
	Coral-algal reef	2. 6	Kaneohe Bay	Webb 1979
	Sand / rubble flat	0. 3	Lizard Island	Kinsey 1979

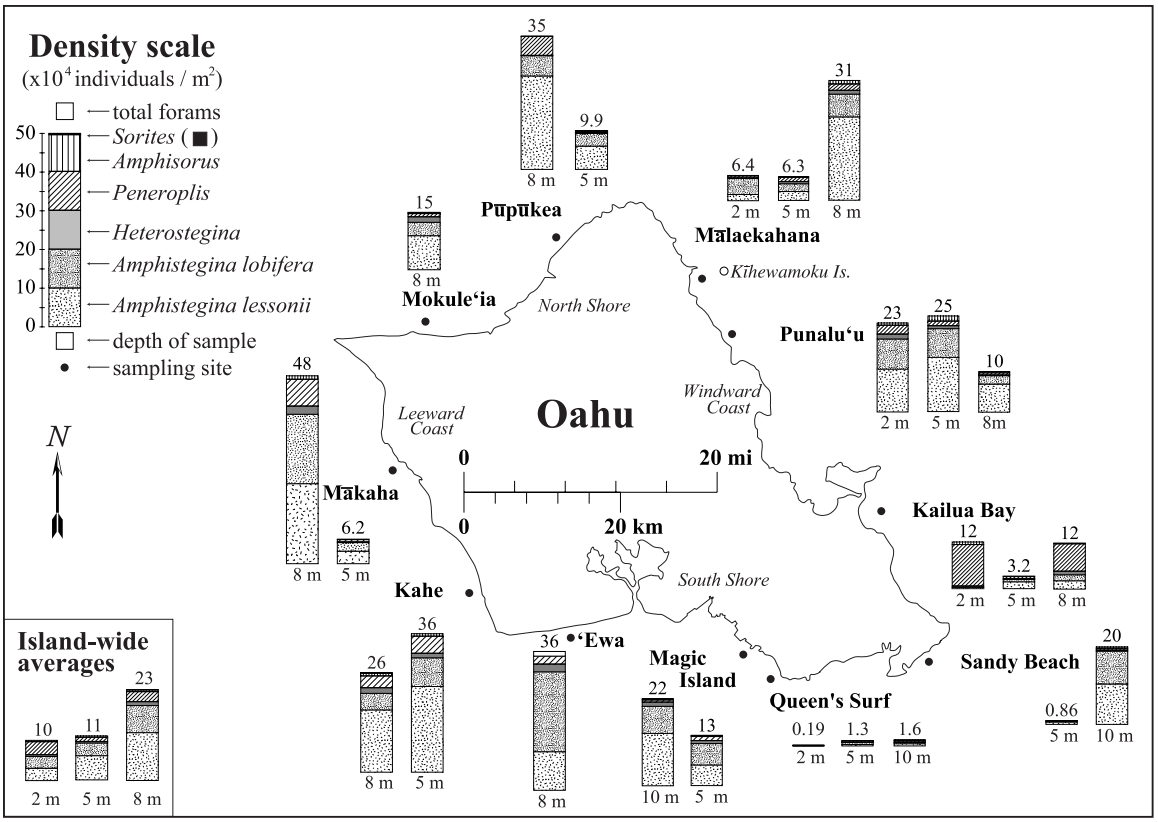

Figure 1-2. Sampling locations and population density data of six groups of symbiont-bearing benthic foraminifera collected from nearshore waters of Oahu, Hawaii.

Samples were also collected at Pūpūkea along the stretch of Oahu's famous North Shore between the popular beaches of Waimea 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 Oahu's waters (35 x 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 Oahu is influenced by the northeast trade 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, Punaluu, 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 Kīwehamoku Island, 1.5 km offshore. 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 substrate. 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 x 10^4 individuals per square meter).

At Punaluu, 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 quality, 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 islandwide 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 Oahu.

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 (>70 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 x 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 Oahu receive long-period swells of moderate height (1 –3 m) from storms generated in the southern hemisphere. 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 Oneula 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 foraminfera (20 x 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 Oahu, by at least an order of magnitude.

Magic Island is semiprotected within the naturally embayed curve of Oahu'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 x 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 Oahu's southern shore. In 8-m water depth offshore of Oneula 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 x 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 (Waianae) 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 Waianae 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 x 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 x 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 Hawaii, 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 Oahu'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 biodensity, 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 Oahu'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 Hawaii'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 Oahu. 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 Oahu's nearshore waters at depths <10 m.

Carbonate Production

Rates of carbonate production by corals and coralline algae are reasonably well known (see Table 1-2), 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 biodensity 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 (number of specimens per square meter) to production values (kg $CaCO_3$ per square meter per year).

Estimates of annual carbonate production by symbiont-bearing benthic foraminifera and other reef-dwelling organisms are presented in Table 1-2, 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 Oahu.

CONCLUSIONS

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 Oahu'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 Oahu'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. Oahu, the most populated island in the Hawaiian Archipelago, 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 Oahu'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 Oahu 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.

CHAPTER 2

AGE AND COMPOSITION OF CARBONATE SHOREFACE SEDIMENTS, KAILUA BAY, OAHU, HAWAII

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ABSTRACT

The Kailua Bay shoreface (from the shoreline to 4 km offshore) consists of a broad (10 km^2) fringing coral reef ecosystem bisected by a sinuous, shore-normal, sand-filled paleostream channel 200–300 m wide. The median grain diameter of surface sands is finest on the beach face (<0.3 mm) and increases offshore along the channel axis. Kailua sands are >90% biogenic carbonate, dominated by skeletal fragments of coralline algae (e.g. *Porolithon*, up to 50%) followed by the calcareous green alga *Halimeda* (up to 32%), coral fragments (1–24%), mollusc fragments (6–21%), and benthic foraminifera (1–10%). Sand composition and age across the shoreface are correlated to carbonate production. Corals and coralline algae, principal builders of the reef framework, are younger and more abundant in sands along the channel axis and in offshore reefal areas, while *Halimeda*, molluscs, and foraminifera are younger and more dominant in nearshore waters shoreward of the main region of framework-building. Shoreface sediments are

relatively old. Of 20 calibrated radiocarbon dates on skeletal constituents of sand, only three are younger than 500 yr BP; six are 500–1000 yr BP; six are 1000–2000 yr BP; and five are 2000–5000 yr BP. Dated fine sands are older than medium to coarse sands and hence may constitute a reservoir of fossil carbonate that is distributed over the entire shoreface. Dominance of fossiliferous sand indicates long storage times for carbonate grains, which tend to decrease in size with age, such that the entire period of relative sea-level inundation (~5000 yr) is represented in the sediment. Despite an apparently healthy modern coral ecosystem, the surficial sand pool of Kailua Bay is dominated by sand reflecting an antecedent system, possibly one that existed under a +1–2 m sea-level high stand during the mid- to late Holocene.

INTRODUCTION

During the last decade, the composition of unconsolidated, shallow-marine carbonate sediments has been utilized to study depositional patterns and pathways (Gischler and Lomando 1999, Kench 1997), the zonation of reefal and lagoonal sediments (Chevillon 1996), and the sedimentological importance of *Halimeda* bioherms (Roberts et al. 1988). Although some compositional studies are concerned with the early diagenesis of sediments and include petrographic analysis of skeletal materials (e.g. Furukawa et al. 1997), most do not integrate detailed binocular, petrographic, mineralogic, and geochemical examination. Thus many aspects of carbonate sand origin, compositional diversity, and mineralogic diagenesis are poorly known.

Similarly, although radiocarbon age-dating of consolidated, shallow-marine carbonates has proven a valuable tool in paleoenvironmental reconstructions and in studies of reef stratigraphy, contemporaneous unconsolidated carbonate sands have received less attention. Work with various aspects of carbonate sand and clast age in Pacific locales has contributed to our knowledge of Holocene sea-levels and shoreline evolution (e.g. Grossman and Fletcher 1998, Calhoun and Fletcher 1996, Fletcher and Jones 1996, Athens and Ward 1991), sedimentation histories (e.g. James et al. 1994, Roy 1991, Harris et al. 1990), and the accumulation of *Halimeda* bioherms (e.g. Davies and Marshall 1985). Understanding the age of sand in various depositional environments aids in the interpretation of sediment production, transport, and storage time within diverse "shoreface" subenvironments (within the region of wave disturbance from shoreline to offshore). The purpose of this paper is to characterize carbonate sediment origin, age, and dynamics in a windward Hawaiian coral reef setting.

Study Area

Kailua Bay is located on the northeast (windward) coast of Oahu (21°25' N, 157°43' W) in the Hawaiian Archipelago (Figure 2-1, location map). Northeast tradewinds blow onshore between 10–25 knots 90% of the summer months (April-September), generating waves that average 1–3 m in height with periods of 6–12 seconds. Ocean surface temperatures during these months are 25°–28°C. During winter months (October-March), storms in the North Pacific produce large swells on Oahu's north shore that occasionally refract into Kailua Bay as waves up to 4 m in height with periods of 10–20 seconds.

During winter months, trade winds are more variable, and ocean surface temperatures range between 22°–25°C.

A georeferenced mosaic of airborne multispectral data collected over Kailua Bay (Isoun et al. 1999) illustrates the distribution and morphology of benthic substrates and reef environments in the study area (Figure 2-1). Dark areas are consolidated substrate, living coral, and algae; light areas are typically sandy regions. The shoreline is rimmed by an arcuate, carbonate sand beach 3.5 km in length which grades seaward to a shallow (<5 m depth), lithified limestone seafloor with a veneer of sand that is generally thin ("hardgrounds"). This nearshore region is dominated by sand, rubble, outcrops of fossil reef, meadows of calcareous *Halimeda* and fleshy algae (e.g. *Sargassum*), and occasional coalesced colonies of the coral *Porites lobata*. In the central nearshore region, a large sand field exists in marked contrast to the generally sand-poor regions characterizing the shallow shoreface to the north and south. The 4 km^2 fringing reef platform is deeply bisected by a sinuous paleostream channel 200–300 m wide that originates in the nearshore sand field. The total length of the channel axis is nearly 2 km, and the area of sandy seafloor between its walls is ~$3x10^5$ m^2.

Detailed bathymetry of the offshore region illustrates varied water depths over the broad fringing reef (5–20 m) (Figure 2-1). Aspects of coral morphology and community structure have been qualitatively observed over the broad reef platform by large-scale reconnaissance dives and tows. Values of live coral cover were based on visual estimates. The landward portion of the reef platform (5–8 m water depth) is largely composed of fossil reef with relatively low substrate relief (<3 m) supporting ~25–50% living coral cover (typically encrusting *Porites lobata* and *Montipora* sp. or stoutly-branched

Pocillopora meandrina). Large sand bodies and partially-buried outcrops of scoured limestone are also common. As the reef platform gradually slopes seaward to depths as great as 20 m, substrate relief (3–8 m) and percent living coral cover (50–75%) increase toward the fore-reef nearly 3 km offshore. Branching *Porites compressa* and platy coral morphologies are abundant on the seaward portion of the reef platform. Portions of the reef slope support luxuriant growth and 100% living coral cover. The top of the fore-reef edge lies in ~15 m water depth and slopes steeply seaward (in some places as talus and elsewhere as continuous living coral cover) to abut a sand field in 25 m water depth. A detailed description of the fore-reef environment of Kailua is found in Hampton et al. (1998).

MATERIALS AND METHODS

Sample Collection

Sediment samples were collected in order to describe their composition, age, and geochemical properties. Samples were collected in Kailua Bay by divers pressing core jars (500 cm^3 volume) into unconsolidated sediment along a transect from the landward edge of the beach (B–series) in a shore-normal direction along the channel axis (C–series) (Table 2-1). The location of samples collected from the beach face (B1–5) are shown in detail in Figure 2-2: B1 was collected above sea level from an excavation pit ~1.8 m deep below B2 at the landward edge of the beach; B3 and B4 were surficial

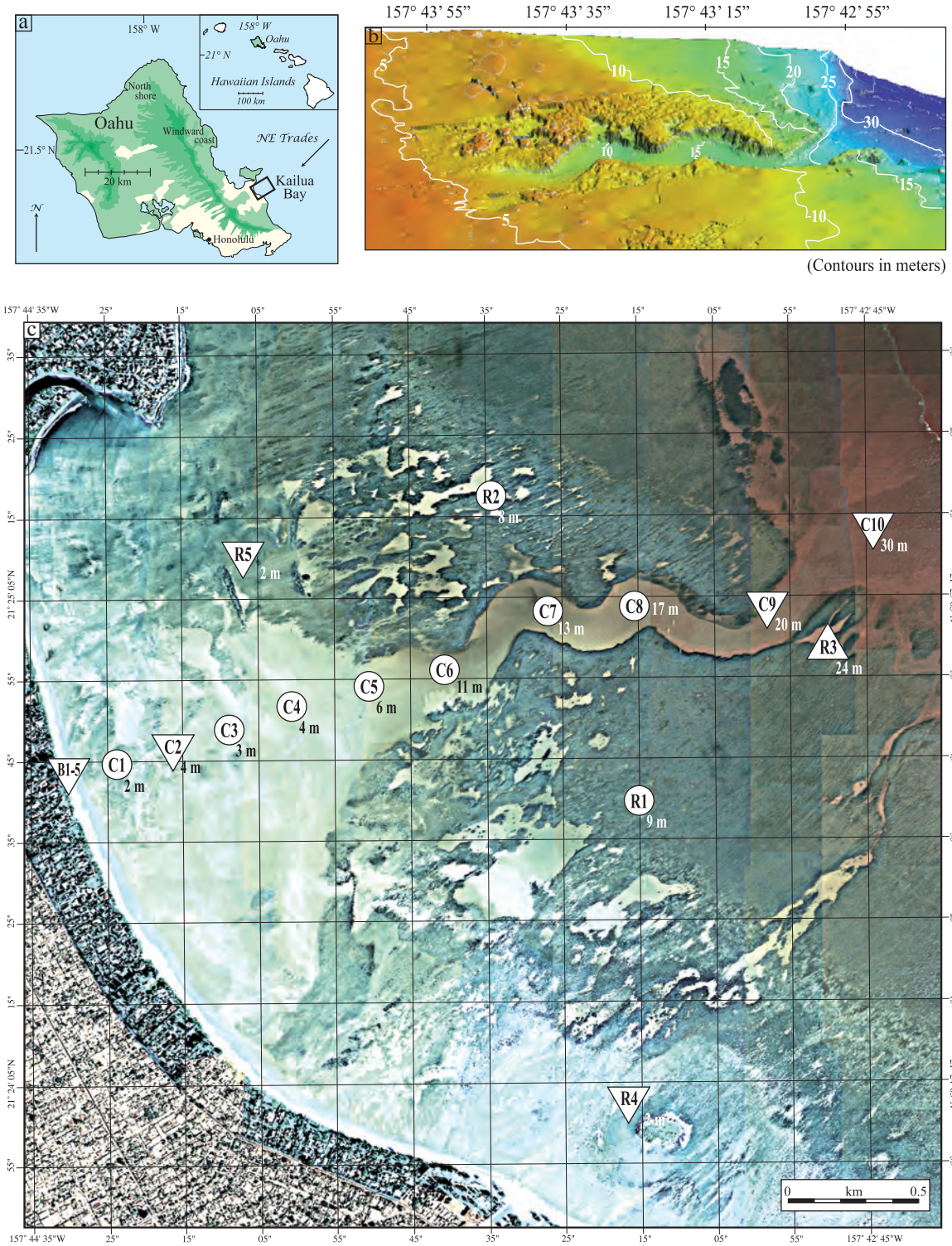

Figure 2-1. Location map (a), bathymetry (b), and reef environments (c) of Kailua Bay, Oahu, Hawaii. Sample location and water depths (in meters) are shown (see also Table 2-1). Georeferenced multispectral image in (c) after Isoun et al. 1999.

Table 2-1. Summary of mean sediment grain size (mm), sorting index (see text), and percent composition of samples in this study. Shoreface sites and elevations are listed from the beach excavation (B1) to the seaward mouth of the channel (C10-Trough and C10-Crest). Samples R1, R2, and R3 are reef platform sands; R4 is sand collected between fossil reef outcrops covered with coralline algae; R5 is sand from a *Halimeda* meadow. Skeletal grains are separated as to origin: framework production and direct production. [a] "Other" direct sediment producers are bryozoans and serpulids. Diagenetic (nonskeletal) grains are intraclasts and crystalline fragments (see text for descriptions). Total sediment is composed of carbonate particles, volcanic minerals, and unidentifiable grains. The last column summarizes the origin of carbonate grains in each sample.

SEDIMENT ORIGIN and Abundance (%)					FRAMEWORK-DERIVED		DIRECTLY-PRODUCED					DIAGENETIC (NONSKELETAL)		TOTAL SEDIMENT			SUMMARY OF $CaCO_3$ ORIGIN		
	SITE	Elevation (m)	Size (mm)	Sorting	Coral	Coralline algae	*Halimeda*	Mollusc	Foram	Echinoid	Other[a]	Intraclast	Crystalline clast	$CaCO_3$	Volcanic	Unid.	Framework	Direct	Diagenetic
BEACH	B1	0	0.30	0.6	12	32	3	16	2	2	1	12	10	90	10	0	44	24	22
	B2	+2	0.30	0.6	12	40	12	16	5	2	0	2	8	97	3	0	52	35	10
	B3	+1.5	0.30	0.7	13	36	12	17	3	1	1	9	6	97	3	1	49	33	15
	B4	0	0.21	0.7	13	24	17	17	9	3	1	4	9	97	2	1	35	47	13
	B5	-1	0.12	0.7	6	18	30	21	6	2	1	0	10	94	6	0	24	60	10
NEARSHORE	C1	-2	0.12	0.6	3	16	31	11	7	5	1	2	17	94	4	2	19	55	19
	C2	-4	0.46	0.8	12	35	13	11	5	2	0	7	9	94	6	0	47	31	16
	C3	-3	0.40	0.7	13	28	16	12	8	3	4	7	6	97	1	2	41	43	13
	C4	-4	0.51	0.7	8	38	8	11	6	4	2	10	9	96	3	1	46	31	19
	C5	-6	0.45	1.1	12	36	2	9	4	1	3	14	9	90	7	3	48	19	23
OFFSHORE	C6	-11	0.83	1.0	9	51	8	6	5	1	0	12	5	97	3	0	60	20	17
	C7	-13	1.26	1.1	10	39	32	8	1	1	2	6	1	100	0	0	49	44	7
	C8	-17	0.70	0.9	11	48	12	7	3	1	1	11	5	99	1	0	59	24	16
	C9	-20	0.68	0.8	9	44	10	10	4	1	0	16	4	98	1	1	53	25	20
	C10-T	-30	0.72	1.6	8	49	4	7	2	0	1	17	5	93	7	0	57	14	22
	C10-C	-30	0.57	0.8	2	41	16	6	10	3	0	5	15	98	2	0	43	35	20
REEF PLATFORM	R1	-9	1.05	0.6	18	42	4	10	6	2	1	16	1	100	0	0	60	23	17
	R2	-8	0.71	0.6	11	46	10	11	4	1	1	16	0	100	0	0	57	27	16
	R3	-20	0.85	1.1	24	33	14	6	3	1	0	16	3	100	0	0	57	24	19
	R4	-2	1.10	0.8	5	38	32	19	0	0	1	2	3	100	0	0	43	52	5
	R5	-2	0.60	0.9	1	25	31	13	5	1	2	15	5	98	2	0	26	52	20

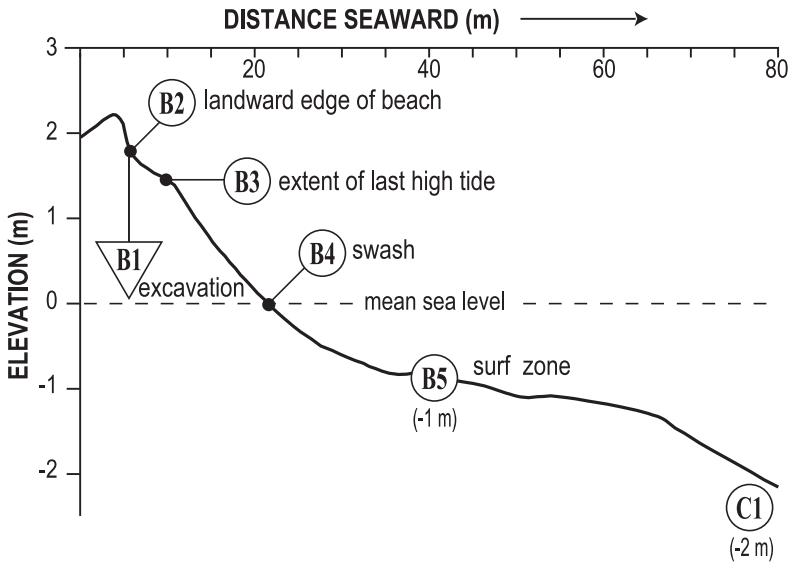

Figure 2-2. Beach profile (distance seaward vs. elevation) of shoreline sites on sampling transect. Site B1 is an excavation pit 1.8 m deep beneath B2 at the landward edge of the beach. B3 is the high tide line. B4 is in the swash zone, approximately the position of mean sea level. Sites B5 and C1 are submarine (depths given in parentheses).

samples of the subaerial beach face at the high-tide line and in the swash zone (approximate mean sea level), respectively; B5 was collected from the turbulent surf zone in 1 m water depth. Offshore sampling continued just seaward of the breaking waves (C1, –2 m). The nearshore sand field was sampled in a broad region of small sand ripples (C2, –4 m), in a macroalgal shoal (C3, –3 m), and landward of the channel opening (C4, –4 m). The channel was sampled at its landward mouth (C5, –6 m), along its axis (C6, –11 m; C7, –13 m; C8, –17 m; C9, –20 m), and at its seaward mouth in the rippled fore-reef sand field (C10, –30 m).

Samples from sand bodies within the reef (R–series) in Kailua Bay were also collected for comparison with channel and beach sediments. Sample R1 was collected from the southern reef platform in 9 m water depth from a small depression 0.5 m wide. This slender sand body is flanked by spurs of 1 m in height covered by platy and encrusting *Montipora verrucosa*. Sample R2 was collected from the northern reef platform in 8 m water depth from a sand-filled depression 10 m wide. This sand body is flanked by talus and sloping walls covered by live coral rising 45° to the top of the reef platform in 5 m water depth. Sample R3 was collected on the south side of the channel mouth in 24 m water depth. This 8000 m^2 reef-top sand body is enclosed by steep spurs 8 m in relief covered with living coral. From the exposed base of the reef spurs at this site, fossil pieces of the coral *Porites lobata* were sampled from the *in situ* framework for geochemical analysis. Shoreward of this site, around Popoia Island on the south side of the bay, sample R4 was collected from the sandy floor in 2 m water depth between fossil limestone outcrops. At this site, shallow mounds of fossil reef are topped by thickets of the branching coralline alga *Porolithon gardineri*; living specimens of the alga were

collected for geochemical analysis. Sample R5 was collected north of the channel adjacent to an extensive nearshore meadow of living *Halimeda* growing along a shore-parallel ridge of fossil carbonate in 2 m water depth. Living specimens of the aragonitic green algae at this site were collected for geochemical analysis.

Sedimentology and Composition

Sand samples were washed with deionized water over a 63-μm-mesh sieve. The filtrate was collected in a 1-L graduated cylinder, stirred for several minutes, and sampled by pipette. A 20-mL aliquot was drawn from the slurry and dried; the weight of the residue (multiplied by a factor to bring the aliquot volume to that of the filtrate) was then used to calculate the total weight percent of silt-sized particles (<63 μm) in the bulk sediment sample. The sand fraction retained by the sieve was oven-dried, weighed, examined under a binocular microscope, and described with respect to texture and composition. Subsamples were sieved into eight grain-size classes based on the Wentworth (1922) scale, and cumulative size-frequency distributions were assembled using the weight percent of each sieve fraction. Mean grain size and sorting index were calculated using both Folk and Ward (1957) formulae and the method of moments (cf. Tucker 1991), yielding similar results.

Sample splits were embedded in epoxy, thin-sectioned, and examined using a petrographic microscope. A minimum of 300 grains were point-counted to determine the composition of each sample, and replicate counts yielded compositional results within 2%. Skeletal particles were identified (after Adams et al. 1994, Tucker 1991, Majewske

1969, and Johnson 1961) and classified by origin: coral, coralline algae, *Halimeda*, mollusc, benthic foraminifera, echinoderm, bryozoan, or worm tube. Nonskeletal carbonate particles included intraclasts (aggregates and micritic grains composed of microskeletal debris) and crystalline fragments. Crystalline fragments (generally <0.7 mm in diameter) lacked discernible skeletal structure and displayed no clear evidence of origin. All noncarbonate sediments were classified as "volcanic." A small percentage of grains were unidentifiable.

Geochemical Analyses

Geochemical analyses included X-ray diffraction, stable carbon isotope composition, and radiocarbon age-dating. Two "bulk" samples (from C2 and C9) consisted of undifferentiated sediment splits. In all other cases, clean subsamples were examined under a binocular microscope and skeletal components were separated into five groups of certain skeletal origin (coral, coralline algae, *Halimeda*, molluscs, and forams). Representative grains were chosen from these groups for analyses, and two samples were prepared for all materials. Samples for mineralogical analysis were ground to a fine powder with an agate mortar and pestle, mixed with an internal fluorite standard (10% by weight), applied to a glass smear slide, and analyzed using a Scintag V powder X-ray diffractometer (XRD). Mineralogic composition of each sample was determined from the resulting diffractogram by calculating the area under curves fitted to major aragonite and calcite peaks (Neumann 1965). The mole percentage of magnesian calcite was determined from the d-spacing offset of primary calcite peaks (caused by magnesium ion

substitution in the crystal structure) using the internal fluorite standard (Bischoff et al. 1983).

Radiocarbon ages were obtained from the Center for Accelerator Mass Spectrometry (CAMS) at Lawrence Livermore National Laboratory and the National Ocean Sciences Accelerator Mass Spectrometry (NOSAMS) facility at Woods Hole. A detailed summary of the weight, grain size, and number of particles of the materials submitted to each lab is listed in Table 2-2. Accelerator mass spectrometry (AMS) ^{14}C measurement techniques require only 0.5 mg of carbon (Pearson et al. 1998) and we generally submitted small samples (<30 mg) to minimize the number of grains contributing to each date. In some cases, skeletal materials were analyzed in two different size classes from the same sample (e.g. coralline algae and *Halimeda* from C10). Other dated materials include two fossilized pieces of *Porites lobata* (removed from the reef framework at R3), living coralline algae (*Porolithon gardineri* from R4), and living *Halimeda* (from R5).

Both CAMS and NOSAMS provided a conventional radiocarbon age and 1σ error that included corrections for isotopic fractionation based on $\delta^{13}C$ values collected during AMS analysis of each sample. These ages were calibrated using Calib software version 3.0.3c (Stuiver and Reimer 1993) with a regional age correction (ΔR) of 117±51 years for the Hawaiian Islands (Broecker and Olson 1961; Stuiver and Braziunas 1993). Calibrated "best" ages were calculated via the intercept method; 2σ age ranges are reported with 95% certainty.

Table 2-2. Summary of sediments analyzed and geochemical results. *Modern* indicates samples are post-1950 in age. An *X* in the calibrated best age column indicates that the sample cannot be calibrated (i.e. modern samples and marine materials when the radiocarbon age minus ΔR becomes less than 460 ^{14}C yr BP, after Stuiver and Reimer 1993).

MATERIAL DESCRIPTION						LABORATORY RESULTS				CALIBRATED AGES[c]		MINERALOGY[d]			
SITE		Sample	Grain size (mm)	Weight (mg)	# grains	Lab ID[a]	Conv. age[b] (^{14}C yr	±)	δ^{13}C (‰)	**Best age (yr BP)**	2σ range (yr BP)	Aragonite %	Calcite %	Mol % Mg (LMC)	(HMC)
BEACH	B1	coralline algae[f]	0.25–0.50	11	93	OS16967	4400	40	0.97	**4522**	4380–4784	10	90	2	16
		Halimeda[f]	0.25–0.50	14	many	OS16968	1420	60	3.44	**943**	782–1129	98	2	0	16
NEARSHORE	C2	bulk	0.25–2.0	104	bulk	OS14781	2230	30	1.93	**1818**	1683–1950	56	44	3	16
		coral	< 0.5	12	many	OS14776	1720	40	0.17	**1267**	1131–1382	88	12	<1	15
		coralline algae	0.4–1.5	13	25–30	OS14777	2020	35	2.09	**1556**	1415–1709	18	82	0	17
		coralline algae	0.4–1.5	18	25–30	OS14789	2710	30	1.26	**2354**	2284–2633	18	82	0	16
		Halimeda	1.0–2.0	24	7	OS14780	730	25	3.90	**353**	273–463	97	3	0	16
		Halimeda	1.0–2.0	24	8	OS15028	455	50	3.88	X	<250	98	2	0	16
		mollusc	0.4–2.0	33	39	OS14778	605	25	2.29	**259**	72–361	98	2	0	13
		foraminifera	0.4–2.0	33	124	OS14779	1100	25	0.86	**649**	548–735	0	100	3	13
OFFSHORE	C9	bulk	0.25–2.0	73	bulk	LL42599	1040	50	1.41	**1001**	889–1174	77	23	3	16
		coral	<1.0	25	100	LL42601	930	50	–0.40	**895**	715–1009	80	20	3	16
		coralline algae	0.75–1.5	26	5	LL42602	550	40	2.50	**540**	473–645	27	73	0	16
		Halimeda	1.0–2.0	29	2	LL42603	2920	40	4.40	**3217**	3038–3361	93	7	0	14
		mollusc	0.25–2.0	26	50	LL42600	810	70	2.20	**737**	625–923	87	13	3	15
		foraminifera	0.4–2.0	24	101	LL42604	1310	50	1.20	**1270**	1116–1402	0	100	3	13
	C10	coralline algae[e]	1.0–2.0	14	3	OS16711	1000	25	2.33	**558**	502–651	22	78	0	16
		coralline algae[f]	0.25–0.50	11	60	OS16712	3380	55	2.01	**3236**	3020–3394	20	80	3	16
		coralline algae[g]	2.0	15	4	–	–	–	–	**–**	–	8	92	0	16
		Halimeda[e]	1.0–2.0	16	3	OS16713	2480	50	3.96	**2114**	1951–2299	97	3	0	16
		Halimeda[f]	0.25–0.50	9	many	OS16714	2280	30	3.37	**1870**	1725–2003	88	12	0	16
		Halimeda[g]	4.0	12	2	–	–	–	–	**–**	–	96	4	0	16
REEF PLATFORM	R3	*Porites lobata*[h]	3.0	25	1	OS16929	640	55	–1.88	**276**	80–440	100	0	0	0
		Porites lobata[h]	3.0	25	1	OS16930	modern	–	–0.53	···	···	100	0	0	0
	R4	*Porolithon*[i]	5.0	20	4	OS16969	modern	–	–1.32	···	···	0	100	0	19
	R5	*Halimeda*[i]	5.0	20	4	OS16966	modern	–	0.00	···	···	100	0	0	0

[a] Laboratory identifier and accession number (*OS*: NOSAMS, *LL*: CAMS).
[b] Conventional ages and errors reported by the laboratories in radiocarbon years, including corrections for isotopic fractionation using the δ^{13}C values collected during AMS analysis.
[c] "Best" ages (intercepts) and 2σ error ranges (95.6% certainty) determined using Calib software, reported here in calendar years before present (cal yr BP).
[d] Mineralogical composition in % aragonite and calcite determined by XRD (see text); *LMC* is low-Mg calcite (<5 mol % Mg substitution in calcite); *HMC* is high-Mg calcite.
[e] Skeletal materials selected from coarse fractions.
[f] Skeletal materials selected from fine fractions.
[g] Sample for XRD only.
[h] Fossil coral samples removed from *in situ* framework.
[i] Algal specimens that were living at the time of collection.

RESULTS

Sedimentology and Composition

Grain size distributions for representative sites given in Figure 2-3 illustrate a general trend of decreasing mean grain size along the channel axis in the shoreward direction. The coarsest sands (mean 0.7–1.3 mm) are found on the reef platform and along the deeper channel axis (C6–C10). Shoreward of C5, sediments become increasingly finer in size (mean <0.5 mm), presumably in response to nearshore wave abrasion. This is particularly evident at C1 and in the surf zone (B5), where grain size is at a minimum (0.12 mm). Sands collected at the high tide line (B3), at the edge of the beach (B2), and in the excavation pit (B1) all have mean diameters of 0.3 mm and identical size distributions, represented by one curve (B*) in Figure 2-3. Additionally, sediments collected from the channel axis and reef platform are moderately to poorly sorted, while those shoreward of C5 are well-sorted.

The relative abundance of the primary constituents in sediments from the beach, channel, and reef-top sand bodies is depicted in Figure 2-4. Sand from various morphologic features of the beach face (B1, B2, B3) are nearly identical in composition; coralline algae constitute 32–40% of these beach sands, coral 12–13%, *Halimeda* 3–12%, molluscs 16–17%, forams 2–5%, intraclasts 2–9%, and crystalline fragments 6–10%. In sand collected from high-energy zones near shore (sites B4, B5, C1), the relative abundance of coralline algae is 16–24%, corals 3–13%, *Halimeda* 17–31%, fine mollusc

shell debris 11–21%, and forams 6–9%; crystalline fragments dominate (9–17%) over intraclasts (0–4%).

The abundance of coralline algae increases in the seaward direction along the channel axis, representing 28–38% of nearshore samples C2, C3, C4, and C5. Coral constitutes 8–13% of these samples, *Halimeda* 2–16%, molluscs 9–12%, forams 4–8%, intraclasts 7–14%, and crystalline fragments 6–9%. Offshore channel sands from sites C6, C7, C8, and C9 are dominated by coralline algae (39–51%); coral constitutes 9–11% of these sands, *Halimeda* 8–32%, molluscs 6–10%, forams 1–5%, intraclasts 6–16%, and crystalline fragments 1–5%.

Individual grains in bedform trough and crest samples collected from site C10 in the fore-reef sand field vary in preservation from relatively unaltered to extensively bored and pitted. Coralline algae constitutes nearly half the sand-sized sediment at this site, while coral is a minor component (8% in trough, 2% in crest). *Halimeda* flakes are less abundant in ripple trough sediment (C10-T, 4%) than in crest sediment (C10-C, 16%). The abundance of mollusc fragments is approximately the same in both samples (6–7%); foram tests constitute 2% of trough and 10% of crest sediment. Micritic intraclasts are more abundant in the trough (17% vs. 5% in crest), as are volcanic grains (7% vs. 2% in crest). The reverse is true for crystalline fragments (5% vs. 15% in crest). These observations are consistent with hydrodynamic sorting of bedform sediment such that denser particles dominate trough sediments.

Samples collected from reef-top sand bodies in Kailua Bay differ markedly from those of the beach and channel. Reef platform sand at sites R1 and R2 are the coarsest of all samples and are dominated by coralline algae (42–46%). Corals (11–18%) and

intraclasts (16%) are more dominant in these sands than are *Halimeda* (4–10%), molluscs (10–11%), and forams (4–6%); crystalline fragments are nearly absent (<1%). Sample R3 contains the greatest abundance of coral fragments of all samples (24%). Coralline algae constitutes one-third of this sand; *Halimeda* and intraclasts contribute 14% and 16%, respectively. Other constituents are minor contributors (forams 3%, molluscs 6%, crystalline fragments 3%). Sand collected from the shallow sea floor near Popoia Island (R4) is composed of 38% coralline algae, 5% corals, 32% *Halimeda*, 19% molluscs, and <3% each of intraclasts and crystalline particles; forams are absent. Nearly one -third of the sand from site R5 is *Halimeda*; 25% are contributed by coralline algae, 15% by intraclasts, and 13% by molluscs. Crystalline fragments are 5% of the sand; coral and echinoderms are rare (each <2%).

Mineralogy of Skeletal Constituents

The relative percentage of carbonate phases in samples of both living material and non-living biogenic sediments are reported in Table 2-2. Two samples of *in situ* fossil coral (*Porites lobata*) collected from the base of the reef framework at site R3 are 100% aragonite, while coral grains analyzed from sediment samples C2 and C9 contain 12% and 20% high-Mg calcite (HMC), respectively. Low-Mg calcite (LMC) is also present in grains of coral from these sediments (<1 mole % Mg at C2, 3 mole % Mg at C9). Living coralline algae (R4, *Porolithon gardineri*) is composed entirely of high-Mg calcite (19 mole % Mg) but in sediment are up to 27% aragonite (B1, C2, C9, C10). Coralline algae grains in the 0.25–0.5 mm size fraction from B1 and C10 also contain low-Mg calcite (2–

3 mole % Mg). Living *Halimeda* (R5) is 100% aragonite. Plates and fragments of the green algae in sediments contain 2–12% calcite with 14–16 mole % Mg content and lack a low-Mg calcite component (B1, C2, C9, C10). Molluscs exhibit a range of normal mixed aragonitic and calcitic mineralogies with varying Mg contents in sediments, as do bulk sand samples (C2, C9). Foram tests in sediments from these sites exhibit normal Mg-calcite mineralogies.

Radiocarbon Age-dating

Table 2-2 and Figs. 2-5 and 2-6 summarize the radiocarbon age results for samples dated across the shoreface. All ages are reported in calendar years before present (1950) and are hereafter abbreviated "yr BP." Of two *in situ* samples of nonliving coral (*Porites lobata*) removed from the exposed base of the seaward reef platform in 18 m water depth (R3), one yields a "modern" (post-1950) age, and one is 276 yr BP. Coral grains in sediment of the adjacent channel are 895 yr BP (C9,–20 m). Coral grains in nearshore sediment are 1267 yr BP (C2, –4 m).

The ages of living specimens of *Porolithon* (a coralline red alga, R4) and *Halimeda* (a calcareous green alga, R5) are modern. Coralline algae in shoreface sediments exhibits a wide range of ages. Like coral, it is younger in offshore sediments (540 yr BP at C9, 558 yr BP at C10) than in nearshore sediments (1556 yr BP and 2354 yr BP at C2) of similar size classes. Coralline algae in fine-grained beach sand (0.25–0.5 mm diameter range) is 4522 yr BP (B1); similarly, in this size fraction of sand from offshore, it is 3236 yr BP (C10).

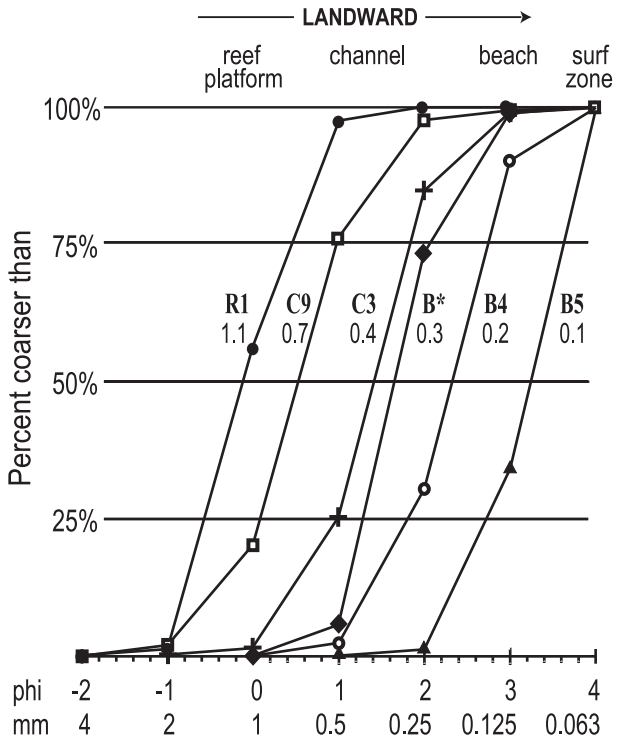

Figure 2-3. Cumulative size frequency distributions for representative sites. Line B* represents three sites from the beach face (B1, B2, B3) with identical distributions. Mean grain size (given in mm beneath site ID) is greatest offshore and decreases in the landward direction.

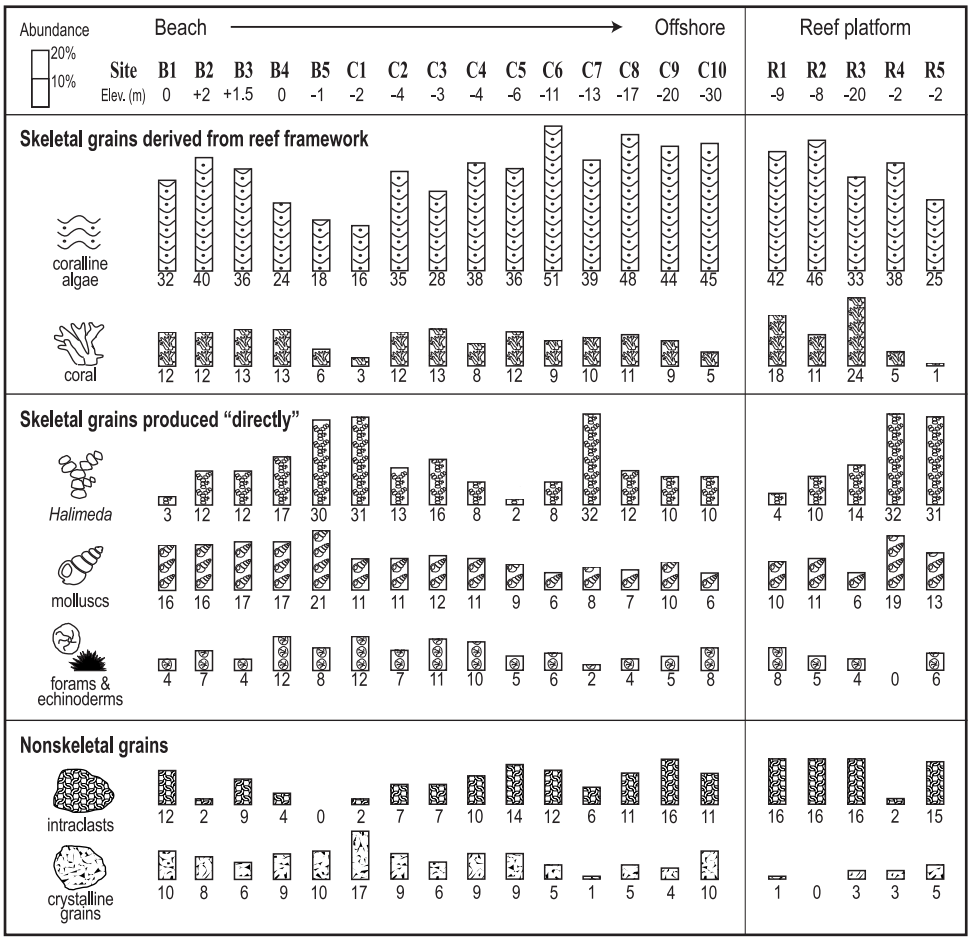

Figure 2-4. Composition of carbonate sediments of Kailua, Oahu. Shoreface transect sites begin at the beach (B1) and continue in the offshore direction to the seaward mouth of the channel (C-series). Elevation of each site is given in meters beneath the sample ID. Refer to Fig. 1 for exact site locations. The composition of sediments collected from other sand bodies is shown for comparison: R1, R2, and R3 (reef series) are from reef-top sand fields; R4 is from the seafloor between fossil reef outcrops near Popoia Island (R4); R5 is from a nearshore *Halimeda* meadow. Components are grouped in terms of their origin (reef framework, direct production, and diagenetic products). The percent abundance of each constituent at each site is given beneath the vertical histogram bars. C10 is the average of C10-T (ripple trough) and C10-C (ripple crest) The abundance of foraminifera and echinoderms are combined for this figure. The volcanic component is not shown. Refer to Table 1 for detailed compositional results.

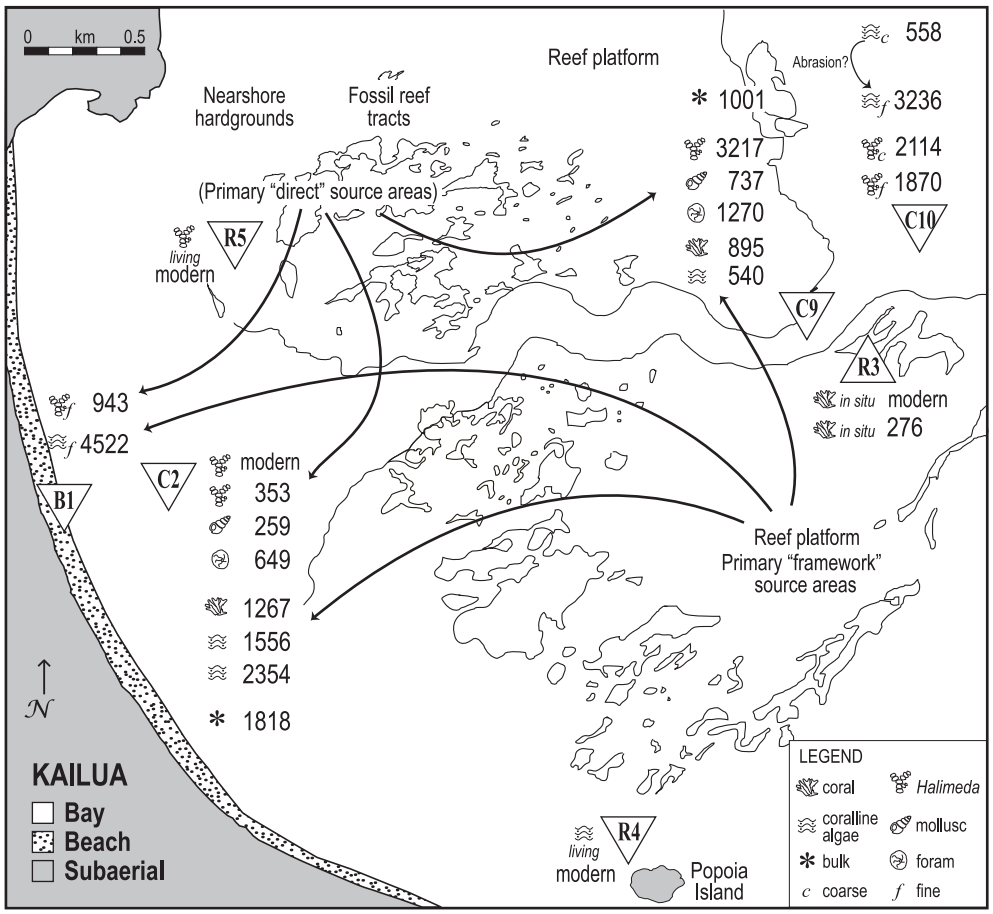

Figure 2-5. Radiocarbon age results of sediments and primary skeletal constituents calibrated to years before present (yr BP). See Table 2 for details on materials and the 2σ age range. Legend of components shown in lower right corner. Coarse and fine size fractions are denoted *c* (1–2 mm) and *f* (0.25–0.5 mm) respectively where appropriate. Arrows show inferred patterns of sediment movement from primary source areas to the sites at which samples were collected. The primary source of "directly-produced" sediments (*Halimeda*, mollusc, and foram) is in nearshore areas (hardgrounds, sand flats, and fossil reef tracts). The primary "framework-derived" sediment source (coral and coralline algae) is in offshore reef platform areas. Four ages from three sites are not of sediment: two fossilized pieces of the coral *Porites lobata* removed from the in situ framework at R3, living *Porolithon* at R4, and living *Halimeda* at R5. "Modern" indicates a post-1950 (modern) age.

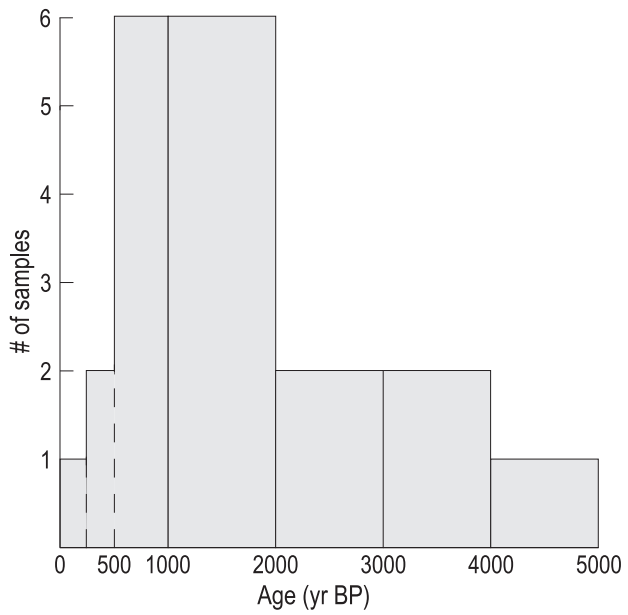

Figure 2-6. Distribution of ages collected on shoreface sediments in this study (in calendar years before present). Twelve of 20 calibrated ages fall between 500 and 2000 yr BP; five are between 2000 and 5000 yr BP, indicating that long storage times dominate the contemporary signature of the present benthic community.

Medium-grained and coarse fragments (1–2 mm) of *Halimeda* in sediment from nearshore site C2 (–4 m) are the youngest found ("modern" and 353 yr BP), while offshore at C9 and C10, *Halimeda* fragments of similar size are 3217 yr BP and 2114 yr BP, respectively. In the fine-grained size fraction (0.25–0.5 mm), *Halimeda* is 943 yr BP on the beach (B1) but twice as old offshore (1870 yr BP at C10). Mollusc debris is also younger in nearshore sediment (259 yr BP at C2) than in offshore sediment (737 yr BP at C9); the same is true for benthic forams (649 yr BP at C2, 1270 yr BP at C9). Bulk sediment is older nearshore (1818 yr BP at C2) than offshore (1001 yr BP at C9).

DISCUSSION

Origin of Carbonate Sediments

Shoreface sediments of Kailua Bay are almost entirely composed of the skeletal remains of marine organisms, particularly that of coralline (red) algae which constitutes one-quarter to one-half of beach, channel, and reef top sediment assemblages. Its abundance drops below 20% at only two sites in the nearshore zone (<2 m depth). The benthic topography, relief, and vigorous circulation in Kailua Bay provide ideal habitats for these rhodophytes. *In situ* growth-rate measurements of articulated *Porolithon gardineri* living in waters around Oahu correspond to a carbonate production rate of ~20 $kgm^{-2}y^{-1}$ (Agegian 1985). Estimates of carbonate production by crustose *Porolithon onkodes* are lower (e.g. ~2.1 $kgm^{-2}y^{-1}$, Agegian et al. 1988; 3.6 $kgm^{-2}y^{-1}$, Soegiarto 1972),

but these forms occupy a greater range of depths (subtidal to 100 m) and colonize a variety of substrates including patch reefs, fossil limestone outcrops, coral skeletons, mollusc shells, loose rubble debris (forming rhodoliths), and even individual sand grains. These levels of productivity are consistent with our observations of the dominance of coralline algae in nearly all beach and submarine sediments.

"Coral sand" is a misnomer commonly used to describe the white carbonate sediments of volcanic islands and atolls, when more often coral fragments are a minor constituent (cf. Chevillon 1996). Such is the case in Kailua, where coral contributes <15% of sediments analyzed from the shoreface transect. However, in sediments collected from on or near the reef platform at sites R1 and R3, grains of coral constitute one-fifth of the sediment assemblage. This preservation of coral grains in close proximity to the source framework likely reflects negligible transport following deposition.

Compared to their abundance in the modern benthic community, corals are under-represented in shoreface sediments. If coral has made a significant contribution to the Holocene reef framework but not to the surficial sediment pool, taphonomic processes may be primarily responsible for this observation. Coral fragments may be eroded or otherwise removed from the system more rapidly than other sediment components. Sites of the most prolific coral growth in Kailua Bay generally occur along fore-reef slopes and channel margins in 15–20 m water depths. The presence of talus deposits along the seaward base of these features suggests that rubble and sediment resulting from their destruction may be transported downslope and offshore rather than distributed landward over the reef platform. Similarly, encrusting corals that are abundant over the shallow,

landward portion of the fringing reef have little potential to be transferred from framework to sediments.

Alternatively, the paucity of coral in sediments may suggest that the relative contribution of corals to the Holocene reef framework has been low. If reef accretion in this windward, energetic environment has been dominated by coralline algae for the last 5000 years, the sediments resulting from reef erosion would also reflect the dominance of algae, as we observe. Knowledge of the nature and rate of Holocene reef accretion in Kailua is needed to answer these basic questions.

Whole and fragmented *Halimeda* segments are present in varied abundance in all beach and sublittoral sands of Kailua Bay, contributing nearly a third of the sediments in energetic waters <2 m deep. We had not anticipated the skeletal remains of this aragonitic green alga to predominate in wave-dominated environments, as its perforated segments have generally been thought to quickly disintegrate into fine sediments characteristic of lagoonal environments (e.g. Neumann and Land 1975). This view is changing in light of detailed studies of extensive *Halimeda* banks and associated sediments of the Great Barrier Reef (e.g. Davies and Marshall 1985, Phipps et al. 1985) and of biomineralization in this and other calcareous algae (Macintyre and Reid 1992, 1995; Reid and Macintyre 1998). *Halimeda* exhibits a wide range of growth forms and habitats and is no longer considered a predominantly lagoonal algae (Hillis 1997). When living, the plant bodies ("thalli" composed of consecutive, branching, calcified segments connected by longitudinal coenocytic filaments) may grow attached to hard substrates by a meshwork of filaments or anchored in unconsolidated sediments by a single, buried holdfast (Hillis 1991). In nearshore Kailua Bay, we have found dense, sandy meadows and extensive

epilithic mats of *Halimeda* flourishing in 2–10 m water depths. Clumps of the alga are abundant in well-lit areas landward of the reef platform but are generally rare to absent within the reef tracts offshore. Death and the natural process of senescence shed aragonitic segments to the surrounding sea floor, where they are then subjected to sedimentary and taphonomic processes. Estimates of *Halimeda* production in subtropical populations around the world are on the order of 2 kg $CaCO_3$ $m^{-2}y^{-1}$ (Hillis 1997), attesting to the significance of this green alga as a sediment producer.

Mollusc shells are common constituents of most sediments in Kailua Bay. Shell hash, intact helices, and fragmented valves are most concentrated in beach sands and nearshore areas and reflect the great diversity in size and number of molluscs in Hawaiian waters. Past studies suggest that benthic foraminifera would occur in similar abundance, having been observed to dominate in beach sands (Moberly et al. 1965) and having a high density of living individuals on reefal substrates in Kailua Bay. The genera *Amphistegina*, *Heterostegina*, *Peneroplis*, and *Marginopora* are present in sediments but in generally low numbers, despite their annual productivity of 0.1–0.4 kgm^{-2} at reefal depths (<10 m) in Kailua Bay (Harney et al. 1999). Minor sediment producers include echinoderms, bryozoans, and the tube-building worms; their combined contribution is small.

Skeletal carbonate sediments in Kailua Bay are thus produced by one of two primary processes: progressive destruction (mechanical, chemical, and biological) of reef framework limestone (primarily coralline algae and coral) into rubble and sand ("framework origin"); and "direct sedimentation" upon the death or senescence of calcareous organisms such as *Halimeda*, molluscs, and foraminifera (which seems to primarily occur in nearshore regions and along the landward portion of the reef platform).

Skeletal grains are generally well-preserved and common to abundant in all submarine and subaerial environments in Kailua Bay, particularly when sediments are medium- to coarse-grained.

Nonskeletal carbonate sediments result from the diagenetic alteration of existing particles of various origin by such processes as micritization and recrystallization (cf. Macintyre and Reid 1992). Most intraclasts are of algal origin and are generally more common in offshore sediments (>10 m water depth) where grain size is medium to coarse. Crystalline particles reach their greatest abundance in nearshore and beach sediments where finer grain size distributions are observed. These particles are likely the result of abrasion, but their exact origin remains uncertain.

Mineralogy of Skeletal Constituents

Departure from the normal aragonitic mineralogy of coral in sediments (C2, C9) compared to those still within the fossil reef framework (R3) could be due to the diagenesis and alteration that occurs with age and during transport within the littoral system or simply due to the inclusion of recrystallized material in the coral fragments analyzed. Coral grains in sediments from site C2 contain less total calcite (12%) than those from site C9 (20%). Peak-area analysis of the calcite present in these samples, however, indicates that a greater proportion of the C2 coral grains is low-Mg in character (18%) when compared to the low-Mg content of the C9 sample (2%). Site C2 is located in the nearshore region where wave energy is greater, sand grains are more abraded, and framework-derived components such as coral and coralline algae are older. The

mineralogical differences between C2 and C9 coral grains may thus reflect differences in storage time.

Although living coralline (red) algae is composed of high-magnesian calcite, its skeletal remains in sediments contain up to 27% aragonite. This is likely due to extracellular or cavity-filling cements that form after deposition (cf. Bosence 1991) and are occasionally observed in thin section. A low-Mg calcite component is found in grains of coralline algae from the fine size fraction (0.25–0.5 mm) of sediments from both the beach (B1) and far offshore (C10). These are also the oldest samples found in this study (4522 yr BP at B1, 3236 yr BP at C10) and may reflect the time scale over which resident particles are stored and altered in this carbonate system. After several millenia of storage time, coralline algae sediments are abraded, mineralogically-altered, and relatively far from their original source atop the reef platform.

Living *Halimeda* segments are wholly aragonite, while modern and aged samples show some degree of mineralogical alteration to magnesian calcite (2–12%). In thin section, we observe the progressive micritization and textural alteration of *Halimeda* grains that likely results in the observed magnesian calcite mineralogy (cf. Reid and Macintyre 1998). *Halimeda* grains of the fine fraction from offshore (C10) contained 12% calcite and were twice as old as the fine fraction from the beach (B1), which contained only 2% calcite. The degree of mineralogical alteration in *Halimeda* appears to be related to age, with those farther offshore being older and more altered than those proximal to their shallow-water source.

Radiocarbon Ages and Sources of Uncertainty

Mineralogical alteration in sand grains of various skeletal origin can result in a radiocarbon age that appears younger than the true age. The extent to which our radiocarbon ages are affected by these post-depositional mineralogical changes is unknown, although the degree of diagenetic alteration is generally limited in the materials selected for dating.

Substrate age has been reported as a source of radiocarbon variation in marine shells. Molluscs grazing on Pleistocene limestone substrates can have shells with apparent ages up to 1000 years older than those on adjacent volcanic coasts, owing to the incorporation of "old carbon" in their skeletal materials (Dye 1994). Our dates on molluscan material both nearshore and offshore (259 and 737 cal yr BP, respectively) are younger than most other sediment components at the same sites and thus may not reflect this condition.

In calibrating radiocarbon ages to calendar ages, two corrections are made for marine carbonates: a global reservoir correction of 400 years (due to the slow diffusion of atmospheric CO_2 into the surface ocean) and a regional reservoir correction ($\Delta R=117\pm51$). The regional correction for Oahu (Stuiver and Braziunas 1993) was determined based on the offset of a single radiocarbon date of a mollusc shell of known historical age (~1840) collected from Pearl Harbor (Broecker and Olson 1961). Further radiocarbon age determinations should be made on historically-aged marine materials such as coral or coralline algae collected from other Hawaiian localities to refine regional reservoir corrections, particularly because of the false-aging potential in marine mollusc shells.

Since radiocarbon-age data are statements of probability, statistical uncertainties also exist. Although statistical analysis of large quantities of material is required to reduce the range of uncertainty, in the case of unconsolidated sediments, this approach may complicate the analysis. The mixing of a large number of carbonate sediments of various origin, age, and alteration history provides a date that reflects an "average" radiocarbon content of the entire assemblage of grains. In most cases, we date as few grains as possible to reduce the degree of age-averaging.

Bulk sand ages are particularly subject to age-averaging, owing to their highly varied, site-dependent sedimentology and mixed mineralogy. While the age of a bulk sample is not predictable based on the abundance and age of the individual skeletal components, our offshore sample is younger (1001 yr BP at site C9) than our nearshore sample (1818 yr BP at site C2), possibly reflecting the greater proportion of younger, coarser, framework-derived coralline algae that exists in sand collected offshore.

Sediment Source and Storage Time

The age range of various skeletal materials in sediments supports observations of the partitioning of sediment production in "primary source areas" of the Kailua shoreface (Figure 2-5). The primary source of framework-derived sediments (coral and coralline algae) is the reef platform offshore; these components are older in nearshore sand. In contrast, the primary sources of directly-produced sediments (*Halimeda*, molluscs, and forams) are nearshore fossil reef hardgrounds and along the landward portion of the reef platform; these components are older in offshore sand. These differences in sediment-

component ages likely reflect the time spent in storage and transport from the primary source of production.

Benthic forams provide one example. The age of foram tests is younger in nearshore sand (649 yr BP) than in offshore channel sand (1270 yr BP). In Kailua Bay, populations of living benthic forams are most dense in shallow, nearshore waters on relatively barren substrates such as rubble and coral skeletons; they are generally absent on substrates colonized by living coral and coralline algae (Harney et al. 1999). It is thus unlikely that the foraminiferal remains found at site C9 (–20 m) were produced on the adjacent reef platform, which is composed of nearly 100% living coral. In contrast, site C2 lies in a nearshore sand field where limestone outcrops and patches of rubble are the dominant consolidated substrate. Since sediment production by foraminifera is more likely to occur in such areas shoreward of the living reef platform, their test ages in nearshore sediments (C2) would likely be younger than in offshore sediments (C9), as we observe.

Further support of this hypothesis is derived from our studies of coralline algae and *Halimeda*. These calcareous algae are abundant in Kailua Bay, have been characterized in terms of production potential, and possess different mineralogies (high Mg-calcite vs. aragonite), thus providing a range of perspectives in sediment dynamics.

Coralline algae sediments are highly varied in age. Of the shoreface samples analyzed, the oldest grains are found on the beach (4522 yr BP at B1); grains of intermediate ages are found nearshore (1556 yr BP and 2354 yr BP at C2); the youngest grains are found offshore (540 yr BP at C9, 558 yr BP at C10; except for fine size fraction at C10, see below). Coralline algae is the only sediment producer that exploits every habitat and depth within the bay. Atop the extensive reef platform and on isolated

outcrop surfaces, it is the most ubiquitous marine taxa and data shows the most prolific producer of sediment. The age distribution of coralline algal fragments reflects the probability that most of the sediment production by these red algae is accomplished atop the reef platform. In sediments collected from the seaward mouth of the channel (C10) offshore, fine grains of coralline algae are distinctly older (3236 yr BP) than coarse grains (558 yr BP), suggesting that coralline-algal grains have long sediment storage times between initial production and loss by abrasion or by transport to deep water.

Halimeda sediments are distinctly younger in nearshore samples ("modern" and 353 yr BP) than in all others, presumably due to their proximity to *Halimeda* production sites in shallow meadows. Fragments on the beach, all very small in size (0.1–0.4 mm), are of intermediate age (943 yr BP at B1) but are younger than those offshore (3217 yr BP at C9, 2114 yr BP and 1870 yr BP at C10), perhaps reflecting a time lag associated with transport of these shallow-water sediments to deeper waters. We do not find a significant age difference between coarse and fine *Halimeda* fragments collected from the channel's seaward mouth in 30 m water depth, suggesting that the transport of *Halimeda* segments from their shallow-water source occurs without size preference. Its greatest contribution is made to sea floor sediments adjacent to its shallow meadows, but its sedimentary products are found on the beach, in the channel body, and far offshore, reflecting storage times as great as 3200 years.

The most surprising result of this work is that the skeletal sediments of this productive, well-circulated system are very old. Even coralline algae, the most ubiquitous modern producer, is not represented in the sediments by a dominant modern-aged signal. Of 20 radiocarbon dates on sediment constituents in this study, only one is of modern

(post-1950) age (*Halimeda* grains from nearshore site C2; other modern ages are from living materials or *in situ* coral). Similar millenial-aged *Halimeda* fragments and other skeletal materials have been found in shelf sediments of the Great Barrier Reef, apparently deposited during post-glacial sea-level rise and subsequently buried 2–3 m below the sea floor (Harris et al. 1990). Could an aragonitic grain even up to 1 cm in size survive abrasion and transport in the windward turbulence of Kailua Bay for several thousand years? Sediment confinement by shallow burial in the channel and other sand bodies would retard the processes that surficial particles are subjected to, thereby reducing the loss of grains by erosion and abrasion or transport to deep water. The deeply-incised Kailua channel represents an *in situ* storage capacity for carbonate sediments produced atop the reef platform and in shallower back-reef areas. The fact that the channel is not filling up with sediment along its length suggests that sand is continually transported in or out of the channel. Recent work on sediment dynamics in the Kailua channel has revealed that migrating bedforms proceed shoreward at a rate of 0.5 m per day during tradewind conditions and seaward at approximately the same rate during winter ground swell conditions (Cacchione 1998). Loss of carbonate particles by abrasion and/or transfer across the "littoral fence" to deep water may not necessarily be a rapid process, as there remains a strong fossil component in sediments of the shoreface. The relationship between circulation, wave forcing, and sediment movement in Kailua Bay is still poorly understood but is an important subject for future research.

Modern and Paleoproductivity

The minor importance of volcanic minerals and the great areal extent and age of carbonate sand contained in the beach and channel reservoirs indicate that the storage time of biogenic carbonate sediment in Kailua Bay is of millennial scale. While the composition of surficial sands in Kailua broadly reflects the existing zonation of benthic habitats and production areas, the distribution of ages (Figure 2-6) may also reflect changes in carbonate productivity during the Holocene. Under a +1–2 m mid- to late Holocene sea-level high stand (Grossman and Fletcher 1998), the flooding of Kailua's broad, low coastal plain would have resulted in significant expansion of shallow, nearshore areas (Athens and Ward 1991, Kraft 1982). The production of calcareous algae and their sediments may have proliferated in this back-reef lagoon zone, and (in part due to long storage times) their fossil signature may be significant in the present surficial sediment pool. The long-term storage and release of fossil sediments and the affects of fluctuating sea level on shallow-marine productivity may have moderated the contemporary signature of the present benthic community but do not completely mask background patterns of partitioned sediment production. A numerical carbonate sediment budget is necessary to further investigate differences in modern and paleoproductivity.

CONCLUSIONS

1. The composition of carbonate sediments across the tradewind-dominated Kailua shoreface broadly reflects modern patterns of zoned carbonate sediment production. Coralline algae, the most abundant component of nearly all sediments, is particularly significant in offshore and reefal sediments where the dominant benthic substrate is a reef framework composed of coral and coralline algae communities. The aragonitic green alga *Halimeda* is most abundant in sediments of the nearshore region where its most prolific production areas are found. Coral is a minor component of most shoreface sediments, although it is more abundant in coarse sand pockets within the reef platform. Molluscs and foraminifera are important but also relatively minor sand constituents. Other calcifying organisms (e.g. echinoderms, bryozoans, serpulids) are minor contributors of sediment.
2. The paucity of coral in sediments (despite their abundance in the modern benthic community) suggests that production of framework-building corals during the Holocene in Kailua Bay has been low or that the rates of erosion of coral particles is high.
3. Despite apparently high modern carbonate productivity by a variety of calcareous organisms in the waters of Kailua Bay, shoreface sediments are predominantly fossil-aged. Only three of 20 calibrated radiocarbon dates on skeletal constituents of sand are younger than 500 yr BP; six are 500–1000 yr BP; six are 1000–2000 yr BP; five are 2000–5000 yr BP.

4. The storage time of individual sand components can be inferred from the ages of skeletal constituents. Coralline algae have storage times as great as 4500 years. *Halimeda* fragments remain in the carbonate sediment system for more than 3000 years; coral fragments and the tests of benthic foraminifera for at least 1300 years; and mollusc shell debris appears for ~500 years. We infer from these relatively long storage times in this well-circulated, windward embayment that the processes which remove sediments from the system (e.g. abrasion and transport to deep water) are slow.
5. Sediment constituents in fine size classes are the oldest found, both on the beach and far offshore. The relationship between fine size and fossil age may reflect the time it takes for coarse, fresh material produced in primary submarine sediment source regions to be reduced to fine sand and transported to distant reservoirs. Fine-grained size classes may constitute a reservoir of fossil ages that can be readily distributed over the shoreface. Further size-specific age dating is needed to investigate the relationship between sand size and age.
6. The long-term *in situ* storage and release of fossil sediments and the affects of fluctuating sea level on shallow-marine productivity may have altered the contemporary signature of the present benthic community but do not completely mask background patterns of partitioned sediment production.

CHAPTER 3

A BUDGET OF HOLOCENE CARBONATE SEDIMENTS KAILUA BAY, OAHU, HAWAII

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ABSTRACT

A comprehensive sediment budget is a quantitative estimate of the production, storage, flux, and loss of particulates within a geographically well-defined natural system. Sediments of the bay and coastal plain of Kailua (Oahu, Hawaii) are >90% biogenic carbonate produced by two means: destruction of reef framework (coral and coralline algae) and direct sedimentation through the biological activity of calcifying organisms (the green alga *Halimeda*, molluscs, foraminifera, and articulated coralline algae). Carbonate dynamics in this system are controlled by physiographic setting (e.g. depth, substrate type, and hydrodynamics), structure and function of the carbonate-producing community, and changing environmental regimes.

This comprehensive model of sediment production in various habitats of Kailua Bay quantifies the modern rates of gross carbonate framework construction, bioerosion, and direct sedimentation. Using field data collected in various physiographic regions of

Kailua Bay, gross framework production by corals and coralline algae is estimated to be 23190 ± 1391 x 10^3 kgy^{-1}. Bioerosion of the reef edifice produces unconsolidated carbonate sediment at a rate of 2983 ± 179 x 10^3 kgy^{-1} (or 2536 ± 337 m^3y^{-1}). Additional carbonate sediment is produced directly by *Halimeda*, molluscs, foraminifera, and articulated coralline algae at a total rate of 4498 ± 565 x 10^3 kgy^{-1} (4503 ± 835 m^3y^{-1}). The total rate of sediment production in Kailua Bay is thus the sum of these sources, amounting to 7481 ± 744 x 10^3 kgy^{-1} (or 7039 ± 1172 m^3y^{-1}). Applying these rates over the 5000 years that Kailua Bay has been wholly inundated by post-glacial sea level (Fletcher and Jones 1996, Grossman and Fletcher 1998), an estimated 351.95 ± 58.62 x 10^5 m^3 of detrital carbonate sediment has been produced in the system since the mid-Holocene.

The estimated cumulative production volume is compared to that which is currently stored in submarine and subaerial reservoirs of the bay and coastal plain. The volume of sediment stored in the bay's various reef channels and pockets (calculated using areas and jet-probed thicknesses of submarine sediment deposits in 3–30 m water depths) is 3726 ± 336 x 10^3 m^3, or 11% of that produced since 5000 yr BP. The volume of sand in the modern beach (estimated from profile data; Norcross et al. 1998) is 600 ± 30 x 10^3 m^3 (2% of Holocene production). The volume of Holocene-aged carbonate sediment stored in the coastal plain is estimated, using core log data, to be 10049 ± 1809 x 10^3 m^3 (29% of Holocene production). Combined, these reservoirs store 143.75 ± 2174 x 10^5 m^3 of calcareous Holocene-aged sediment, 41% (±7%) of the sediments estimated to have been produced since 5000 yr BP. By these calculations, 59% (±7%) of the sediments produced in our mid-to late- Holocene model are unaccounted for. This imbalance may represent

sediment loss due to dissolution, abrasion, and/or transport offshore; it may arise from the inaccuracy of some model parameters (e.g. annual carbonate production rates); or it may be due to the application of modern production rates over a 5000-year period.

INTRODUCTION

The morphology and evolution of coastal margins are dependent on antecedent topography, tectonic setting, sediment type and availability, the position and history of relative sea level, wave and current processes, and the nature of adjacent (terrestrial and oceanic) environments (Carter and Woodroffe 1994). The volume and type of coastal sediments in a system drive the formation and maintenance of beaches and coastal dunes, affect the style and rate of reef accretion, and dictate coastal change under steady or slowly-rising sea levels. Sediment budgets are quantitative estimates of the sources, sinks, fluxes, and losses of sediment within a geographically well-defined natural system; they can be instrumental in predicting and interpreting coastal behavior over both space and time. Erosion and shoreline transgression characterize a region with a negative sediment budget, while one with a positive sediment budget will gradually accumulate material (i.e. coastal sedimentation) (Carter and Woodroffe 1994). A dynamic system can switch between positive and negative budgets.

In Hawaii and on other oceanic islands lacking a continental sand source, coastal sediments are often highly calcareous. The primary control of sediment supply in such environments is carbonate productivity associated with coral reefs. In addition to being

diverse ecosystems, monumental bioconstructions, and settings in which biology controls geomorphology, coral reefs are prodigious sediment factories. A robust carbonate sediment budget can thus also be a vehicle for understanding reef form and function, community structure, and benthic diversity. Oceanic islands in subtropical settings offer the opportunity to pair studies of reef growth and productivity with a quantitative budget of carbonate sediments. Such a quantitative budget of the production, storage, flux, and fate of sediments provides an understanding of the processes that govern shoreface variability and evolution.

Purpose and Overview

The purpose of this paper is to construct and discuss a quantitative, field-based budget describing the production, storage, and loss of calcareous sediment during the last 5000 years in a carbonate reef-dominated embayment in the Hawaiian Islands (Kailua Bay, Oahu). Part I of this **Introduction** section summarizes previous work in aspects of shallow-water carbonate dynamics. It describes an important field-based approach that considers reef zonation in sediment budget models and presents in detail two case studies that utilize quantitative, field-collected data in constructing such budgets. Part II of this Introduction section provides an overview of the sediment budget for Kailua Bay, including a description of the study area in terms of hydrographic setting, age and composition of calcareous sediments (briefly summarized from Chapter 2), and benthic community structure. The second section, **Methods and Field Results**, also consists of two parts. Part I describes the physiographic zonation of the carbonate reef system in

Kailua Bay, including the methodology used to map substrates. Part II describes the collection, interpretation, and use of organism-based carbonate production data (gross framework production, reef bioerosion, and direct sediment production). The third section, **Results**, tabulates and describes the data, variables, equations, and results of the sediment production model components: gross framework production, reef bioerosion, and direct sediment production by *Halimeda*, benthic foraminifera, molluscs, and articulated coralline algae. The fourth section, **Discussion**, consists of four parts. Part I describes the storage of calcareous sediment in submarine, beach, and subaerial reservoirs in Kailua. Sediment storage is volumetrically compared to sediment production over 5000 years (predicted by the model) to 'balance' the budget. Part II of the Discussion section ('Analyzing Production and Comparing to Previous Studies') considers the results of each component of the sediment production model (gross framework production, reef bioerosion, and direct sediment production) and compares them to the results of previous studies. Part III ('Sources of Uncertainty') discusses important aspects of a sediment budget that could not be directly and rigorously assessed in this study, including the modes and rates of sediment loss, Holocene reef accretion, and mechanical erosion, as well as examines the assumptions involved in applying modern production rates over the last 5000 years. Part IV discusses the significance of the Kailua budget to oceanic island systems, and the relationship between reefs and beaches in affecting coastal stability. It also examines the importance of coralline algae in Hawaiian reef systems and suggests a role in the pelagic alkalinity balance of the North Pacific. The final section, **Conclusions**, summarizes the findings of this interdisciplinary

approach to carbonate sediment dynamics. A numbered list of the primary quantitative findings is provided.

PART I: Previous Work

Carbonate accumulation on reefs has been estimated using growth rates and abundances of reef-dwelling organisms; accretion histories from age-dated reef cores; rates of $CaCO_3$ extraction from seawater based on alkalinity changes; and changes in reef topography. Drilled cores collected from modern and fossil reef systems have been instrumental in developing Holocene reef accretion histories in tropical and subtropical settings around the globe (e.g. Easton and Olson 1976, Macintyre and Glynn 1976, Davies and Hopley 1983). Although such histories are detailed accounts of the modes and rates of the (net) accumulation of reefal substrates, they focus largely on constructional processes and biolithologic structure. A multitude of biological, chemical, and mechanical processes act to reduce a reef edifice to unconsolidated sediment. Any reef, living or fossil, is thus the cumulative result of constructional and destructional processes.

Among the first quantitative 'carbonate budgets' were systems-level geochemical process studies of calcification on reefs (e.g. Smith and Kinsey 1976, Lewis 1977, Kinsey 1983, Smith 1983, Kinsey 1985). The 'currency' in such studies is *carbon* rather than carbonate, and rates of growth and erosion are expressed in terms of $CaCO_3$ pathways through reefs. In his review of metabolism and calcification in coral communities, Kinsey (1985) estimated 10–30% of the total carbon fixed in reef systems goes into the production of carbonates. The parameter *P* (photosynthetic fixation) for most reefs is

between 1–14 g C $m^{-2}d^{-1}$, with most estimates falling within 2–10 g C $m^{-2}d^{-1}$ (e.g. Lewis 1977, Sournia 1977), while the parameter *G* is a measure of the *inorganic gain* of biogenic carbonate, generally expressed in $kgm^{-2}y^{-1}$. Most 'complete' reef systems have *G* values <2 $kgm^{-2}y^{-1}$ while highly productive, coral-covered slopes can gain carbonate at rates as great as 12 $kgm^{-2}y^{-1}$ (Kinsey 1985).

Chave et al. (1972) assessed carbonate production by coral reefs and associated environments, dividing it into three categories: *Potential*, *Gross*, and *Net* production of carbonate (*not* carbon as above). *Potential* production (also abbreviated *P*, but note the difference in meaning) was defined as the amount of $CaCO_3$ produced by an organism (or colony) per unit area of the reef surface it covered. This quantity was calculated by multiplying the standing crop of the organism (in $gm^{-2}y^{-1}$) by its annual population turnover rate. In order-of-magnitude calculations of *P* for *Halimeda*, red algae (both encrusting and articulated), micro- and macromolluscs, echinoderms, and foraminifera, Chave et al. found (to their surprise) that the potential production abilities (*P*) of these diverse organisms were all ~10^4 g $CaCO_3$ $m^{-2}y^{-1}$ (~10 $kgm^{-2}y^{-1}$). Potential production by corals was highly variable depending on the species, location, and morphology, but estimates of *P* were generally 10^4–10^5 $gm^{-2}y^{-1}$ (~10–100 $kgm^{-2}y^{-1}$).

The Chave et al. model defined gross production (*G*) as the amount of $CaCO_3$ produced by the reef community per unit area of sea floor. This quantity *G* was calculated by multiplying the *P* value of each organism by its areal coverage. The authors described four typical reef-associated habitats in terms of their gross production: (1) back-reef sand flats with calcareous algae, molluscs, and foraminifera produced 400 g $CaCO_3$ $m^{-2}y^{-1}$; (2) coral mounds on sand (with associated algae, molluscs, echinoderms, and forams)

produced 13000 $gm^{-2}y^{-1}$; (3) algal ridges produced 9000 $gm^{-2}y^{-1}$; (4) gardens of 100% living coral produced 55000 $gm^{-2}y^{-1}$. Combinations of these four typical habitats can be used to model whole-reef environments in terms of *G*. For example, a 'lower reef slope' might be characterized as 20% sand flat, 20% coral mound, 10% coral garden, and 50% barren, yielding an estimate of gross production on lower reef slopes of ~8000 $gm^{-2}y^{-1}$.

The authors admitted their model was oversimplified, largely hypothetical, and speculative but maintained their results were reasonable and testable. The model did indeed provide useful, order-of-magnitude estimates of carbonate productivity from the scale of individual reef inhabitants to whole-reef environments.

Land (1979) proposed a simple reef mass-balance equation: *Gross = Net + Sediment removed*. He calculated total coral productivity of the fringing reef in Discovery Bay, Jamaica, to be 3.1 $kgm^{-2}y^{-1}$. Lacking data on red and green algae production, he added in their productivity based on their proportion in sediments, acknowledging this was a giant assumption. 'Non-coral' productivity totaled 2.1 $kgm^{-2}y^{-1}$, bringing the *Gross* term of the mass balance equation to 5.2 $kgm^{-2}y^{-1}$. From cores, he calculated the *Net* term ($CaCO_3$ within the reef edifice) to be 1.1 $kgm^{-2}y^{-1}$. He found an average of 1.2 kg of sediment were lost from every square meter of the reef each year (= *Sediment removed*). To satisfy the mass-balance equation, 2.9 $kgm^{-2}y^{-1}$ must be lost in solution (5.2 – 1.1 – 1.2 = 2.9). This relationship suggested only 21% of gross productivity was retained in the reef edifice and that the majority of the carbonate budget (56%) was lost in solution.

These early studies of carbonate production and cycling in reefal environments and at the geochemical level were valuable in understanding the general gains and losses

incorporated in a reef 'budget,' although they self-admittedly lacked systematic and extensive data collection from a specific reef setting.

Field-based Approach

Among the most important field observations that should be incorporated in any detailed reef budget is quantitative mapping of various benthic substrates over a range of depths and spatial scales in the system. The surface of most reefs is best described in terms of various sub-environments (or 'zones'), each with a suite of specific characteristics. The zones themselves may cover vast areas and support diverse and complex benthic communities, or they may be restricted in size and/or abundance of living occupants. Such zones should be identified, described, and accurately characterized in terms of physiographic setting, substrate type, species diversity, and organism abundance. This can be accomplished by quantitative mapping of the reef surface. The term 'reef' in this context refers to an entire 'carbonate reef complex' and encompasses all subenvironments within the near- to offshore package.

The rates at which sediment is created and destroyed on the reef and within its different zones can also be quantified by identifying the organisms and processes responsible for the construction and destruction of calcareous material, both consolidated and unconsolidated, over the entire system. Such a carbonate budget analyzes reef-based community structure, composition, and carbonate production while utilizing an understanding of the geological processes in and history of reef environments.

Since carbonate sediment is also produced directly by the biological activities of reef-dwelling organisms such as *Halimeda*, molluscs, foraminifera, and echinoderms, analysis of the living population and annual turnover of each group should be combined with an understanding of the framework components of the reef system.

The most comprehensive sediment budgets for shallow-marine carbonate reefs address the processes of initial (gross) carbonate production of corals and coralline algae, the bioerosion and degradation of the resulting reef edifice, and the direct addition of calcareous sediment through the biological activities of reef-dwelling, calcifying organisms. A comprehensive budget also recognizes the source and role of allochthonous sediments (if they exist in the system). Figure 3-1 illustrates a conceptual box model of a reef-based carbonate budget.

The storage, flux, and loss of sediment are also important components of a reef budget. Reefs are such prolific producers of sediment that self-burial in their own biocoenosic debris can occur. Unconsolidated sediments produced on reefs can be more significant than skeletal structures when considered in terms of volume of total carbonate (Stoddart 1969, Milliman 1974). Sand channels, chutes, and fields in reefs act to remove and/or store sediments to prevent such self-imposed burial. The volume of sediment storage and exchange in a system should thus be quantified in a comprehensive budget.

In the last 25 years, two field-based carbonate sediment budgets have availed from systematic and extensive data collection in specific reef environments. Presented below are two case studies summarizing the work published in a series of papers on the two research areas: Bellairs Reef, Barbados (Stearn and Scoffin 1977, Stearn et al. 1977,

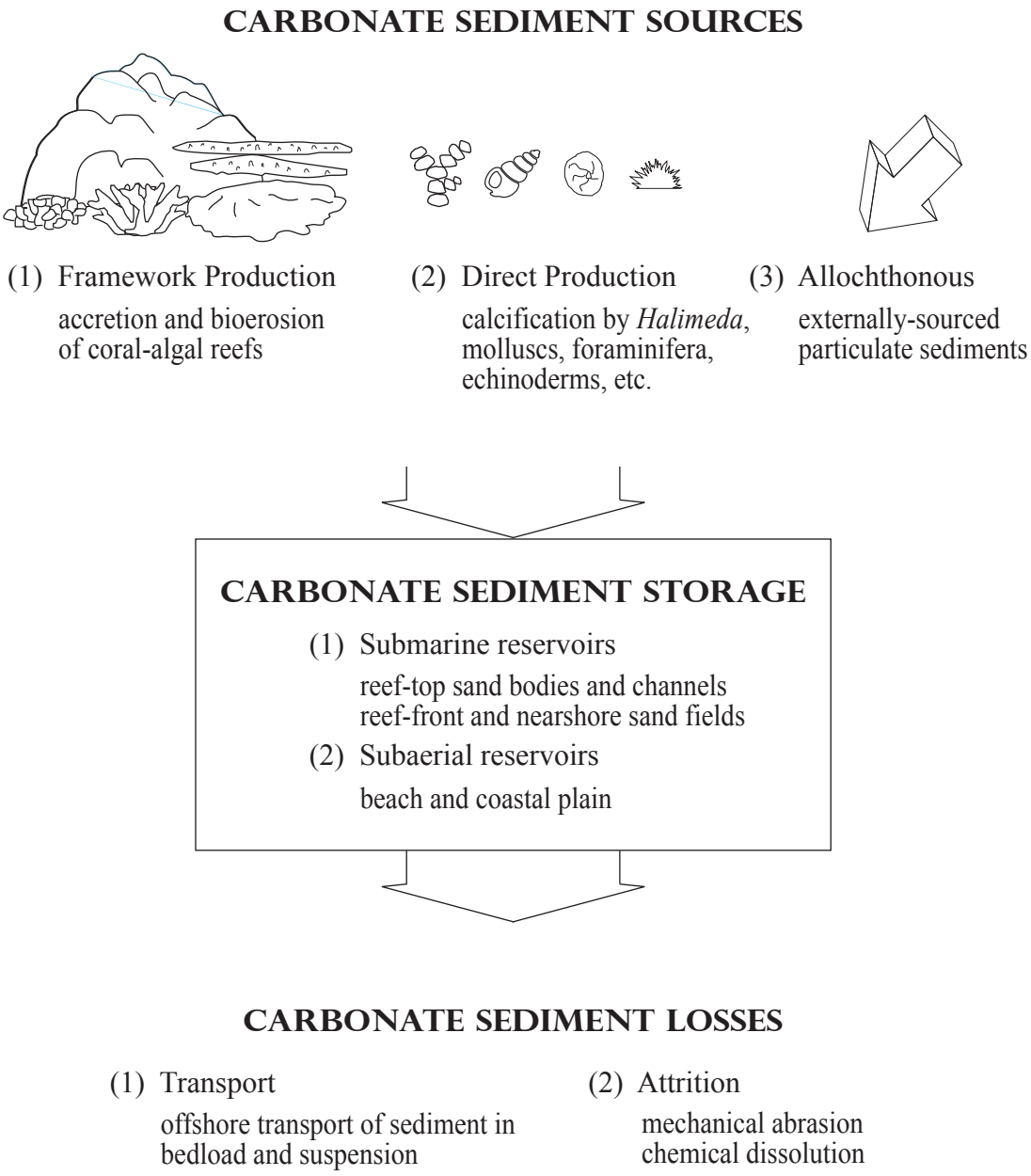


Figure 3-1. Conceptual model of a reef-based carbonate sediment budget for Kailua Bay. Processes involved in the production of silts and muds are not shown.

Scoffin et al. 1980) and Cane Bay, St. Croix, U. S. Virgin Islands (Sadd 1984, Hubbard et al. 1990, Hubbard 1992).

Case Study: Bellairs Reef, Barbados

The carbonate budget for Bellairs Reef, a small, leeward fringing reef on the west coast of Barbados, was the first of its kind to utilize actual field-based measurements of hard tissue growth and destruction. Stearn and Scoffin (1977) recognized the complexity of a growing tropical reef, extolling it as a 'super-organism.' To construct the budget, the authors measured $CaCO_3$ production by corals and coralline algae over the 10800 m^2 reef area, mapped the distribution and abundance of coral and coralline-algal species, assessed reef rugosity, and calculated an estimate total (gross) reef productivity. They investigated reef bioerosion in detail, quantifying the boring and grazing rates of various bioeroding inhabitants of the reef.

The distribution and abundance of corals and coralline algae were determined from point-counting along six transects (2175 points total) over Bellairs Reef. Twelve 'ecological zones' were delineated and described using the transect data (e.g. swash zone, sand zone, rubble zone, pillar-coral zone, dome-coral zone, spur and groove zone). Substrate area was calculated by multiplying the planimetric area of the reef by its rugosity (a roughness factor collected by dividing a known length of chain by the lateral distance it covers when draped over a topographic surface; rugosity is usually between 1 (flat) and 4 (high relief)). The habitat area for each species is the product of its percent cover and the substrate area.

Coral growth rates in the Bellairs study were either extracted from published literature or determined by sclerochronology (in which coral specimens are slabbed, x-rayed, and their annual rates of linear extension are measured directly). The encrusting coralline algae *Porolithon* grows at a rate of 2 mmy^{-1} in this region (Stearn et al. 1977). Using a density of 1.56 gcm^{-3}, the gross production rate can be converted to 3.12 $kgm^{-2}y^{-1}$. This rate was applied to all types of encrusting coralline algae on Bellairs Reef (e.g. *Neogoniolithon*, *Lithophyllum*, and *Mesophyllum*). *Halimeda* and other types of calcareous algae were entirely absent on Bellairs Reef. Carbonate production by molluscs, forams, bryozoans, serpulids, and crustaceans was considered insignificant compared to corals and crustose coralline algae, thus their sediment contribution was ignored. The contribution of branching coralline algae was also considered minor and not included.

Gross $CaCO_3$ production rates for each type of coral and coralline algae were calculated by multiplying the respective growth rate by the habitat area the organism occupied on the reef. Gross production rates averaged 6.35 $kgm^{-2}y^{-1}$ for corals and 2.55 $kgm^{-2}y^{-1}$ for encrusting coralline algae, yielding a whole-reef gross carbonate production total of 163.3 x 10^3 kgy^{-1} (116.5 x 10^3 kgy^{-1} contributed by corals; 46.8 x 10^3 kgy^{-1} by coralline algae).

The authors suggested that mechanical erosion was unimportant in this leeward setting and instead studied the organisms and processes responsible for biological degradation of the reef edifice. The amount of skeletal material removed by boring organisms was estimated from x-radiographs of several species of massive corals. When paired with known growth rates for each coral, boring rates between 80–382 $gm^{-2}y^{-1}$ were

calculated. (Very high rates of boring were reported for samples of dead coral (507 $gm^{-2}y^{-1}$)). By these calculations, a total of 25 x 10^3 kg $CaCO_3$ were removed from the reef each year due to boring alone, or 15% of the annual gross carbonate production.

In assessing the relative importance of grazing organisms (e.g. fish, gastropods, urchins, and worms), the authors determined that only the large 'stoplight' parrotfish (*Sparisoma viride*) and the abundant *Diadema antillarum* sea urchin participated significantly in reef destruction. The behavior, biomass, and gut contents of these two organisms were studied in detail to determine their grazing rates over Bellairs Reef: 36 $gm^{-2}y^{-1}$ for parrotfish (or 1 x 10^3 kgy^{-1}); 9000 $gm^{-2}y^{-1}$ for urchins (or 163 x 10^3 kgy^{-1}). By these calculations, borers and grazers removed a total of 189 x 10^3 kgy^{-1} from the reef edifice.

These results indicated a considerable deficit in the reef budget, in which bioerosion (boring + grazing) was greater than production. Scoffin et al. (1980) suggested that the high rates of reef destruction by grazing organisms did not take into account the likely possibility that up to a third of the parrotfish's and half the urchin's excreta is actually reworked sediment, not fresh destruction. Although the studies discussed the reincorporation and cementation of bioeroded sediment within the reef edifice (a process that added almost 30 x 10^3 kgy^{-1} to the reef structure), storage and loss of sediment from Bellairs Reef was not discussed; sub-surface processes and cryptic bioeroders were not observed; and direct sedimentation by molluscs, forams, and echinoderms was not assessed. The authors acknowledged not all aspects of reef construction and destruction were included in the study, but the order-of-magnitude rates were the first to be based on field-collected data and remain useful in understanding 'real reef' carbonate dynamics.

Case Study: Cane Bay, St. Croix

Hubbard et al. (1990) constructed a carbonate budget that attempted to quantify influences on Holocene reef development, emphasizing the importance of secondary depositional processes in 'restructuring' a reef's interior. The detailed study of the production and cycling of $CaCO_3$ in Cane Bay on the island of St. Croix (U.S. Virgin Islands) addressed three reef-scale processes: initial (gross) carbonate production (Pg), its subsequent bioerosion (some of which is retained in the reef edifice), and the redistribution of a portion of unconsolidated sediments (derived from bioerosion) outside the reef edifice. The methods of Hubbard et al. were instrumental in the development of the sediment budget for Kailua Bay and are thus described here in some detail.

In the Hubbard et al. model, the total volume of unconsolidated sediment produced by and released from the reef edifice in Cane Bay annually is defined as SEDt ($kgm^{-2}y^{-1}$):

$$SEDt = SED + SEDca + SEDd \qquad \text{(Eq. 1)}$$

where SED is bioeroded sediment released from the reef edifice into channels, SEDca is the contribution of encrusting coralline algae, and SEDd is the volume added by direct sediment production by accessory organisms. Each of these parameters is described below. The extent and effect of micritization processes and mechanical erosion were not assessed in the Cane Bay study.

Bioeroded sediment (SED)

The amount of bioeroded sediment not incorporated in the reef edifice (SED) is calculated using the following equation, initially argued by Land (1979):

$$SED = Pg - Pn \qquad \text{(Eq. 2)}$$

where Pg = gross carbonate production (calculated from growth rates) and Pn = net carbonate production (determined from cores).

Hubbard et al. defined gross carbonate production (Pg) as the 'amount of calcium carbonate produced by the organisms inhabiting the reef,' primarily corals and coralline algae, with lesser contributions made by molluscs, forams, echinoderms, serpulids, and bryozoans (*Halimeda* is conspicuously absent from the Cane Bay reef). Gross production was a function of three major factors: relative abundance of calcifying organisms, habitat area occupied by the carbonate producers, and production rates of each organism. Species abundance was determined from quantitative mapping at 46 sites (10-m transect per site) in Cane Bay. Habitat area was calculated by multiplying the species abundance by the surface area of the reef. Coral growth rates were either extracted from published literature or measured directly in sclerochronologic sample analysis. Gross production by each coral species was the product of its growth rate and the habitat area it occupied. The sum of gross production by all coral species in Cane Bay was 1.13 $kgm^{-2}y^{-1}$. A small contribution made by coralline algae (SEDca = 0.02 $kgm^{-2}y^{-1}$, described below) was added to this to obtain a total gross production rate of Pg = 1.15 $kgm^{-2}y^{-1}$.

Net carbonate production (Pn) was the amount of carbonate incorporated in the reef edifice, derived from the linear amount of solid core recovered plus 67% of the intervals containing sand and rubble. The '67%' correction value was derived from the ratio

between bulk densities measured for the coral (1.8 gcm^{-3}) and dry sand (1.2 gcm^{-3}) collected in cores. The total length was multiplied by 1800 kgm^{-3} to yield an equivalent net production rate of Pn = 0.91 $kgm^{-2}y^{-1}$.

Using Eq. 2 above, the amount of bioeroded sediment not incorporated in the reef edifice was calculated as the difference between Pg and Pn, or SED = 0.24 $kgm^{-2}y^{-1}$.

Coralline algae production (SEDca)

The paucity of coralline algae in the Hubbard et al. reef cores led the authors to assume coralline algae growth was balanced by herbivory. Thus, the rate of sediment generated by the breakdown of corallines through bioerosion was approximately equal to their rate of gross production, calculated as:

$$SEDca = SEDt \times ABNca \qquad \text{(Eq. 3)}$$

where SEDt was the rate of total sediment production (see below) and ABNca was the abundance of coralline algae fragments in sediment samples. The amount of sediment produced by the growth and bioerosion of coralline algae was SEDca = 0.02 $kgm^{-2}y^{-1}$.

Direct production (SEDd)

The contribution of direct sediment production (SEDd) by 'accessory' organisms in Cane Bay (molluscs, foraminifera, and echinoderms) was approximated by:

$$SEDd = SEDt \times ABNd \qquad \text{(Eq. 4)}$$

where SEDt = total sediment production (in $kgm^{-2}y^{-1}$) and ABNd = proportion of direct producers in the sediment. The contribution of accessory organisms was SEDd = 0.06 $kgm^{-2}y^{-1}$.

Total sediment production (SEDt)

The total rate of unconsolidated sediment produced and released into channels of Cane Bay ($kgm^{-2}y^{-1}$) was expressed as the sum of bioeroded sediment released (SED = Pg – Pn = 0.24 $kgm^{-2}y^{-1}$) and direct sources (SED ca and SEDd):

$$SEDt = SED + SEDca + SEDd \qquad \text{(Eq. 1)}$$

$$0.32 = 0.24 + 0.02 + 0.06$$

thus SEDt = 0.32 $kgm^{-2}y^{-1}$. This is the rate at which unconsolidated sediment is produced and released from the reef in Cane Bay. The production of sediment actually occurs at a greater rate, owing to the proportion of bioeroded material that remains incorporated in the reef edifice. The authors assess this by examining total bioerosion.

Total bioerosion

Although bioerosion rates by sponges, fish, echinoderms, and other organisms are widely available (e.g. Moore and Shedd 1977, Ogden 1977), the task of applying bioerosion estimates to each bioeroding species over a large reef area is 'herculean' and unnecessary. An estimate of 'total' bioerosion in Cane Bay was instead determined by adding the amount of detrital sediment reincorporated into the reef fabric (0.41 $kgm^{-2}y^{-1}$ determined from cores) to SED (0.24 $kgm^{-2}y^{-1}$), for an estimate of 0.65 $kgm^{-2}y^{-1}$. Adding this to SEDca (0.02 $kgm^{-2}y^{-1}$) and SEDd (0.06 $kgm^{-2}y^{-1}$) allows the true rate at which the reef produces unconsolidated sediment to be discerned (0.73 $kgm^{-2}y^{-1}$):

$$\text{Rate Sed. Prod.} = \text{Reincorporated} + SED + SEDca + SEDd \qquad \text{(Eq. 5)}$$

$$0.73 = 0.41 + 0.24 + 0.02 + 0.06 \qquad (kgm^{-2}y^{-1}).$$

Noteworthy is the result that this rate of sediment production is 60% of gross carbonate production (Pg = 1.21 $kgm^{-2}y^{-1}$) and was close to the rate of net reef accretion (Pn = 0.91 $kgm^{-2}y^{-1}$).

Balancing the Cane Bay budget

The average total carbonate production over Cane Bay's fringing reef ranged between 0–5.78 kgm^{-2}. A reef-wide average of 1.21 $kgm^{-2}y^{-1}$ was reported, with 1.13 $kgm^{-2}y^{-1}$ contributed by corals, 0.02 $kgm^{-2}y^{-1}$ by coralline algae, and the remaining 0.06 $kgm^{-2}y^{-1}$ contributed by 'accessory organisms' (primarily molluscs, forams, and echinoderms). Seven reef cores from Cane Bay indicated that of this average, 0.91 kg $CaCO_3$ $m^{-2}y^{-1}$ was retained in the reef edifice as both consolidated and unconsolidated material. The remaining 0.30 $kgm^{-2}y^{-1}$ was flushed from the reef as unconsolidated sediment. Thus, 25% of total gross production was converted into unconsolidated sediment and released into channels outside the reef edifice. If the sediment released was confined only to channels within the reef (roughly one-quarter of the total reef area of 412,200 m^2), the sediment accumulation rate would be 1.20 m / 1000 y. This exceeds the rate of reef accretion!

Hubbard et al. suggested the fate of such prodigious sediment production lay in the following processes: re-incorporation of sediment into the reef edifice, storage in channels, loss to off-shelf transport, winnowing of fine sediments in suspension, and mass removal during hurricanes. The rate of sediment export along the shelf edge was estimated to be 65 kgm^{-2} in fair weather and 1130 kgm^{-2} during annual storms (~55,100 kgy^{-1}). No other rates of sediment removal were assessed.

The Hubbard et al. (1990) Cane Bay study represents the most detailed carbonate reef budget of its kind to that date, incorporating quantitative data on substrate type and distribution, coral growth rates, drilled reef cores, and sediment export. Ultimately, Hubbard et al. discovered that 60% of the carbonate produced in Cane Bay was reduced to sediment by bioerosion, and of that, 40% was released from the reef (and subsequently removed during storms; see Hubbard 1992). Two points of emphasis emerged from the work of Hubbard and colleagues: (1) recognizable coral (41% of cores) was less important in the reef than sediment (45% of cores), with void space alone accounting for 14% of cores; (2) a definitive 'framework' of in-place and interlocking coral (see Dunham (1970) for a discussion of stratigraphic vs. ecologic reefs) was difficult to detect, suggesting that such a characteristic may be the exception rather than the rule in the preservation of reefs in the rock record (Hubbard 1997).

Previous reef budget studies remain useful in designing methodologies for studying reefs as geological systems controlled by biological activities. In his synopsis of the dynamics of reef systems, Hubbard (1997) reiterates the complex interplay of construction, destruction, and redistribution in the development of reefs and suggests they are integral parts of any 'reef equation.'

PART II: Sediment Budget for Kailua Bay, Oahu, Hawaii

Critical to an understanding of carbonate systems are detailed field observations on reef production, accretion, and destruction; sediment production, flux, and loss; and the volume of sediment storage reservoirs. Kailua Bay is an ideal location for developing a

high-resolution sediment budget and for improving our understanding of reef function through time and the role of geologic processes. In our carbonate sediment budget of Kailua Bay, we construct a production model in which we consider details of benthic community structure, biogenic carbonate production by reef-dwelling and frame-building organisms, large-scale physiographic and hydrodynamic conditions, and small-scale life habits of reef-associated, calcifying flora and fauna. We refer to reef cores drilled in Kailua Bay to understand reef accretion and destruction (Grossman and Fletcher 1999), and we utilize existing (Harney et al. 2000) and new radiocarbon ages of the reef and sediments in Kailua to integrate carbonate dynamics over the last 5000 years. We consider the extensive carbonate sediment stored in the coastal plain, in the sandy accretion barrier behind Kailua Bay, in the beach, and in the submarine realm from sea level to -30 m. Finally, in 'balancing' the budget, we consider sediment loss in terms of dissolution, abrasion, and offshore transport of suspended and bedload materials.

Study Area

Kailua Bay is a carbonate reef-dominated embayment on the northeast coast of Oahu in the Hawaiian Islands (Figure 3-2). The bay is positioned windward to Trades, which prevail northeasterly to easterly at average 10–20 knot speeds ~70% of the year. Wind-generated waves 1–3 m in height with periods of 6–9 s dominate hydrographic conditions in summer months (April–September). Winter months bring lighter, more variable winds and 'Kona conditions,' in which southerly low pressure cells cut off prevailing Trade winds for periods of days to weeks. Winter storms generated in the North Pacific deliver

long-period (10–20 s) swells to north-facing shores that occasionally refract into Kailua Bay as waves up to 4 m in height.

Although Kailua Bay lacks a restricted seaward mouth, lateral boundaries of the study area are defined as Mokapu Peninsula in the north and Alala Point in the south. Hydrographic conditions and benthic characteristics of the two boundary regions are quite different. A shallow reef flat contiguous with that off Lanikai exists at the southern end of the bay off Alala Point, while the waters off Mokapu Peninsula are deep close to shore and lack a shallow reef setting of Holocene age.

Circulation in Kailua Bay is described in Krock and Sundararaghavan (1993) in terms of three 'zones' in which the processes governing water and sediment movement are wind-, wave-, and/or tide-dominated. Across the broad, shallow 'reef flat' region landward of the 5 m bathymetric contour, circulation is dominated by breaking wave-induced flow, particularly at the shallower sites north and south of the central portion (Figure 3-3, dark red arrows). Onshore flow at these shallower sites is balanced by offshore flow through the relatively deeper central region of the bay (a triangular sand field). This general circulation pattern is typical of most reef flat settings.

Krock and Sundararaghavan (1993) report that the circulation of mixed-layer surface waters (to 5 m below sea level) outside the 5 m bathymetric contour is tide-related, parallel to bathymetric contours, and maintained by the dominantly-onshore wind pattern (Figure 3-3, orange arrow). As wind-generated currents approach the littoral cell boundaries of Kailua Bay, transport is diverted, generating a more northward component at Mokapu and a more southward component at Alala (Figure 3-3, dark blue arrows), possibly caused by the submarine 'canyon' directly seaward of Kailua Bay. Onshore

winds and the effect of nearshore set-up also cause transport to be diverted parallel to bathymetric contours inside the littoral cell.

A carbonate reef platform comprises most of the seafloor of the study area to -25 m and supports a diverse assemblage of substrates and reef communities. The high-resolution, central portion of image C in Figure 3-2 is a georeferenced, orthographically-rectified, digital mosaic of airborne multi-spectral data collected over Kailua Bay (Isoun et al. 1999). Bisecting the broad reef platform is a 200-m wide sand-floored channel that maintains the antecedent topography of a meandering stream that likely drained the windward Koolau mountains during Pleistocene sea level low-stands. The seaward mouth of the channel opens into a broad, reef-front sand field lying in 30–70 m water depth atop a gradually-sloping limestone terrace (Hampton et al. 1998). In the landward direction, the channel widens to a triangular nearshore sand deposit characterized by shallow depths (<5 m) and occasional fossil reef outcrops.

Age and composition of sediments

Beach and submarine sediments of Kailua Bay are primarily composed of carbonate skeletal fragments (>90%) produced by two processes: mechanical, chemical, and biological destruction of reef framework limestone (coralline algae and coral) into rubble, sand, and silt; and direct sedimentation upon the death of organisms such as *Halimeda*, molluscs, and foraminifera. Although coral is abundant atop the reef platform, it is a minor constituent (<15%) of most sediment assemblages (Harney et al. 2000). Shoreface sands are instead dominated by coralline algae (up to 60%) and *Halimeda* (up to 35%). Other constituents include molluscs (15–20%), benthic foraminifera (<10%), and

echinoderms (<5%). Volcanic fragments and unidentifiable components account for <10% (but are generally 0–4%).

Despite an apparently healthy ecosystem engaging in active carbonate production, sediments in Kailua are dominantly fossil-aged. Of 20 accelerator-radiocarbon ages, only one dates post-1950; twelve ages are 500–1000 calendar years before present (cal yr BP); five are 2000–5000 cal yr BP (Harney et al. 2000). Sand composition and age across the shoreface broadly reflect a spatial relationship to carbonate production. Corals and coralline algae, principal builders of the reef framework, are younger and more abundant in sands along the channel axis and in offshore areas, while *Halimeda*, molluscs, and foraminifera are younger and more dominant in sediments landward of the main region of framework-building. Dated fine sediment is older than medium to coarse sediment and hence may constitute a reservoir of fossil ages. Dominance of fossiliferous sand suggests that ~5000 years of relative sea-level inundation is represented in the sediment.

Benthic community structure

The distribution of benthic substrates in Kailua Bay is well illustrated by the multispectral image (Figure 3-4). Dark areas are consolidated substrate, living coral, and algae; light areas are typically sandy regions. Seaward of sandy shoreline lie scoured fossil limestone surfaces, some covered with a veneer of loose sediment. Jet-probing in the central, triangular region landward of the channel reveals sediment thicknesses <1 m over much of the sand field. In the generally sand-poor regions directly north and south of the triangle, limestone outcrops to 1 m in height are often covered by clumps or meadows of calcareous *Halimeda* and fleshy algae (e.g. *Sargassum*) or encrusted by

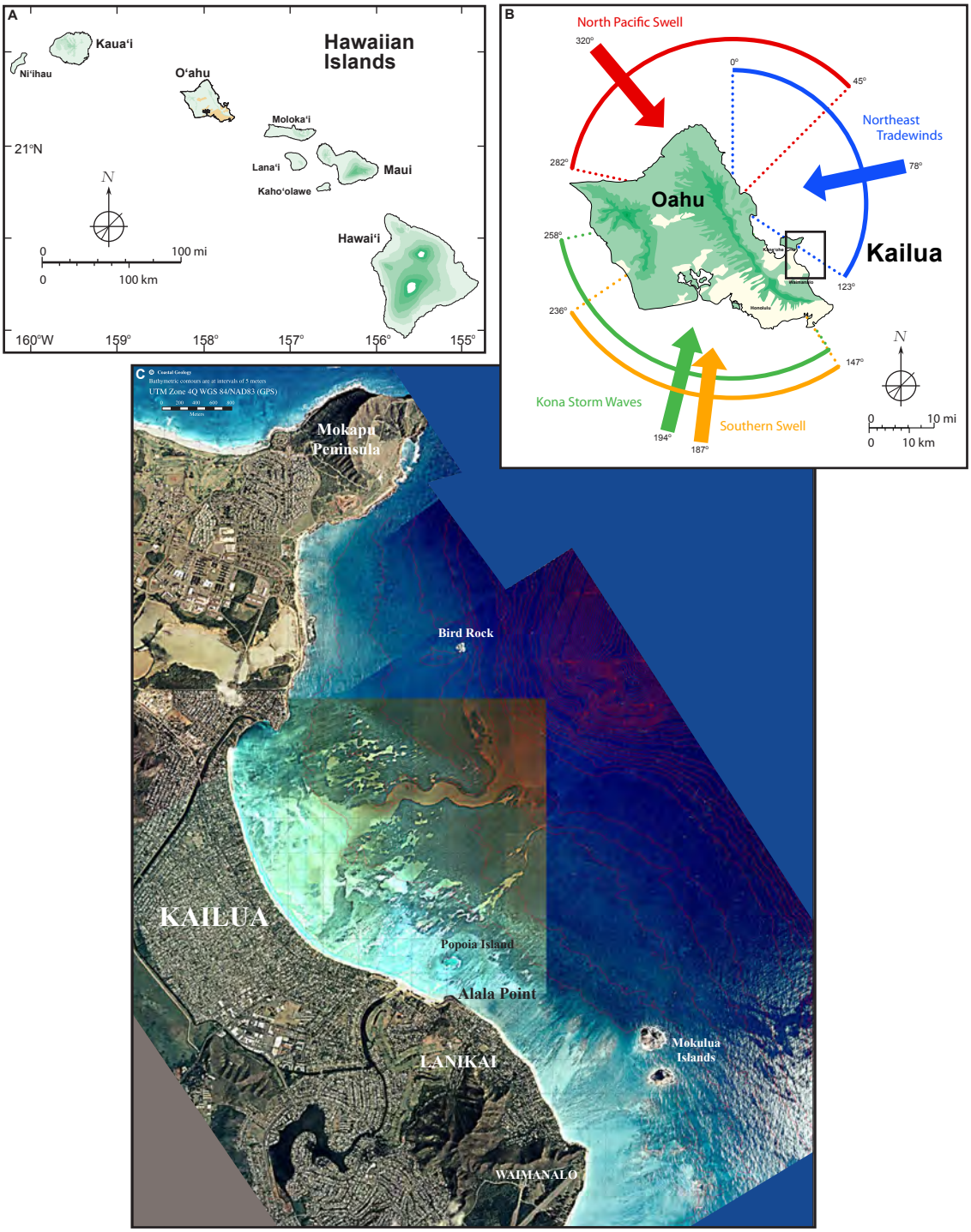


Figure 3-2. Location map of the Hawaiian Islands (A), the island of Oahu (B, after Moberly et al. 1965), and of the study area, Kailua Bay (C). Central, high-resolution region of C is a mosaic of multispectral data (Isoun et al. 1999).

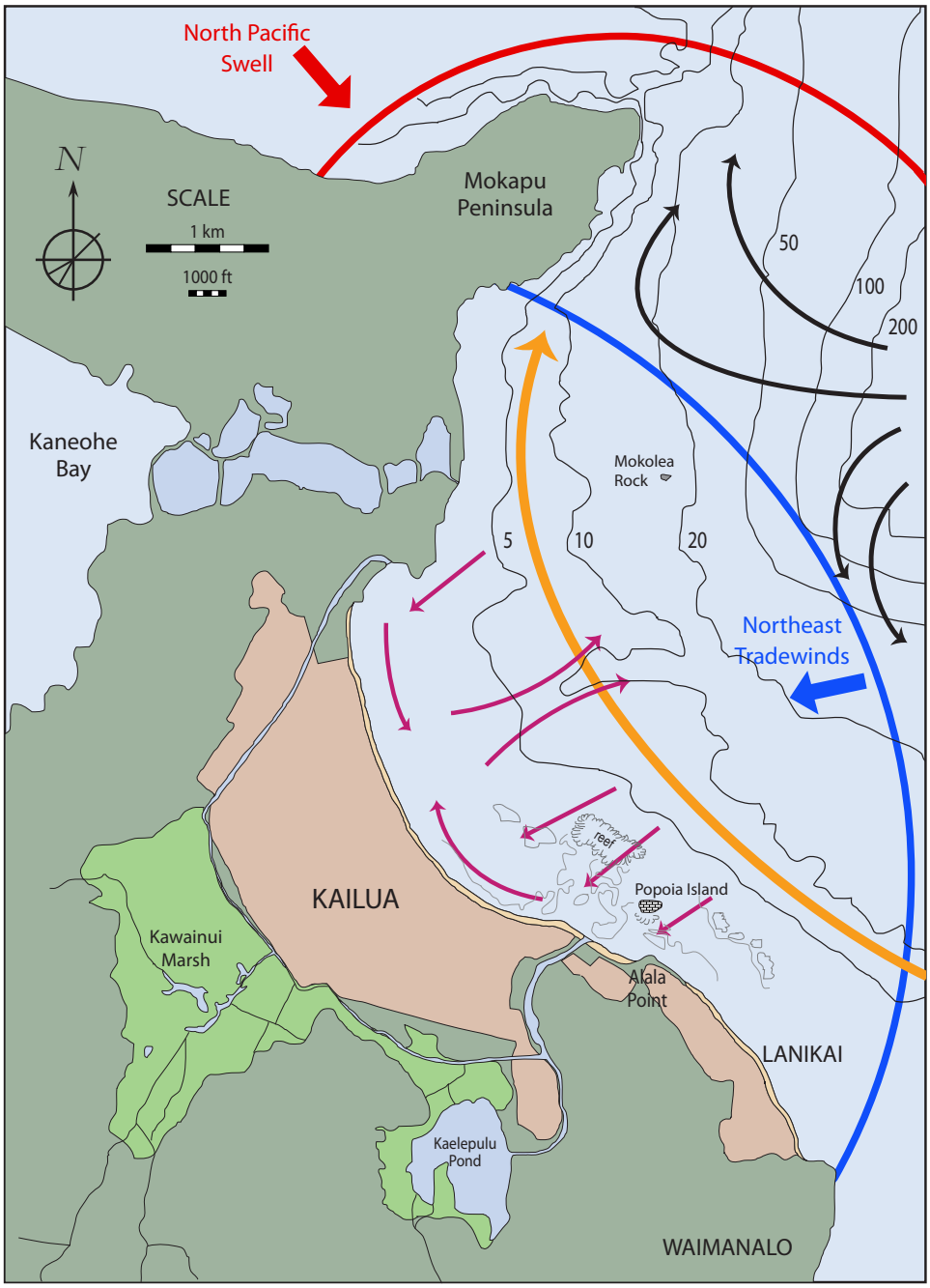


Figure 3-3. General ocean circulation in Kailua Bay (after Krock and Sundararaghavan, 1993). In the nearshore region landward of the 5 m bathymetric contour, circulation is dominated by breaking wave-induced flow onshore balanced by offshore flow through the relatively deeper central region of the bay (dark red arrows). Outside the 5 m contour, circulation of mixed-layer surface waters is tide-related, parallel to bathymetric contours, and maintained by the dominantly-onshore wind pattern (orange arrow). As wind-generated currents approach the littoral cell boundaries of Kailua Bay, transport is diverted, generating a more northward component off Mokapu Peninsula and a more southward component off Alala Point (black arrows), possibly caused by the submarine 'canyon' directly seaward of Kailua Bay.

Figure 3-4. A georeferenced, orthographically-rectified, digital mosaic of airborne multi-spectral data collected over Kailua Bay (Isoun et al. 1999). Dark areas are consolidated substrate, living coral, and algae; light areas are typically sandy regions. Bisecting the broad reef platform is a 200-m wide sand-floored paleostream channel. Its seaward mouth opens into a broad, reef-front sand field lying in 30–70 m water depth atop a gradually-sloping limestone terrace (Hampton et al. 1998). In the landward direction, the channel widens to a triangular nearshore sand deposit.

coralline algae. No coral growth occurs in this nearshore region of mixed sand and hardgrounds.

Porites, *Montipora*, and *Pocillopora* are the most common genera of living scleractinian corals growing on the reef platform. Their distribution, abundance, and morphology vary with depth and hydrodynamic energy. For example, encrusting *P. lobata*, *M. patula*, and *M. verrucosa*, although present at all depths, are most dominant in shallow and/or energetic settings. In contrast, the branching finger coral *Porites compressa* is generally found on reef slopes in deeper or calmer water. Robust, stoutly-branching *Pocillopora meandrina*, a 'pioneer species' (Grigg 1982), is most abundant in shallow, energetic environments. Massive or head-like forms of *Porites lobata* are common in shallow to moderate water depths, while platy forms of this species and both *Montipora* sp. are generally found in deeper waters or on relatively steep slopes. Other less common coral species include *Pavona varians*, *Pavona duerdeni*, *Leptastrea purpurea*, and *Cyphastrea ocellina*.

Encrusting coralline (red) algae are prolific inhabitants of the benthic community at all depths. *Porolithon onkodes* is among the most ecologically-important of the tropical crustose coralline algae (Littler and Doty 1975) and the single most common crustose species in Hawaii (Adey et al. 1982). Articulated *Porolithon gardineri* is most abundant in shallow, energetic habitats where it grows as stout or ramose clumps 5–50 cm in diameter. Extensive meadows of the calcareous green alga *Halimeda* are abundant in shallow, well-lit areas near shore, growing on both sandy and rocky substrates. In addition, scattered clumps of both *H. opuntia* and *H. discoidea* are common across the reef platform in water depths <15 m. Nonsessile macromolluscs and echinoderms, as well

as epilithic benthic foraminifera and micromolluscs, are common to abundant in all habitats and at all depths on the reef platform. The assessment of their distribution and abundance is discussed in a later section.

The broad fringing reef, with its diverse benthic community structure and large sand bodies, offers a unique setting in which to study the production and storage of calcareous sediment. Based on the multispectral image, quantitative data collected from the reef surface, and knowledge gained from large-scale reconnaissance, this study characterizes substrate type, benthic community structure, the distribution and abundance of reef-dwelling organisms, and general hydrodynamic conditions over a 10-km^2 region of Kailua Bay.

METHODS AND FIELD RESULTS

Part I: Physiographic Zonation

Substrate mapping

Figure 3-5 illustrates the locations of 51 sites on the reef platform in Kailua Bay where quantitative data on substrate type was collected. Some mapping sites were chosen randomly on the reef surface; others were selected specifically for their location on the platform, to follow a depth contour, to characterize the nature of a wall or sloping surface, or to answer other specific questions. At each site, GPS locations, water depths,

and hydrodynamic conditions were recorded. Quantitative substrate mapping was accomplished by SCUBA divers employing a continuous line-transect method (cf. English et al. 1997). A 30-m polypro line labeled at 50-cm intervals is mounted on a large, durable plastic reel. One end of the marked transect line is secured on the seafloor with a small anchor, the transect line is unspooled by a diver swimming along a compass bearing, and the opposite end is secured to the bottom. The line remains straight and does not follow benthic contours. If surge or current is present, the line is weighted to prevent movement. Using standardized data sheets printed on underwater paper (Figure 3-6), the diver works from one end to the other, continuously recording the substrate type and any living inhabitants encountered under the transect line. At each point where the benthic substrate, living organism, or morphology changes, the data collector records the transition point in meters and the name or code corresponding to the substrate type (Figure 3-7). During processing of the transect data, the length of each different substrate type is determined by the difference between the numbered transition points. The percent coverage for each substrate type is then calculated by dividing the sum of its occurrences by the total transect length.

Substrate types recorded include: fossil reef (bare, with sediment veneer, encrusted with coralline algae, grown over with fleshy or turf algae), living coral (species and morphology), recently dead coral, coralline algae (encrusting or articulated), rubble, and sand. Living corals are identified to the species level and their growth form recorded (e.g. *Porites lobata* encrusting).

The presence of every individual colony encountered is also recorded, yielding species 'counts' as well as percent cover. Such counts are useful in calculating a standard diversity index, Hc:

$$Hc = -\Sigma\,(p_i \times ln\ p_i) \qquad \text{(Eq. 6)}$$

where p_i is the percent cover of the ith coral species (Zar 1984). Values <0.5 indicate low species diversity.

At each transect site, the three-dimensional reef surface topography is quantitatively expressed using a 'rugosity' value that is collected directly from the reef surface. A 2-m chain is draped over the sea floor, conforming to the topographic variation of the substrate; the linear distance the chain stretches over the substrate is measured, and rugosity is calculated by dividing the total chain length (2 m) by that distance. Rugosity values are 1.0 on a flat surface and up to 4.0 on topographically-variable surfaces or slopes.

After processing, the quantitative data are sorted, grouped, and analyzed in terms of general substrate type, community structure, coral species composition, dominant coral morphologies, appearance of fossil substrate, abundance and type of algae, and other parameters. The author was the sole collector and processor of all mapping data in this study. A subset of the data is provided as an example in Table 3-1. The complete set of transect data from all 51 sites can be found in Appendix C.

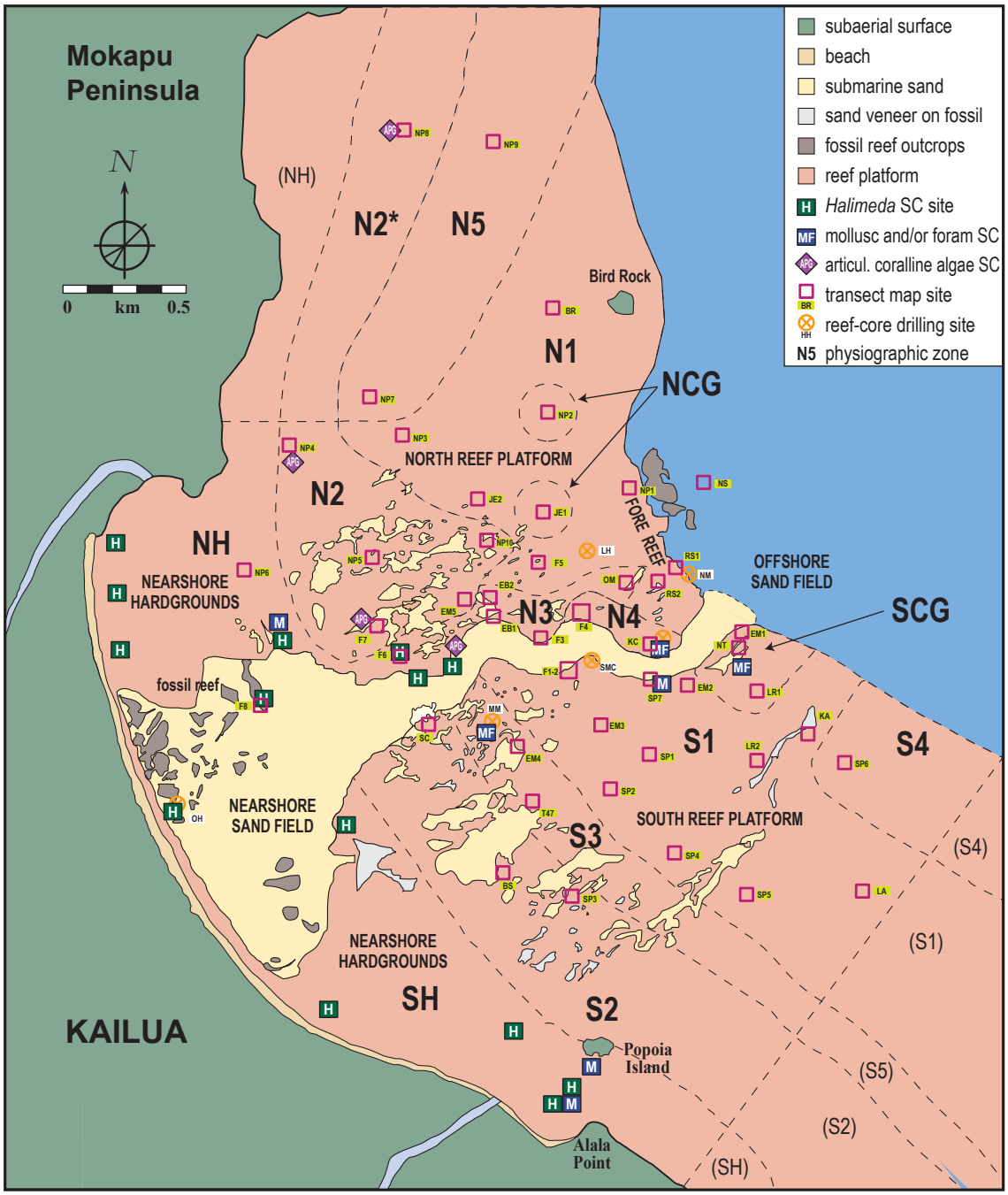
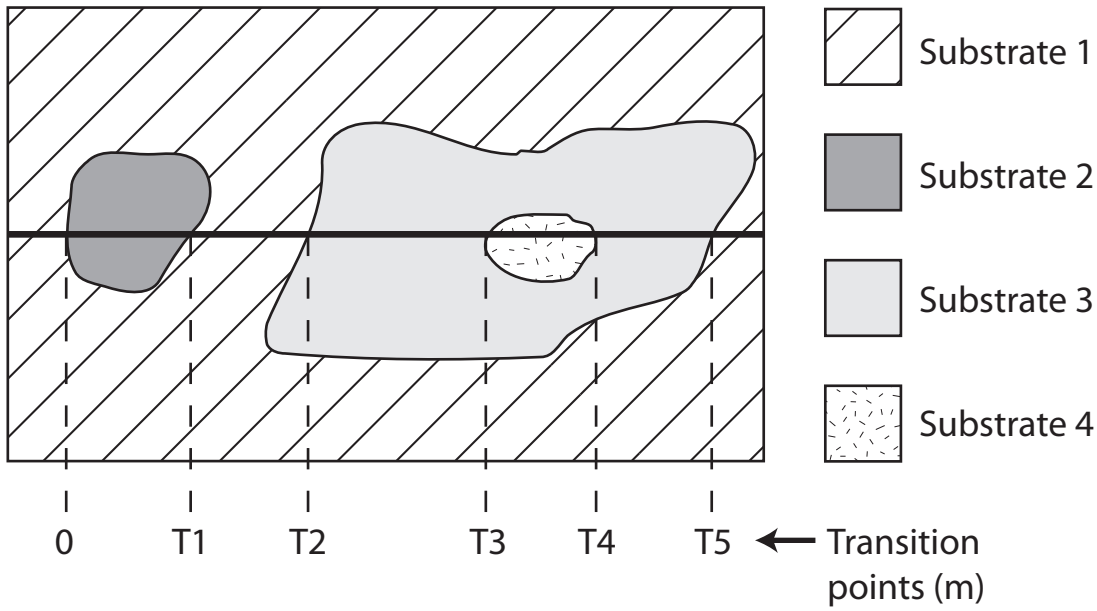


Figure 3-5. Fringing reef platform of Kailua Bay, illustrating mapping and sampling locations and physiographic zone designations. Boxed letters (H, M, F, and APG) indicate sites where samples for standing crop (SC) analyses were collected.

SITE		LAT
DATE		LON
DEPTH		BEAR
RUG		TR LN (m)
#	Substrate	Genus, species, morphology

SUBSTRATE	FR	fossil reef (note spur height)
	FRH	hardground
	LC	living coral
	DC	recently dead coral
	R	rubble
	S	sand
	X	blocks
CORAL COMMUNITY	PL	*Porites lobata*
	PC	*Porites compressa*
	PE	*Porites evermanni*
	PR	*Porites rus*
	MV	*Montipora verrucosa*
	MP	*Montipora patula*
	MF	*Montipora flabellata*
	MS	*Montipora studeri*
	OM	*Pocillopora meandrina*
	OE	*Pocillopora eydouxi*
	OD	*Pocillopora damicornis*
	VD	*Pavona duerdeni*
	VV	*Pavona varians*
	LB	*Leptastrea bottae*
	LP	*Leptastrea purpurea*
	FS	*Fungia scutaria*
MORPHOLOGY	M	massive, head, mound
	E	encrusting
	P	platy
	SB	stout branching
	FB	finger branching
	BL	bladed
ALGAE	ACE	encrusting coralline algae
	ACO	*Porolithon onkodes*
	ACG	*Porolithon gardineri*
	H	*Halimeda*
	AF	fleshy (color B, R)
BIOERODERS	BU	urchins
	BW	boring worms
	BM	boring molluscs
	BF	(parrot) fish
OTHERS	ZP	*Palythoa tuberculosa*
	ZZ	*Zoanthus pacificus*
ABUNDANCE	0	absent
	1	<10%
	2	11-30%
	3	31-50%
	4	51-75%
	5	76-100%

Figure 3-6. Example data sheet used in quantitative line transect mapping of benthic substrates in Kailua Bay.



Length (m)		Category
T1-0	= L1	Substrate 2
T2-T1	= L2	Substrate 1
T3-T2	= L3	Substrate 3
T4-T3	= L4	Substrate 4
T4-T4	= L5	Substrate 3

$$\% \text{ Cover Substrate 3} = \frac{\text{S Lengths (Substrate 3)}}{\text{Total transect length}}$$

Figure 3-7. Continuous line-transect method of quantitative benthic substrate mapping.

Table 3-1. Subset of quantitative data collected during line-transect mapping in Kailua Bay. The complete set of data for all 51 sites can be found in Appendix B.

Site	Site #	34	35	36	37	38	39	40	41	42	43	44
information	Date collected	02.06.00	02.06.00	02.06.00	02.16.00	02.16.00	02.16.00	02.16.00	02.16.00	02.16.00	02.16.00	02.16.00
	Site name	NP8	NP9	NP10	F1	F2	F3	F4	F5	F6	F7	F8
	Longitude	-157.72894	-157.72486	-157.72547	-157.72161	-157.72161	-157.72294	-157.72108	-157.72297	-157.72967	-157.73078	-157.73628
	Latitude	21.44106	21.44047	21.42228	21.41653	21.41653	21.41803	21.41917	21.42122	22.41717	23.41847	24.41497
	EPE (m)	14	14	14	19	19	19	19	19	19	19	19
	Bearing	0	0	90	165	225	45	180	225	0	255	0
	Depth_min	7.6	15	6	9	8	6	7	7	8	2	3
	Depth_max	7.6	15	8	13	10	6	14	9	8	3	3
	Depth_mean	7.6	15	6	11	9	6	11	8	8	2.5	3
	Rugosity	1.0	1.0	1.2	1.5	1.2	1.2	1.2	1.2	1.1	1.4	1.0
	Zone	N2	N5	N2	S1	S1	N3	N4	N1	N3	N2	FRS
Substrate	Fossil reef - bare	83%	65%	0%	12%	21%	0%	2%	2%	20%	0%	0%
type	FR w/ encrusting coralg	0%	0%	59%	3%	12%	35%	60%	26%	17%	59%	73%
	FR w/ branching coralg	0%	0%	0%	0%	0%	0%	5%	0%	5%	23%	0%
	Coral - living	12%	34%	12%	72%	64%	42%	24%	57%	47%	9%	0%
	Coral - dead / bare	0%	0%	0%	6%	0%	1%	0%	0%	0%	0%	0%
	Coral - dead w/ encrust alg	0%	1%	24%	4%	3%	21%	7%	14%	0%	8%	0%
	Coral - dead w/ branch alg	0%	0%	3%	0%	0%	0%	0%	0%	0%	0%	0%
	Coralline algae - encrust	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
	Coralline algae - branch	4%	0%	1%	0%	0%	1%	0%	0%	2%	1%	0%
	Rubble	0%	0%	0%	4%	0%	0%	0%	0%	2%	0%	0%
	Rubble w/ encrust coralg	0%	0%	0%	0%	0%	0%	0%	0%	2%	0%	0%
	Sand	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	15%
	Zoanthid	0%	0%	0%	0%	0%	0%	2%	0%	0%	0%	0%
	Other	0%	0%	0%	0%	0%	0%	0%	0%	5%	0%	11%
Coral	Total	12%	34%	12%	72%	64%	42%	24%	57%	47%	9%	0%
cover	Porites lobata - sum of all	4%	5%	0%	1%	1%	1%	2%	14%	0%	1%	0%
	Montipora verrucosa - sum	6%	8%	1%	10%	10%	3%	0%	2%	29%	0%	0%
	Montipora patula - sum	0%	17%	7%	60%	54%	28%	10%	38%	17%	7%	0%
	Porites lobata - encrusting	4%	5%	0%	0%	1%	1%	0%	4%	0%	1%	0%
	Porites lobata - massive	0%	0%	0%	0%	0%	0%	0%	9%	0%	0%	0%
	Porites lobata - plate	0%	0%	0%	1%	0%	0%	2%	0%	0%	0%	0%
	Porites compressa	0%	0%	0%	0%	0%	0%	0%	1%	0%	0%	0%
	Montipora verrucosa - encr	6%	8%	1%	1%	10%	3%	0%	2%	29%	0%	0%
	Montipora verrucosa - plate	0%	0%	0%	9%	0%	0%	0%	0%	0%	0%	0%
	Montipora patula - encrust	0%	17%	7%	50%	54%	28%	8%	38%	17%	7%	0%
	Montipora patula - plate	0%	0%	0%	11%	0%	0%	2%	0%	0%	0%	0%
	Montipora flabellata - encrust	1%	2%	0%	0%	0%	0%	0%	1%	0%	0%	0%
	Pocillopora meandrina	2%	2%	4%	0%	0%	6%	0%	2%	1%	2%	0%
	Pocillopora eydouxi	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
	Pavona varians	0%	0%	0%	0%	0%	0%	8%	0%	0%	0%	0%
	Pavona duerdeni	0%	0%	0%	0%	0%	3%	4%	0%	0%	0%	0%
	Leptastrea purpurea	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
	Cyphastrea ocellina	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
	Other	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
Coral	Encrusting	11%	31%	8%	51%	64%	33%	16%	46%	46%	8%	0%
morphology	Massive	0%	0%	0%	0%	0%	0%	0%	9%	0%	0%	0%
	Plate	0%	0%	0%	21%	0%	0%	4%	0%	0%	0%	0%
	Stoutly-branched	2%	2%	4%	0%	0%	6%	0%	2%	1%	2%	0%
	Finger-branched	0%	0%	0%	0%	0%	0%	0%	1%	0%	0%	0%
	Bladed	0%	0%	0%	0%	0%	3%	4%	0%	0%	0%	0%
	Other	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%

Defining physiographic zones

Line transect mapping of the reef surface at 51 sites over a range of depths and hydrodynamic conditions in Kailua Bay provides quantitative data on benthic community structure and reveals aspects of zonation in terms of the distribution and abundance of living organisms, growth forms, and life habits. Based on the multispectral image, quantitative transect data, and observations from large-scale reconnaissance tows and SCUBA dives in Kailua Bay, the reef platform can be divided into a series of 'physiographic zones,' each with a suite of physical and biogeological characteristics (e.g. living vs. dead substrate, form and abundance of corals, amount of encrustation by algae) (Figure 3-7). Table 3-2 presents a statistical summary of some basic characteristics of each zone derived from field observations. The minimum, maximum, mean, and median values of each parameter measured at transect mapping sites within each zone are provided. Budget calculations use median values of data collected within each zone.

The surface area (A_s) of each physiographic zone is measured using NIH image analysis software (available at http://rsb.info.nih.gov/nih-image) by tracing its boundaries on the multispectral image of the Kailua reef surface. Areal measurements in NIH have an average uncertainty of ±5%, owing to the 3 m-per-pixel resolution of the image and to the spatial limitations of the software. The areas of non-reef features within some zones (e.g. sand bodies, islands, and other superimposed zones) are also measured in image analysis and are subtracted from the zone area in which they occur. In this manner, only hard substrates are included in the surface area of each physiographic zone. Due to the rugose nature of the reef's surface, the planimetric area measured in two-dimensional

image analysis (A_s) is an underestimate of actual habitat area. This can be corrected by applying the rugosity factor for that portion of the reef (discussed later in this section).

Zone descriptions

It is noteworthy to mention that the zonation of the Kailua reef complex is not typical of 'classic' fringing reef environments commonly illustrated in profile (e.g. Boggs 1987). For example, back reef and reef crest zones present in most reef profiles are not clearly discernible in the Kailua complex. Analogous settings and the terminology used are described in detail here.

The northern portion of the reef platform is divided into seven physiographic zones: N1, N2, N3, N4, N5, NCG, and NH; similarly, the southern: S1, S2, S3, S4, SCG, and SH. Across the seaward portion of the reef platform (physiographic zones **N1** and **S1**), substrate relief (3–8 m) and percent living coral cover (40–75%) are generally high (Table 3-2, Figure 3–8). Broad topographic highs and steeply-sloping margins support areas of particularly diverse coral growth, where thickets of branching *Porites compressa* and stacks of foliose corals may dominate the reef substrate. The seaward reef platform and its sloping walls along the channel and reef front are characterized by a diverse array of coral species and growth forms. The median coral diversity index (Hc) is relatively high in both zones (0.88 in N1, 0.94 in S1). The sea floor in depressions and grooves of these regions is generally fossil limestone, bare or covered with a thin veneer of loose sediment. The fore-reef margin (also called the reef front) is defined as the seaward edge of the reef platform, approximately contiguous with the 20-m bathymetric contour running north and south of the channel mouth. Along the margin, the coral-covered

platform slopes seaward to a fossil limestone terrace at ~30 m depth (consisting of rubble, limestone hardgrounds, and loose sediment). The zones **NCG** and **SCG** within N1 and S1 are regions of particularly luxuriant coral growth, where living corals cover 75–100% of the bottom and species diversity is the highest encountered in Kailua (medians 1.06 and 1.19, respectively).

The central portion of the northern reef platform (zones **N2** and **S2**) lies in 5–8 m water depth and is characterized by limestone substrate that has apparently undergone extensive karstification, evidenced by underwater caves, sand-filled reef holes, and overhanging ledges. Fossil spurs and topographic highs are 1–3 m above the sea floor, and nearly all substrates are heavily encrusted with living coralline algae. Coral cover reaches 15% in some places (typically encrusting *Porites lobata* and *Montipora* sp. and stoutly-branching *Pocillopora meandrina*); diversity is generally low (~0.3). Large sand bodies and partially-buried outcrops of scoured limestone are common in these 'karstified' regions.

Bottom characteristics of the narrow band of zone **S3**, also in the central portion of the southern reef platform, differ from those flanking it in that the percent cover of living coral is between 25–40% and large-scale spur-and-groove morphologies are more common. Substrate relief is generally 2–4 m. The sea floor of depressions and grooves may be bare fossil limestone or loose calcareous sediment. S3 represents a zone of transition between S2 and S1 and has a median species diversity index of 0.59. Zone **N3** bears characteristics similar to S3, although it lies along the channel margin rather than situated as a transition between landward and seaward zones. The region is characterized by 25–40% coral cover, moderate diversity (0.73), spur-and-groove relief on the order of

2–4 m, and fossil surfaces that are heavily encrusted with coralline algae. Zone **N4** also lies along the channel margin but is characterized by a lower percentage of living coral (15–35%) and lower species diversity (0.58). Encrusting coralline algae is abundant in this region (covering 74% of the sea floor). Spur-and-groove reef topography is on the order of 2–4 m.

Zone **S4** lies along the south-central reef-front where a fossil carbonate platform ramps seaward to meet the offshore sand field. Living coral cover is generally 15–25%, diversity is moderate (0.64), and the benthic community is dominated by encrusting forms of coral and algae. Zone **N5** lies on the northern, central-seaward portion of the reef platform outside the multispectral image. Living coral covers 25–40% of the substrate, diversity is 0.81, and corals and algae are primarily of encrusting morphology.

Limestone hardgrounds of zones **NH** and **SH** are characterized by low-relief outcrops of fossil limestone encrusted by living coralline algae or covered with a thin veneer of sediment. Living coral is entirely absent. Meadows of *Halimeda discoidea* and *H. opuntia* are common, as are clumps of highly-ramified coralline algae (*Porolithon gardineri*). These hardgrounds are geographically analogous to a classic 'back reef' setting but are not as well-protected (a reef crest is absent in the seaward direction), thus substrates are generally scoured and lack coral growth.

Zone **FRS** is a region of scoured fossil reef that is partially to completely buried by unconsolidated sediment of various thickness. Coralline algae and *Halimeda* are present in some regions, whereas coral is absent.

Table 3-2. Characteristics of physiographic zones in Kailua Bay.

ZONE	Description	Surface area ($x10^3$ m^2)	Habitat area ($x10^3$ m^2)	Transect mapping sites in zone
N1	seaward portion and fore-reef of platform 40–75% coral cover	1244.19	1493.03	NP3, JE2, F5, NP1, RS1, RS2, BR
N2	landward, karstified portion of reef platform <15% coral cover	587.72	764.03	NP4, NP5, F7, EM5, NP10
N2*	northern portion of N2 adjacent to Mokapu (less karstified) <15% coral cover	546.72	546.72	NP8
N3	channel margin along central portion of platform 25–40% coral cover	132.61	159.13	F6, EB1, EB2, F3, OM
N4	margin of seaward platform (shallower, higher energy) 15–25% coral cover	59.60	71.52	F4, KC
N5	northern, central-seaward portion of platform outside image 25–40% coral cover	797.78	797.78	NP9, NP7
NCG	coral gardens of seaward platform and slope >75% coral cover	85.60	102.72	NP2, JE1ab
NH	nearshore hardgrounds 0% coral cover	608.94	608.94	NP6
S1	seaward portion, central margin, and fore-reef 40–75% coral cover	913.88	1096.66	F1–2, SP7, EM2, EM3, SP1, SP2, SP4, SP5, LR2, KA, LA
S2	landward, karstified portion of reef platform <15% coral cover	698.01	1116.81	SC, BS, SP3
S3	central, somewhat-karstified portion of reef platform 25–40% coral cover	345.73	518.60	EM4, T47
S4	southern, central-seaward portion of platform 25–40% coral cover	125.49	138.04	SP6, (BMW)
SCG	coral gardens of seaward channel mouth and slope >75% coral cover	87.51	113.76	NT, EM1, LR1
SH	nearshore hardgrounds 0% coral cover	838.49	838.49	none
FRS	fossil reef outcrops with sand veneer 0% coral cover	350.30	3.99	F8

(Continued)

Table 3-2 (Continued). Characteristics of physiographic zones in Kailua Bay.

ZONE	DEPTH				RUGOSITY				DIVERSITY INDEX (Hc)			
	min	max	mean	median	min	max	mean	median	min	max	mean	median
N1	6.5	16.0	11.5	12.0	1.0	1.5	1.2	1.2	0.79	1.10	0.93	0.88
N2	2.5	6.0	4.7	5.0	1.0	1.5	1.3	1.3	0.11	0.36	0.26	0.31
N2*	7.6	7.6	7.6	7.6	1.0	1.0	1.0	1.0	0.42	0.42	0.42	0.42
N3	6.0	10.7	8.2	8.0	1.1	1.5	1.2	1.2	0.52	0.80	0.71	0.73
N4	10.5	11.0	10.8	10.8	1.2	1.2	1.2	1.2	0.53	0.63	0.58	0.58
N5	6.0	15.0	10.5	10.5	1.0	1.0	1.0	1.0	0.81	0.82	0.81	0.81
NCG	12.2	13.0	12.6	12.5	1.2	1.2	1.2	1.2	1.04	1.28	1.12	1.06
NH	3.0	3.0	3.0	3.0	1.0	1.0	1.0	1.0	0.00	0.00	0.00	0.00
S1	8.0	13.5	10.1	10.0	1.1	1.6	1.3	1.2	0.59	1.16	0.86	0.94
S2	3.0	5.0	4.0	4.0	1.2	2.0	1.6	1.6	0.11	0.32	0.24	0.30
S3	5.0	6.4	5.7	5.7	1.3	1.7	1.5	1.5	0.45	0.73	0.59	0.59
S4	13.0	13.0	13.0	13.0	1.1	1.1	1.1	1.1	0.64	0.64	0.64	0.64
SCG	12.0	13.7	13.1	13.3	1.2	1.5	1.3	1.3	0.98	1.21	1.14	1.19
SH	3.0	3.0	3.0	3.0	1.0	1.0	1.0	1.0	0.00	0.00	0.00	0.00
FRS	3.0	3.0	3.0	3.0	1.0	1.0	1.0	1.0	0.00	0.00	0.00	0.00

(Continued)

Table 3-2 (Continued). Characteristics of physiographic zones in Kailua Bay.

ZONE	LIVING CORAL COVER				CORALLINE ALGAE COVER				ENCRUSTING CORAL			
	min	max	mean	median	min	max	mean	median	min	max	mean	median
N1	0.40	0.73	0.55	0.53	0.11	0.53	0.29	0.21	0.19	0.55	0.39	0.42
N2	0.03	0.12	0.08	0.09	0.15	0.91	0.73	0.86	0.01	0.08	0.06	0.06
N2*	0.12	0.12	0.12	0.12	0.05	0.05	0.05	0.05	0.11	0.11	0.11	0.11
N3	0.38	0.47	0.42	0.42	0.26	0.57	0.40	0.33	0.33	0.46	0.38	0.37
N4	0.16	0.24	0.20	0.20	0.72	0.76	0.74	0.74	0.09	0.16	0.12	0.12
N5	0.34	0.35	0.34	0.34	0.01	0.10	0.05	0.05	0.28	0.31	0.30	0.30
NCG	0.74	0.82	0.78	0.78	0.02	0.11	0.06	0.04	0.60	0.63	0.61	0.61
NH	0.00	0.00	0.00	0.00	0.94	0.94	0.94	0.94	0.00	0.00	0.00	0.00
S1	0.44	0.74	0.62	0.62	0.07	0.54	0.27	0.26	0.42	0.70	0.53	0.52
S2	0.03	0.10	0.07	0.08	0.49	0.53	0.78	0.88	0.00	0.10	0.06	0.08
S3	0.34	0.36	0.35	0.35	0.27	0.64	0.46	0.46	0.31	0.34	0.33	0.33
S4	0.25	0.25	0.25	0.25	0.75	0.75	0.75	0.75	0.23	0.23	0.23	0.23
SCG	0.70	0.85	0.76	0.75	0.08	0.29	0.20	0.21	0.31	0.57	0.43	0.42
SH	0.00	0.00	0.00	0.00	0.94	0.94	0.94	0.94	0.00	0.00	0.00	0.00
FRS	0.00	0.00	0.00	0.00	0.73	0.73	0.73	0.73	0.00	0.00	0.00	0.00

(Continued)

Table 3-2 (Continued). Characteristics of physiographic zones in Kailua Bay.

ZONE	MASSIVE CORAL				STOUT-BRANCHING CORAL				FINGER-BRANCHING CORAL			
	min	max	mean	median	min	max	mean	median	min	max	mean	median
N1	0.05	0.16	0.10	0.09	0.00	0.03	0.01	0.00	0.00	0.10	0.02	0.00
N2	0.00	0.00	0.00	0.00	0.00	0.06	0.03	0.02	0.00	0.00	0.00	0.00
N2*	0.00	0.00	0.00	0.00	0.02	0.02	0.02	0.02	0.00	0.00	0.00	0.00
N3	0.00	0.03	0.01	0.00	0.00	0.06	0.02	0.01	0.00	0.00	0.00	0.00
N4	0.00	0.00	0.00	0.00	0.00	0.02	0.01	0.01	0.00	0.04	0.02	0.02
N5	0.00	0.00	0.00	0.00	0.00	0.02	0.01	0.01	0.00	0.00	0.00	0.00
NCG	0.13	0.17	0.15	0.14	0.00	0.01	0.00	0.00	0.00	0.04	0.01	0.00
NH	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
S1	0.00	0.17	0.05	0.04	0.00	0.08	0.02	0.01	0.00	0.03	0.01	0.00
S2	0.00	0.00	0.00	0.00	0.00	0.03	0.01	0.00	0.00	0.00	0.00	0.00
S3	0.00	0.00	0.00	0.00	0.00	0.03	0.01	0.01	0.00	0.00	0.00	0.00
S4	0.02	0.02	0.02	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
SCG	0.15	0.27	0.22	0.22	0.00	0.03	0.01	0.01	0.00	0.12	0.06	0.06
SH	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
FRS	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

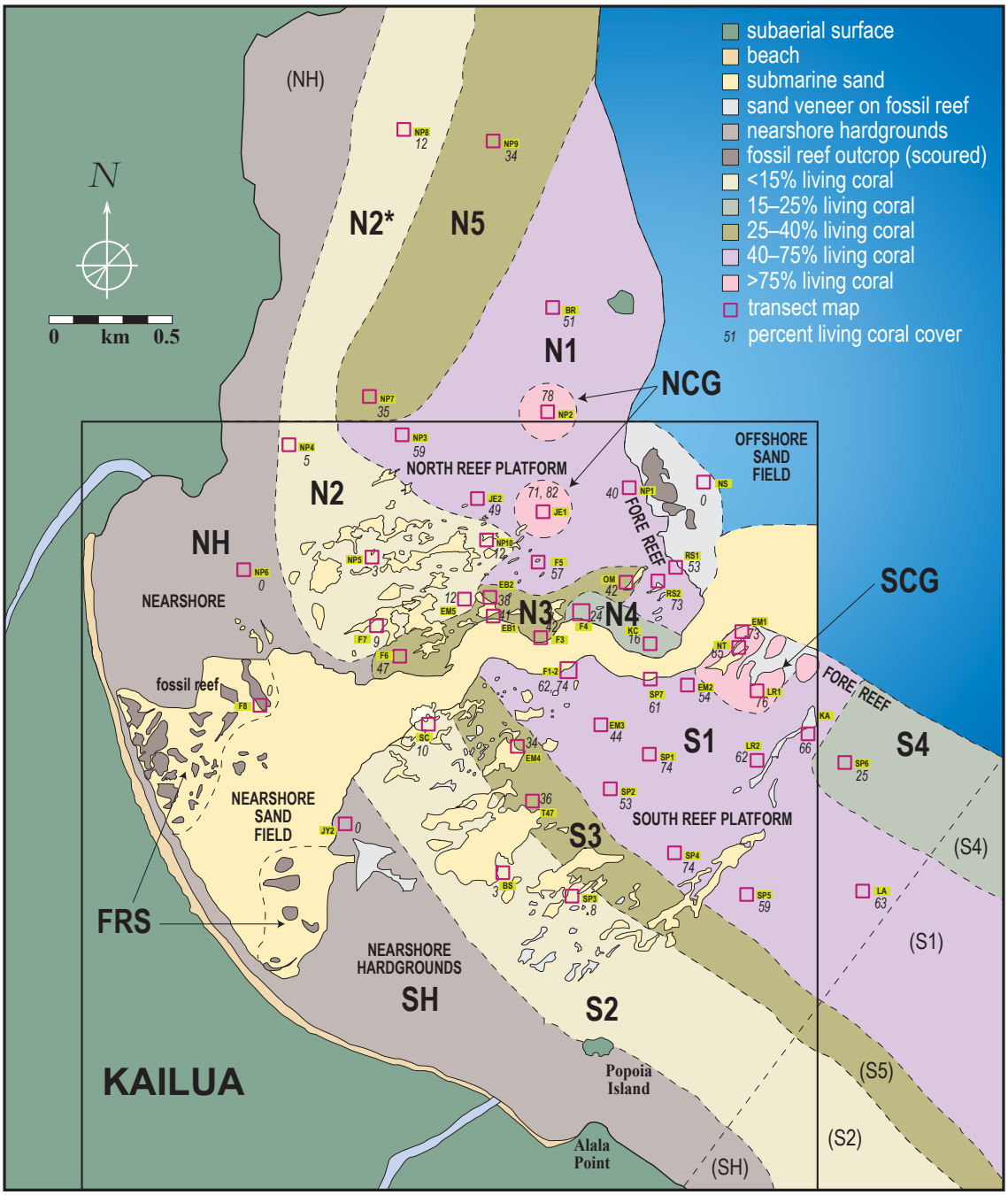


Figure 3-8. Physiographic zones and their respective living coral coverage in Kailua Bay. Zone boundaries and characteristics were determined from benthic substrate data collected during underwater transect mapping. Box illustrates region of multispectral data coverage.

Part II: Modeling Sediment Production

Gross Framework Production

Hawaii's coral reef fauna has been described as 'highly depauperate' compared to the diversity and abundance of Indo-West Pacific reefs (Grigg 1983). Owing to the islands' geographic isolation, only 42 species of 16 genera construct reefs in Hawaiian waters, compared to more than 500 species in the Indo-West Pacific. The structure and development of modern reef communities in Hawaii is a primarily a function of wave exposure, frequent disturbance, and sea-level history (Dollar 1982, Grigg 1983, Grigg 1995, 1998, Grossman and Fletcher 1999). Because conditions for coral growth and reef accretion in Hawaii are unique, this model employs rates of coral growth and carbonate production collected on Hawaiian reefs. References are made to Australian and Caribbean data for comparison and discussion.

Several carbonate production rates for framework-building corals and coralline algae in Hawaii are available. Using drilled reef cores, vertical Holocene fore-reef accretion in Hanauma Bay on southeast Oahu was estimated to be 8 mmy^{-1} (rates of lateral accretion are even greater, up to 22 mmy^{-1}; Easton and Olson 1976). Rates of growth or accretion in mmy^{-1} can be converted to rates of $CaCO_3$ production per unit area by using a density of 1.4 gcm^{-3} (2.9 gcm^{-3} for $CaCO_3$, assuming 50% porosity; after Smith and Kinsey 1976, Grigg 1982). The rate of *net* carbonate production in Hanauma Bay is thus ~11 $kgm^{-2}y^{-1}$ (using rate of upward accretion only). However, reef growth in this protected embayment is not considered representative of conditions generally found in Hawaii and is rather a

maximum rate of potential accretion possible in wave-sheltered environments (Grigg 1998, Grossman and Fletcher 1999).

More representative are direct growth rate measurements of corals in Hawaii determined by sclerochronology and densitometry (cf. Buddemeier et al. 1974). Grigg (1995, 1998) reports growth rates of massive *Porites lobata*, branching *Porites compressa*, and stoutly-branching *Pocillopora meandrina* corals growing in 2–12 m water depths around Oahu determined in sclerochronologic analyses (Table 3-3). Branching *Porites compressa* corals from Kaneohe and Hanauma Bays have linear extension rates averaging 7.66 and 8.13 mmy^{-1}, respectively. Growth rates for massive *Porites lobata* (the most common reef-building coral in Hawaii) in Mamala Bay average 10.1 mmy^{-1}. Colonies of the stoutly-branching 'pioneer' species *Pocillopora meandrina* collected offshore of Sunset Beach have an average annual growth rate of 8.08 mmy^{-1}. These growth rates correspond to gross $CaCO_3$ production rates of 10–14 $kgm^{-2}y^{-1}$.

To assess coral growth in Kailua Bay, digital photos of drilled reef cores from the study area were subjected to image analysis to measure the thickness of annual bands in modern coral skeletons (Figure 3-9). Annual bands measured in five *Porites lobata* colonies at the top of cut core sections averaged 6 mm thickness, corresponding to a gross production rate of 8.4 $kgm^{-2}y^{-1}$ (Table 3-4). Encrusting corals (*Montipora* sp. and *Porites lobata*) had annual layer thicknesses of 2 mm (2.8 $kgm^{-2}y^{-1}$). These observations are consistent with those published for Hawaiian corals, but sclerochronologic analyses should be performed on the samples to confirm these observations. The growth rates of *Porites compressa* and *Pocillopora meandrina* in Kailua Bay were not measured. For *P. compressa*, Grigg's (1995, 1998) rate of 8 mmy^{-1} (11.2 $kgm^{-2}y^{-1}$) is applied, assuming

this coral's growth in moderate water depths in Kailua provides 'protected' conditions and allows for growth rates typical of shallower, wave-protected settings found in Kaneohe and Hanauma Bays. For *P. meandrina*, a conservative rate of 6.7 $kgm^{-2}y^{-1}$ is applied (Eakin 1996).

Coralline (red) algae are important inhabitants of reefs in Hawaii. *In situ* measurements of the crustose coralline alga *Porolithon onkodes* growing in waters around Oahu correspond to carbonate production rates of 2.1 $kgm^{-2}y^{-1}$ (Agegian 1985) and 3.6 $kgm^{-2}y^{-1}$ (Soegiarto 1972). Such encrusting forms occupy a wide range of depths (subtidal to –100 m) and colonize a variety of substrates from fossil limestone and dead coral to shells, rubble, and sand grains. The benthic topography, depth variability, and vigorous circulation in Kailua Bay provide ideal habitats for the ubiquitous coralline algae. Lithology of reef cores from Kailua Bay reflects the abundance of coralline algae as a component of the reef edifice. We apply Agegian's (1985) growth rates for all species of encrusting coralline algae in our reef budget (2.1 $kgm^{-2}y^{-1}$). Clumps of the articulated coralline algae *Porolithon gardineri* are not considered framework-building and are thus discussed in a later section on 'direct' sediment production.

Gross production variables and equations

A summary of the data used in gross framework production calculations appears in Table 3-5. The variables A_s (surface area) and R (rugosity) have been previously discussed. Percent living coral cover (C_c) is determined from analysis of the quantitative mapping data and is specific to each zone. Subscripts denote the coral morphology: encrusting (C_e), massive (C_m), or branching (C_{sb} for stoutly-branching *P. meandrina*, C_{fb}

for finger-branching *P. compressa*). All data used in calculations are median values of transect parameters. For example, the median percent coral cover in zone N1 is 53% (C_c), of which 42% is encrusting (C_e) and 9% is massive (C_m) (Table 3-2).

Table 3-6 summarizes the equations employed in calculating gross production. Each parameter is calculated *by zone* using data unique to that zone. Habitat area (A_h) in each zone is calculated by multiplying the zones' planimetric surface area (measured in image analysis) by its mean rugosity (based on mapping data):

$$A_h = A_s \times R \qquad \text{(Eq. 7).}$$

Gross production by each coral growth form (G_e, G_m, G_{sb}, G_{fb}) *in each zone* is calculated by multiplying its percent cover (C) by the zone's habitat area (A_h) and by each form's rate of calcification (GPR_e, GPR_m, GPR_{sb}, GPR_{fb}). For example, gross production by encrusting corals (G_e in kgy^{-1}) is:

$$G_e = C_e \times A_h \times GPR_e \qquad \text{(Eq. 8).}$$

Gross production by all forms of coral within a single zone is the following sum:

$$G_c = G_e + G_m + G_{sb} + G_{fb} \qquad \text{(Eq. 9).}$$

Total gross production by corals over the entire reef platform is the sum of G_c for all zones:

$$G_{Tc} = \Sigma\, G_{c(\text{all } z)} \qquad \text{(Eq. 10).}$$

Gross production by encrusting coralline algae (G_{ace}) in each zone is similarly calculated by multiplying its percent cover (C_{ace}) by the zone's habitat area (A_h) and by its rate of calcification (GPR_{ace}):

$$G_{ace} = C_{ace} \times A_h \times GPR_{ace} \qquad \text{(Eq. 11).}$$

Table 3-3. Production and accretion rates for various corals, coralline algae, and reef settings.

Approach	Location	Site	Organism / Setting		Growth (mmy^{1})	Gross production (kg $CaCO_3$ m^2y^{-1})[a]	Accretion (mmy^{1})	Reference
Growth rate	Hawaii	Mamala Bay	Coral	*Porites lobata*	10.1	14.1	1.0	Grigg 1998
		Kaneohe Bay		*Porites compressa*	7.66	10.7	5.27	Grigg 1998
		Hanauma Bay		*Porites compressa*	8.13	11.4	5.93	Grigg 1998
		Mamala Bay		*Porites lobata*	7–10	10–14		Grigg 1995
		Mamala Bay		*Porites lobata*	13	18		Grigg 1982
		Sunset Beach		*Pocillopora meandrina*	8.08	11.3		Grigg 1998
	Hawaii	Oahu	Cor. algae	*Porolithon gardineri* (artic.)		20		Agegian 1985
				Porolithon onkodes (encrust.)		2.6		Agegian 1985
				Porolithon onkodes (encrust.)		3.6		Soegiarto 1972
	E. Pacific	Uva Island	Coral	*Pocillopora meandrina*		6.7		Glynn 1977
	Barbados	Bellairs Reef	Cor. algae	*Porolithon* sp. (encrust.)		2.4		Stearn and Scoffin 1977
Whole reef	Hawaii	Hanauma Bay		fringing reef in sheltered bay			8[c]	Easton & Olson
		Kaneohe Bay		coral-algal reef		2.6		Webb 1979
		Kaneohe Bay		barrier reef		3		Smith et al. 1970
		Kona		growth on historic lava flow		1.4		Oostdam 1963
	Enewetak			atoll		1–2		Smith and Harrison 1977
	Pacific			reef flat		3–5		Kinsey 1979
	Pacific			sand-rubble zones		0.5		Kinsey 1979
	Jamaica	Discovery Bay		fringing reef *net* production		1.1[b]		Land 1974, 1979
Model				"Potential"		25		Chave et al. 1972
				"Gross		7–10		
				"Net"		2		

[a] Converted from growth rate in mmy $^{-1}$ using a density of 1.4 gcm $^{-3}$ (after Grigg 1982).

[b] Net reef production from budget.

[c] Holocene reef accretion

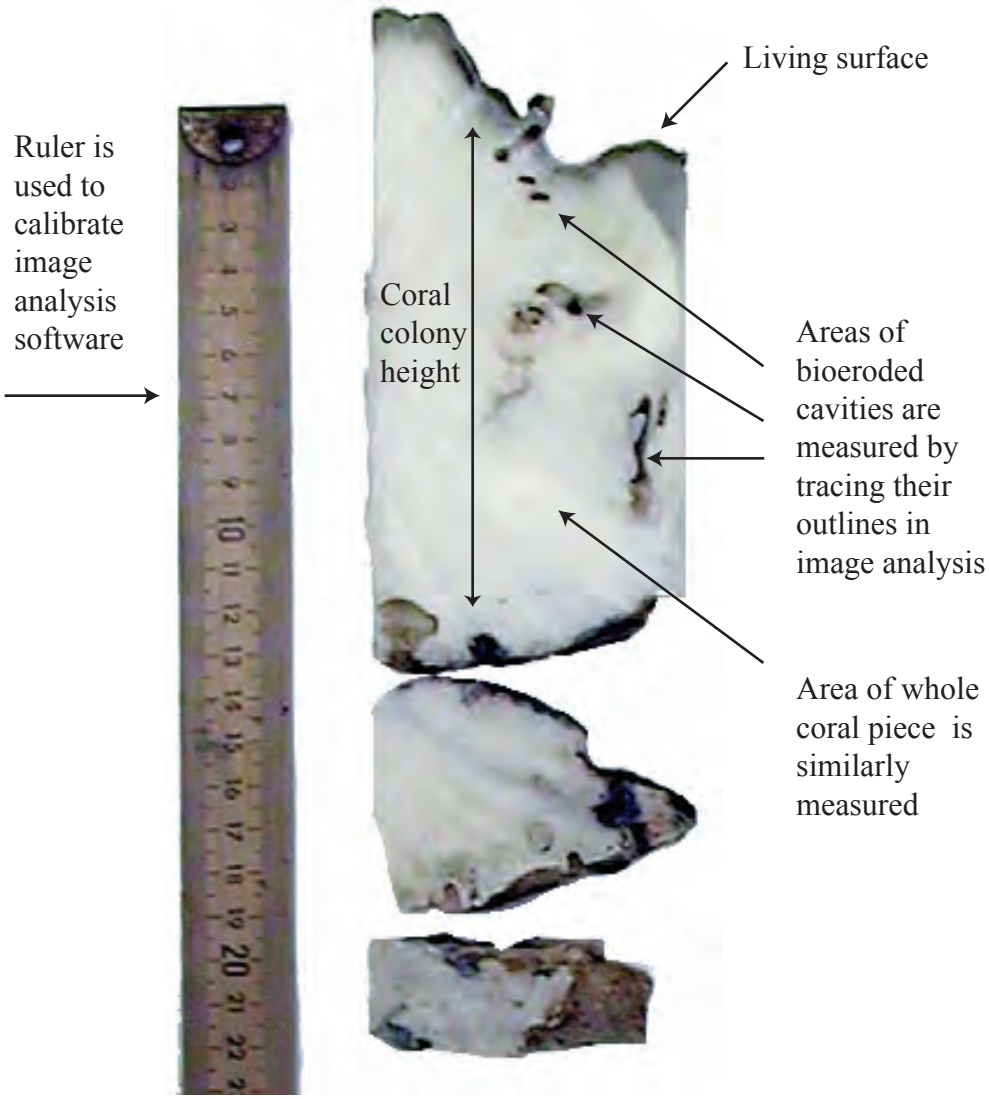


Figure 3-9. Analysis of drilled reef cores to determine rates of growth and bioerosion using image analysis. Sample shown is NM62–D1P1.

Table 3-4. Estimates of coral growth and bioerosion rates in Kailua Bay determined by analysis of drilled reef cores.

Site	Zone	Core ID	Core section[a]	Coral sp.[b]	Coral area (cm^2)	Bioeroded area (cm^2)	% Coral bioeroded [c]	Growth[d] rate (cmy^{-1})	GPR[e] ($kgm^{-2}y^{-1}$)	Bioerosion[f] rate ($kgm^{-2}y^{-1}$)
LH	N1	LH32	all	P. lob.	508.7	6.1	1%	**0.6**	8.4	0.1
		LH32	D1 P1	P. lob.	118.1	0.6	1%	**0.6**	8.4	0.0
		LH32	D2 P1	P. lob.	258.5	4.5	2%	**0.6**	8.4	0.1
		LH32	D2 P2	P. lob.	132.1	1.1	1%	**0.6**	8.4	0.1
NM	N1	NM62	D1 P1	P. lob.	95.1	4.6	5%	0.6	8.4	0.4
		NM62	D1 P2	P. lob.	25.5	0.9	4%	0.6	8.4	0.3
		NM65	D1 P1	P. lob.	38.2	4.6	12%	0.6	8.4	1.0
		NM65	D1 P2	P. lob.	20.1	1.2	6%	0.6	8.4	0.5
KC	N4	KC32	D1 P1	P. com.	76.0	7.8	10%	**0.6**	8.4	0.9
SMC	S1	SMC	D3 P1	P. lob.	210.6	8.7	4%	**0.6**	8.4	0.3
MM	S3	MM20	D1 P1	P. lob.	17.9	0.2	1%	0.6	8.4	0.1
		MM20	D1 P3	P. lob.	72.6	1.1	1%	0.6	8.4	0.1
		MM20	D2 P1	P. lob.	25.5	0.7	3%	0.6	8.4	0.2
		MM20	D2 P2	P. lob.	85.7	4.6	5%	0.6	8.4	0.5

[a] Section of core (Drive and Piece) examined in image analysis (see text).

[b] Coral species analyzed are *Porites lobata* (P. lob.) and *Porites compressa* (P. com.).

[c] Area bioeroded ÷ Area of specimen.

[d] Growth rates in **bold** are measured thickness of upper living surface and underlying annual bands. Others are inferred.

[e] Gross Production Rate, calculated from growth rate using a density of 1.4 gcm^{-3} (see text).

[f] Bioerosion rate is the % coral bioeroded × GPR. These rates are applied in the gross production model.

Table 3-5. Data variables used in gross production model.

Variable	Description	Units
A_s	area surface	m^2
R	rugosity	none
C_c	percent coverage of living coral	decimal %
C_e	percent coverage of encrusting coral	decimal %
C_m	percent coverage of massive coral	decimal %
C_{sb}	percent coverage of stout-branching coral	decimal %
C_{fb}	percent coverage of finger-branching coral	decimal %
C_{ace}	percent coverage of encrusting coralline algae	decimal %
GPR_e	gross production rate of encrusting coral	$kgm^{-2}y^{-1}$
GPR_m	gross production rate of massive coral	$kgm^{-2}y^{-1}$
GPR_{sb}	gross production rate of stout-branching coral	$kgm^{-2}y^{-1}$
GPR_{fb}	gross production rate of finger-branching coral	$kgm^{-2}y^{-1}$
GPR_{ace}	gross production rate of encrusting coralline algae	$kgm^{-2}y^{-1}$
B_K	Kailua modern coral model of bioerosion	$kgm^{-2}y^{-1}$
B_H	Hubbard model of bioerosion	decimal %
B_S	Spencer model of subtidal limestone erosion	$kgm^{-2}y^{-1}$
t	time (5000 y)	y
d	approximate bulk sediment density (1176±80)	kgm^{-3}

Table 3-6. Variables and equations employed in calculating gross and direct production.

GROSS PRODUCTION

Variable	Description	Units	Equation	Eq. #
A_h	habitat area	m^2	$A_h = A_s \times R$	7
G_e	gross production by encrusting coral	kgy^{-1}	$G_e = C_e \times A_h \times GPR_e$	8
G_m	gross production by massive coral	kgy^{-1}	$G_m = C_m \times A_h \times GPR_m$	8
G_{sb}	gross production by stout-branching coral	kgy^{-1}	$G_{sb} = C_{sb} \times A_h \times GPR_{sb}$	8
G_{fb}	gross production by finger-branching coral	kgy^{-1}	$G_{fb} = C_{fb} \times A_h \times GPR_{fb}$	8
G_c	gross production by all coral growth forms	kgy^{-1}	$G_c = G_e + G_m + G_{sb} + G_{fb}$	9
G_{Tc}	total gross production by coral (whole-reef)	kgy^{-1}	$G_{Tc} = \Sigma\ G_{c(all\ z)}$	10
G_{ace}	gross production by encrusting coralline algae	kgy^{-1}	$G_{ace} = C_{ace} \times A_h \times GPR_{ace}$	11
G_{Tace}	total gross production by coralline algae (whole-reef)	kgy^{-1}	$G_{Tace} = \Sigma\ G_{ace(all\ z)}$	12
G_F	gross framework production (corals and encrust. cor. algae)	kgy^{-1}	$G_F = G_c + G_{ace}$	13
G_{TF}	total gross framework production (whole-reef)	kgy^{-1}	$G_{TF} = G_{Tc} + G_{Tace}$	14

DIRECT PRODUCTION

Variable	Description	Units	Equation	Eq. #
SC_H	standing crop of *Halimeda*	kgm^{-2}	see text	15–16
CPP	carbonate production potential	kgm^{-2}	biomass x carbonate content	17
SPR	sediment production rate	$kgm^{-2}y^{-1}$	$CPR \times T$	18
ASP	annual sediment production	kgy^{-1}	$SPR \times Area \times Cover$	19
$SC_{f,m}$	standing crop of forams, micromolluscs	kgm^{-2}	weight shells ÷ area sampled	20
SC_{apg}	standing crop of articulated coralline algae	kgm^{-2}	weight shells ÷ area sampled	21
T	turnover rate	y^{-1}	see text	–

Total gross production by encrusting coralline algae over the entire reef platform is the sum of G_{ace} for all zones:

$$G_{Tace} = \Sigma\ G_{ace(all\ z)} \qquad \text{(Eq. 12).}$$

Gross framework production by corals and encrusting coralline algae is thus expressed for each zone:

$$G_F = G_c + G_{ace} \qquad \text{(Eq. 13).}$$

Total gross framework production by corals and encrusting coralline algae over the entire reef platform in Kailua Bay is the sum of G_F for all zones, or:

$$G_{TF} = G_{Tc} + G_{Tace} \qquad \text{(Eq. 14).}$$

Erosion of the reef edifice is a primary source of unconsolidated sediment in Kailua Bay (Harney et al. 2000), as well as in most other reef settings (Hubbard et al. 1990, Stearn and Scoffin 1977). The rates and processes of biological, chemical, and mechanical erosion operating to break down the carbonate edifice into unconsolidated sediment must be investigated to determine framework-derived sediment production.

Reef Bioerosion

Previous studies of bioerosion

The various activities of reef-dwelling organisms that cause the destruction of coral and algal substrates are collectively known as 'bioerosion,' a term originally used by Neumann (1966). Bioerosion is one of the most important agents of alteration and destruction in reefal habitats. Carbonate borers (cyanobacteria, fungi, algae, sponges, polychaete and sipunculan worms, bivalve molluscs, barnacles, and decapods) and

grazers (fish, echinoderms, and gastropods) play a significant role in the ecology and preservation of modern and fossil reefs (Neumann 1966, Warme 1976, Hutchings 1986, Glynn 1997, Perry 1998a, 1998b, 1999). Reef budgets have demonstrated that over half the annual production of reef-associated carbonate framework material can be reduced to sediment by contemporaneous bioerosion (Land 1979, Hubbard et al. 1990, Hubbard 1992). In some cases, the rate of bioerosion may exceed the rate of reef construction, resulting in a net budget 'deficit' (e.g. Stearn and Scoffin 1977, Scoffin et al. 1980).

Quantifying bioerosion in a carbonate sediment budget may be accomplished in several ways. The distribution, abundance, individual habits, and process rates of bioeroding organisms in various physiographic zones over the reef can be assessed and their cumulative impact on the reef calculated. This approach may utilize estimates of the amount of sediment produced by grazing and boring organisms (such as fish, polychaete worms, molluscs, echinoderms, and sponges) that are available for reefal and lagoonal habitats around the globe (Table 3-7).

Although these rates are useful in identifying the most important organisms and processes operating in an environment, the task of mapping the distribution and abundance of every borer and grazer on and in a reef's various habitats is not only 'herculean' (Hubbard et al. 1990) but is fraught with limitations and uncertainties:

1. Published rates for the same organism can differ significantly. For example, Neumann (1966) estimated clionid sponges are capable of excavating 1.0–1.4 cm^3 of reef limestone each year, corresponding to a bioerosion rate of 20–25 $kgm^{-2}y^{-1}$. In contrast, both Moore and Shedd (1977) and Scoffin et al. (1980) found clionids reduce reef to sediment at rates an order of magnitude lower.

2. Bioeroders are most often cryptic organisms that are difficult to see or count on the reef surface. Bivalve molluscs (e.g. *Lithophaga* and *Gastrochaena*) burrow into massive coral skeletons at rates of 8.4–9.1 mmy^{-1} (Trudgill 1983), but it is difficult to apply these rates to a population of cryptic bivalves living on the reef at any given time.
3. Bioeroding organisms, processes, and rates vary significantly in different settings (e.g. lagoon vs. fore-reef), therefore individual observations cannot be applied to an entire reef system.
4. Underestimating bioerosion is easily done, owing to a host of other reef-dwelling organisms which graze, browse, and scrape the reef surface (e.g. puffer, surgeon, and butterfly fish, chitons, littorinids), removing carbonate material in a less obvious fashion that is exceedingly difficult to measure.
5. Overestimating bioerosion is also easily done, owing to the activities of many fish and echinoderms that ingest unconsolidated sediment as well as attack solid reef substrate. A significant portion of the excreta of these organisms may thus be reworked sediment and not entirely representative of bioerosional processes.

Secondly, bioerosion can be estimated as a proportion of the gross carbonate production that is reduced to unconsolidated sediment over some time period. This can be done using drilled cores or limestone samples collected from the reef. Based on reef cores, Hubbard et al. (1990) determined 54% of gross carbonate production in Cane Bay is reduced to unconsolidated sediment each year by bioerosion alone. The unconsolidated sediments generated are either retained in the reef edifice (56%) or released into channels

(44%). By these calculations, 24% of gross annual carbonate production is converted to loose sediment and released from the reef.

Using slabbed sections of 54 samples of dead coral and rubble, Perry (1998b) determined the percent of each sample affected by boring activities and the relative abundance of the macro-endolithic borers responsible. Average surface areas bored were greater on patch reefs (16.0%) and on the fore-reef (16.7–25.3%, 12–30 m) than in the lagoon (13.2%) or on the reef crest (8.6%). Clionid sponges accounted for 55–98% if all boring; polychaete and sipunculan worms were also very important (up to 43% relative abundance); bivalves, barnacles, and decapods were of minor importance. Perry also recognized a trend in coral species susceptibility to bioeroder infestation.

In a third method, integrated mechanical, biological, and chemical erosion can be assessed using various techniques (e.g. micro-erosion metering or MEM) to measure substrate 'surface lowering' (see review by Sunamura 1992). Surface lowering of reef limestone substrates in intertidal (1.5–2.7 mmy^{-1}, Viles and Trudgill 1984; 0.88–1.12 mmy^{-1}, Spencer 1985; 1–1.6 mmy^{-1}, van de Plaasche 1986) and subtidal (0.63–1.26 mmy^{-1}, Kiene 1985; 1.12–1.79 mmy^{-1}, Spencer 1985) settings are generally consistent and offer an interesting approach to quantifying the integrated and complex processes of reef erosion (Table 3-7). Limitations to this technique lie in its observance of only surface erosion, failing to quantify bioerosion occurring within the reef edifice. These examples demonstrate that care must thus be taken to assess the organisms and processes responsible for bioerosion in different settings within a single reef system.

Table 3-7. Rates of bioerosion by organisms and in various reef settings.

ORGANISM	Location	Erosion rate ($kgm^{-2}y^{-1}$)	Reference	Comment
Cyanobacteria	Davies Reef, GBR	0.35	Tudhope and Risk 1985	2–6 μm particles
Clionid sponges	Barbados	1.12 – 1.80	Scoffin et al. 1980	x-ray of coral head
	Bermuda	20.0 – 25.0	Neumann 1966	transplanted block
	St. Croix	0.21 – 3.50	Moore and Shedd 1977	thin sections
Polychaetes, sabellariids, sipunculans	Lizard Isl., GBR	0.10 – 0.93	Kiene 1985	coral blocks
	Lizard Isl., GBR	0.69 – 1.79	Davies and Hutchings 1983	coral blocks
	Lizard Isl., GBR	0.33 – 13.23	Hutchings and Bamber 1985	coral blocks
Barnacles	Aldabra Atoll	(0.8 cm^3y^{-1} per indiv.)	Trudgill 1976	
	Barbados	0.14	Scoffin et al. 1980	
Bivalve molluscs	Aldabra Atoll	(8.4–9.1 mmy^{-1})	Trudgill 1976	burrowing rate
	Costa Rica	9.0	Scott et al. 1988	1870 bivalves / m^2
	Florida	0.18	Hein and Risk 1975	
	Lizard Isl., GBR	0.01 – 0.15	Kiene 1985	
Echinoderms	Barbados	9.0	Stearn and Scoffin 1977	7.4 gd^{-1} per indiv.
	Barbados	5.0 – 5.6	Scoffin et al. 1980	*Diadema antillarum*
	Moorea, Fr. Polynes.	0.46	Le Campion et al. 1993	1.26 $gm^{-2}d^{-1}$
	St. Croix, Virgin Isl.	3.90 – 4.6	Ogden 1977	0.5 kgy^{-1} per indiv.
Parrot fish	Barbados	0.036	Stearn and Scoffin 1977	
	St. Croix, Virgin Isl.	0.49	Ogden 1977	
	Bermuda	0.017 – 0.21	Gygi 1975	
SETTING	**Location**	**Erosion rate (mmy^{-1})**	**Reference**	**Comment**
Intertidal	Aldabra Atoll	0.6 – 4.0	Trudgill 1976	MEM
	(Indian Ocean)	1.5 – 2.7	Viles and Trudgill 1984	MEM
Subtidal	Grand Cayman	1.12 – 1.79	Spencer 1985	MEM
		0.46	Spencer 1983	weight-loss tablet
Intertidal		0.88 – 1.2	Spencer 1985	MEM
		0.56	Spencer 1983	weight-loss tablet
Subtidal	Bermuda	1.30	Bromley 1978	rock pedestal
Subtidal	Lizard Island	0.63 – 1.26	Kiene 1985	coral surface lowering
Intertidal	(Great Barrier Reef)	0.006 – 0.02	Kiene 1985	coral surface lowering
Lagoon		0.22 – 0.93	Kiene 1985	coral surface lowering
Intertidal	Rurutu	1.0 – 1.6	van de Plaasche 1986	notch-cutting

Table 3-8. Bioerosion rates applied to physiographic zones of Kailua Bay in framework model calculations.

Zone	Bioerosion rate [a] (B_K) ($kgm^{-2}y^{-1}$)
N1[b]	**0.5**
N2[c]	0.3
N2*[c]	0.3
N3[d]	0.9
N4	**0.9**
N5[e]	0.5
NCG[e]	0.5
NH	0.2
S1	**0.3**
S2[c]	0.3
S3[b]	**0.3**
S4[g]	0.3
SCG[f]	0.3
SH	0.2
FRS	0.2

[a] Bioerosion rate is based on observations from drilled reef cores (Table 3-4). Values in **bold** are data collected from sites in this study. Other values were assigned based on proximity to those sites and on habitat similarity.

[b] Weighted mean of rates derived from cores collected in the zone.

[c] Extrapolated from data collected in zone S3.

[d] Extrapolated from data collected in zone N4.

[e] Extrapolated from data collected in zone N1.

[f] Extrapolated from data collected in zone S1.

[g] A conservative rate of 0.2 is applied to zones NH, FRS, and SH.

Assessing bioerosion in Kailua from core cavities

Digital images of drilled reef cores collected in Kailua Bay were subjected to image analysis and the surface area of bioeroded cavities measured (Figure 3-9). The percent of substrate removed by bioerosion was estimated by dividing the bioeroded area by the area of the coral (Table 3-4). When this 'percent bioeroded' is multiplied by the gross production rate, it provides an estimate of the 'bioerosion rate' in $kgm^{-2}y^{-1}$. Bioerosion rates were estimated in this manner using drilled cores from five sites in four zones in Kailua Bay. Resultant estimates of the rate at which unconsolidated sediment is produced by bioerosion and released from the reef are between 0.1–1.0 $kgm^{-2}y^{-1}$, consistent with the whole-reef estimate used in the Hubbard et al. (1990) model (0.24 $kgm^{-2}y^{-1}$) and with many published estimates for limestone erosion in reefal settings (Table 3-7). The table illustrates the range of bioerosion rates that occur in various settings, depending on which method is used. The results collected from Kailua cores (Table 3–8) reflect the rate at which coral skeletons near the reef surface are bioeroded, assuming the sediment produced is entirely removed from the cavity. Erosion deep below the reef surface is not included in the annual estimated rate. These results and their application in the sediment budget are further discussed in the following section.

Direct Sediment Production

In addition to the erosion of coral and algal reef framework, unconsolidated carbonate sediments in Kailua Bay are also produced directly by the growth and death of *Halimeda* (the only calcareous green alga in Hawaii; the genus *Penicillus* is absent), molluscs,

benthic foraminifera, and articulated coralline algae. Direct sediment production is quantified for these four organisms based on their living population densities (biomass or 'standing crop' of individuals in kgm^{-2}) and on the number of times per year the population experiences turnover (T in y^{-1}). The methods of calculating standing crop and sediment production of each organism are described below. Table 3-6 summarizes the general equations employed in calculating direct production.

Halimeda

Sediment production by this calcareous alga is a function of standing crop (in kgm^{-2}), the amount of $CaCO_3$ each thallus (plant body) contains (in %), and turnover rate (T in y^{-1}). These characteristics can vary with water depth, light intensity, environmental setting, growth habit, and between species. Standing crop is based on field observations of the distribution and abundance of *Halimeda* meadows, mats, and individual clumps, the type of growth habit (lithophytic or sand-anchored), and the percent plant cover. Carbonate content, easily measured on field-collected samples, is generally 60–90% in mature segments (Hillis 1997).

Biomass turnover is a function of the natural process of senescence ('shedding' of mature segments as the thallus grows), plant death following gamete release, and bed destruction by hydrodynamic events (Hillis 1991). Published turnover rates (T) in the literature are highly variable between species and in various settings. Drew (1983) determined that, on average, half of the reefal standing crop of *Halimeda* in sites on the Great Barrier Reef was lost every 80 days ($T = 2.2\ y^{-1}$). In the same paper, he reported a 15-day turnover time for *H. opuntia* ($T = 24.3\ y^{-1}$). Freile et al. (1995) use a turnover rate

of 3 y^{-1} in their production calculations for *Halimeda* meadows of the Bahama Banks. Other reported turnover times include 32 days for *H. incrassata* in Panama (Freile and Hillis 1997) and 39 days for *H. incrassata* and *H. monile* in Antigua (Multer 1988).

The calcareous green alga *Halimeda* is a prolific producer of sediment in Kailua Bay, particularly in shallow, well-lit areas of the nearshore region. Samples of living *Halimeda* were collected in Kailua Bay to determine the sediment production potential of the algae in various settings (Figure 3-5). At each of 14 sites, the surface area of a small portion of a *Halimeda* 'bed' was measured and the plants within the area harvested. Percent cover of the alga in the region sampled was visually estimated or determined by transect-mapping. In the laboratory, the sample was rinsed in deionized water, oven-dried, and weighed. It was then treated with hydrogen peroxide in a warm oven for 12–24 hours to remove all organic matter, rinsed again, oven-dried, and re-weighed. Biomass, carbonate content, and carbonate production rate were calculated for each sample using the following equations:

Biomass of *Halimeda* (converted to kgm^{-2}):

Dry weight of plant body (g) ÷ Surface area harvested (cm^2) (Eq. 15)

Carbonate content of organism (%):

Dry weight of inorganic remains (g) ÷ Dry weight of plant body (g) (Eq. 16)

Carbonate production by organism (kgm^{-2}):

Biomass (kgm^{-2}) × Carbonate content (%) (Eq. 17).

Applying the results of these calculations to knowledge of the occurrence, extent, and turnover of *Halimeda* meadows in various settings in Kailua Bay, carbonate sediment production can be calculated using the following equations:

Sediment Production Rate, SPR ($kgm^{-2}y^{-1}$):

Carbonate production (kgm^{-2}) × Turnover rate (y^{-1}) (Eq. 18)

Annual Sediment Production, ASP (kg):

SPR ($kgm^{-2}y^{-1}$) × Area (m^2) × Percent cover (%) (Eq. 19).

Scattered clumps and dense meadows of *Halimeda* in Kailua Bay have the capacity for rapid growth and a tendency to be buried, torn up, or otherwise destroyed during wind or swell events. Each turnover converts the standing crop to some volume of sediment, a process observed at least twice in Kailua Bay within an eight-month period. Given the frequency of tradewind and swell events, the observation of event-related turnover, and the consistency with published data, a turnover rate of 2 y^{-1} is applied in Eq. 18. Annual sediment production by *Halimeda* (ASP, Eq. 19) in each meadow and zone where the alga is present is calculated using the habitat area and percent cover data summarized in Table 3-9.

Halimeda covers 60% of the sea floor at sites OKLA 3-1, 3-M, 3-2, OHAN, and OKLA-5 where fossil outcrops close to shore provide shallow, energetic habitats. Elsewhere in zones NH, FRS, and SH, field observations and mapping transects suggest an average percent cover of 20%. One-third of the total habitat area in zone NH (608.9×10^3 m^2) is apportioned to regions of dense *Halimeda* coverage, one-third to regions of 20% cover with an observed SPR of 0.6 $kgm^{-2}y^{-1}$, and one-third to regions of 20% cover with an SPR of 0.9 $kgm^{-2}y^{-1}$. A similar technique is applied to zones FRS and SH where multiple observations exist. Results of these calculations are discussed in the following section.

Benthic foraminifera

At three sites in Kailua Bay, samples of unconsolidated rubble were collected to analyze the living population of benthic foraminifera (Figure 3-5). Sediment and attached fauna were gently scrubbed from the rubble samples, treated with hydrogen peroxide to remove organic material, rinsed over a 63-µm sieve, and oven-dried. Foraminifera that were living at the time of collection (determined by shell condition and color) were then removed from the dry sediment with the aid of a binocular microscope, identified, counted, and weighed. The standing crop of each population sampled was estimated by dividing the dry shell weight by the surface area of the rubble samples (measured in image analysis):

Standing crop of benthic foraminifera (converted to kgm^{-2}):

Dry weight of shells (g) ÷ Area of rubble sampled (cm^2) (Eq. 20).

The standing crop of foraminifera is equivalent to their carbonate production rate (CPR) and does not require an adjustment for organic content. The life span of *Amphistegina* (the most common reef-dwelling, symbiont-bearing foram in Kailua) is 4–12 months depending on the species and the environment (Hallock et al. 1995). A conservative turnover rate of 1 y^{-1} is thus applied to Eq. 18 to determine the sediment production rate (SPR in $kgm^{-2}y^{-1}$) by forams. These standing crop results and those of Harney et al. (1999) are summarized in Table 3-10.

To calculate the mass of sediment produced by forams each year in Kailua Bay, an appropriate CPR (carbonate production rate) is applied to each physiographic zone based on water depth and habitat. The ASP (annual sediment production rate) is then calculated for each zone using Eq. 19. Because forams have not been observed on living coral

surfaces in Kailua, only the non-coral portion of the total habitat area of each zone is used in the calculation. Table 3-11 summarizes the data used in assessing foram production and the resultant ASPs of each zone. Results are discussed in the following section.

Molluscs

Epilithic 'micromolluscs' (<1 cm in diameter) are very common inhabitants on solid reefal substrates, in loose sand, and in clumps and beds of calcareous algae. In a study of micromollusc assemblages in sediments of Kailua Bay (Kay 1973), 82 species were recorded, with three families dominating the assemblages: Phasianellidae (represented by one species, *Tricolia variabilis*), Rissoidae (16 spp.), and Cerithidae (6 spp.). Shell densities of 2–22 shells per cm^3 of sediment were reported, but no information on carbonate productivity or living population densities was provided.

Larger molluscs on Hawaiian reefs include cone shells (*Conus*), miters (*Mitra*), and cowries (*Cypraea*) that live in sand, rubble, and cryptic reef habitats. They are more common at depths of 10–50 m than on shallow reef platforms (Kay 1979), but no quantitative studies of their distribution or population density exist.

Although the ecology of Hawaiian molluscs is well known and their presence in coastal and reef sediments is significant (Moberly et al. 1965, Kay 1973, 1979, Harney et al. 2000), knowledge of their carbonate productivity in Hawaii is entirely lacking. Harney et al. (2000) demonstrated the age of mollusc shells in sediments of Kailua Bay were 259 cal yr BP nearshore and 737 cal yr BP offshore. Owing to long storage times and fossil ages, the abundance of shells in sediments is therefore not a reliable proxy for annual carbonate productivity.

To assess carbonate production by epilithic micromolluscs in Kailua Bay, living populations were analyzed in a manner similar to that described for forams. Samples of *Halimeda* and rubble were collected from various settings, scrubbed free of attached fauna, and their surface areas measured in image analysis. Carbonate production (in kgm^{-2}) was calculated in the same manner as for forams, requiring no correction for organic content (Eq. 20, above). Chave et al. (1972) cite a personal communication with malacologist E. A. Kay in 1970 for their estimate of micromollusc turnover of 10 y^{-1}. This turnover rate is applied to Eq. 18 to determine the sediment production rate (SPR in $kgm^{-2}y^{-1}$) by micromolluscs. The micromollusc standing crop results are summarized in Table 3-12.

To calculate the mass of sediment produced by molluscs each year in Kailua Bay, an appropriate CPR (carbonate production rate) is applied to each physiographic zone based on habitat. The ASP (annual sediment production rate) is then calculated for each zone using Eq. 19. As with forams, only the non-coral portion of the total habitat area of each zone is used in the calculation. Table 3-13 summarizes the data used in assessing micromollusc production and the resultant ASPs of each zone.

Larger molluscs have been observed infrequently in Kailua Bay, and quantification of their distribution has not been attempted. The dominance of micromollusc fragments in Kailua sediments (Harney et al. 2000) suggests that neglecting the production of macromolluscs is not significant within the uncertainty of this study. Carbonate production by littorinids (e.g. *Littorina*), neritids (e.g. *Nerita*), and patellids (e.g. *Cellana*) dwelling in supra- and intertidal zones has also not been assessed. Densities of these molluscs can be quite high in certain environments (up to 930 individuals per m^2, Kay

1979). However, rocky intertidal zones and shoreline 'benches' (settings where these molluscs are most numerous) are uncommon habitats in Kailua, occupying only a small portion of the southeast shoreline along Alala Point. Results of micromollusc production are discussed in the following section.

Articulated coralline algae

In situ measurements of the articulated coralline (red) alga *Porolithon gardineri* growing in waters around Oahu correspond to carbonate production rates of ~20 $kgm^{-2}y^{-1}$ (Agegian 1985). Clumps of this alga are common to abundant in shallow, energetic waters of nearshore hardgrounds (NH, SH) and portions of the shallow reef platform (N1, N2, S1, S2). Samples of whole specimens of articulated *Porolithon gardineri* were collected from five sites on the shallow reef platform (Figure 3-5), bleached, and weighed. Carbonate production estimates were calculated using the standing crop method:

Standing crop of articulated coralline algae (converted to kgm^{-2}):

Dry weight of skeleton (g) ÷ Area of specimen (cm^2) (Eq. 21).

Planimetric surface areas of the 'clumps' sampled were calculated using the formula for the area of a circle ($1/2\pi r^2$). Because the skeletons were bleached, no correction for organic content was necessary. These clumps of *P. gardineri* are easily removed from the reef surface and are probably frequently dismantled by wind and swell events. Applying a conservative population turnover rate of 1 y^{-1} to Eq. 18, the sediment production rate (SPR in $kgm^{-2}y^{-1}$) of articulated coralline algae in Kailua Bay is calculated. These data are summarized in Table 3-14. Table 3-15 summarizes the data used in assessing

Table 3-9. Biomass, carbonate content, turnover, and sediment production of the calcareous green alga *Halimeda* in Kailua Bay.

Sample	Site	Zone	Depth (m)	Biomass[a] (kgm^{-2})	$CaCO_3$[b] (%)	CPR[c] (kgm^{-2})	Turn.[d] (y^{-1})	SPR[e] ($kgm^{-2}y^{-1}$)	Area[f] ($x10^3$ m^2)	Cover[g] (%)	Adj. area[h] ($x10^3$ m^2)	ASP ($x10^3$ kgy^{-1})	Zone ASP ($x10^3$ kgy^{-1})	Zone SPR[j] ($kgm^{-2}y^{-1}$)
H1	KT	meadow[k]	3.7	3.6	90%	3.2	2	6.4	0.50	100%	0.50	3.2	11.4	6.6
H2	SPX	–	11.6	3.7	90%	3.3	2	6.7	0.73	100%	0.73	4.8		
H3	T2	–	7.9	3.7	90%	3.3	2	6.7	0.50	100%	0.50	3.3		
H4	OKLA3-1	NH[l]	1.8	0.4	72%	0.3	2	0.6	203.0	60%	121.8	74.9	137.0	0.2
H5	OKLA3-M	NH	2.4	1.0	72%	0.3	2	0.6	203.0	20%	40.6	24.4		
H6	OKLA3-2	NH	0.9	0.6	72%	0.5	2	0.9	203.0	20%	40.6	37.8		
H7	F6	N3[m]	7.6	1.6	90%	1.5	2	2.9	16.0	4%	0.64	1.9	1.9	0.1
H8	F8	FRS[n]	2.7	1.8	72%	1.3	2	2.6	262.7	11%	28.9	74.9	108.3	0.3
H9	OHAN	FRS	3.0	0.4	86%	0.3	2	0.6	87.6	60%	52.5	33.4		
H10	JY2	SH[o]	3.7	0.8	76%	0.6	2	1.2	184.9	20%	37.0	43.9	331.0	0.4
H11	OKLA-5	SH	3.0	0.5	72%	0.4	2	0.7	184.9	60%	111.0	79.5		
H12	PO1	SH	1.8	3.0	50%	1.5	2	3.0	184.9	30%	55.5	164.6		
H13	PO2	SH	1.8	0.3	50%	0.2	2	0.3	184.9	30%	55.5	18.1		
H14	JY1	SH[p]	2.4	0.8	76%	0.6	2	1.3	98.7	20%	19.7	24.9		
									1815.5		565.5	**589.6**		
TOTAL Annual Sediment Production in Kailua Bay						**589.6 ± 70.2 x 10^3 kgy^{-1}**								

[a] Biomass is the dry weight of the *Halimeda* plants harvested from a known surface area of the sea floor (Eq. 15)
[b] Carbonate content is calculated by dividing dry weight after treatment with H_2O_2 by total biomass (Eq.16).
[c] Carbonate Production Rate is the product of biomass and % $CaCO_3$ (Eq.17)
[d] Population turnover rate (see text).
[e] Sediment Production Rate (the product of $CaCO_3$ production and turnover) (Eq. 18).
[f] Area of the meadows themselves for sites KT, SPX, and T2; area of zone or applicable region within zone for other sites (see text)
[g] Percent cover is the amount of sea floor covered by the algae in the region of the "bed."
[h] The habitat area of each zone is adjusted for the percent cover.
[i] Annual Sediment Production is the product of SPR, area, and % cover (Eq. 19).
[j] Sediment production rate for the zone = Zone ASP / Total area in zone.
[k] Meadows and beds of *Halimeda;* not characteristic of a zone.
[l] The total area of zone NH is divided equally among the three *Halimeda* productivities.
[m] Only a portion of zone N3 (primarily the channel margin) is inhabited by *Halimeda* (area of regional measured in image analysis).
[n] Of the total area of zone FRS, 75% is typical of the F8 data; 25% is typical of the OHAN data.
[o] The total area of zone SH is divided equally among the first four *Halimeda* productivities.
[p] A portion of zone SH in the lee of Popoia Island with different *Halimeda* characteristics (area of region measured in image analysis).

Table 3-10. Standing crop of benthic foraminifera in Kailua Bay.

Sample	Site	Zone	Depth (m)	CPR[a] (kgm^{-2})	Turn.[b] (y^{-1})	SPR[c] ($kgm^{-2}y^{-1}$)	Source
F1	KC	N4	16.8	0.14	1	0.14	this study
F2	MM	S3	6.1	0.11	1	0.11	this study
F3	RG	SCG	21.0	0.02	1	0.02	this study
Shallow reef		~SH[d]	2.0	0.01	1	0.01	Harney et al. 1999
Reef platform		~S2	5.0	0.08	1	0.08	Harney et al. 1999
Reef slope		~S1	8–10	0.13	1	0.13	Harney et al. 1999

[a] Carbonate Production Rate, equal to standing crop (Eq. 20).

[b] Population turnover rate after Hallock et al. 1995 (see text).

[c] Sediment Production Rate (Eq. 18).

[d] Applicable zones inferred from location of sampling sites in Harney et al. 1999.

Table 3-11. Sediment production by benthic foraminifera in Kailua Bay.

Zone	CPR[a] (kgm^{-2})	Turn.[b] (y^{-1})	SPR[c] ($kgm^{-2}y^{-1}$)	Habitat area ($x10^3$ m^2)	Non-coral substrate	Adj. area[d] ($x10^3$ m^2)	ASP[e] ($x10^3$ kgy^{-1})	Zone SPR[f] ($kgm^{-2}y^{-1}$)
N1	0.13	1	0.13	1493.0	47%	701.2	91.1	0.06
N2	0.08	1	0.08	764.0	91%	691.6	55.3	0.07
N2*	0.08	1	0.08	546.7	88%	478.9	38.3	0.07
N3	0.10	1	0.10	159.1	58%	92.1	9.2	0.06
N4	**0.14**	1	0.14	71.5	80%	57.3	8.0	0.11
N5	0.08	1	0.08	797.8	66%	524.4	42.0	0.05
NCG	0.01	1	0.01	102.7	22%	22.1	0.2	0.00
NH	0.01	1	0.01	608.9	100%	608.9	6.1	0.01
S1	0.13	1	0.13	1096.7	38%	412.6	53.6	0.05
S2	0.08	1	0.08	1116.8	92%	1023.0	81.8	0.07
S3	**0.11**	1	0.11	518.6	65%	337.9	37.2	0.07
S4	0.10	1	0.10	138.0	75%	103.9	10.4	0.08
SCG	**0.02**	1	0.017	113.8	25%	28.8	0.5	0.00
SH	0.01	1	0.01	838.5	100%	838.5	8.4	0.01
FRS[g]	0.01	1	0.01	4.0	100%	4.0	0.04	0.01
				8370.2		5925.3	**442.3**	
TOTAL Annual Sediment Production in Kailua Bay						**442.3 ± 69.6 x 10^3 kgy^{-1}**		

[a] Carbonate Production Rate, equal to standing crop (Eq. 20). Values in **bold** are data collected from sites in this study. Other values were assigned based on data from Harney et al. 1999 (see Table 3-10). The value 0.01 kgm^{-2} was assigned to "shallow reef" zones NH, FRS, and SH; 0.08 kgm- ^{2} was assigned to mid-depth "reef platform" zones N2, N5, and S2; 0.13 was assigned to "reef slope" zones N1 and S1.

[c] Sediment Production Rate (Eq. 18).

[d] The habitat area of each zone is adjusted for the percent non-coral substrate (median value in Table 3-2).

[e] Annual Sediment Production (Eq. 19).

[f] Sediment production rate for the zone = Zone ASP / Total area in zone.

[g] Only the area of solid substrate in zone FRS is applied.

Table 3-12. Standing crop of micromolluscs in Kailua Bay.

Sample	Site	Zone	Depth (m)	CPR[a] (kgm^{-2})	Turn.[b] (y^{-1})	SPR[c] ($kgm^{-2}y^{-1}$)
M1	KC	N4	16.8	0.0127	10	0.13
M2	MM	S3	6.1	0.0052	10	0.05
M3	RG	SCG	21.0	0.0034	10	0.03
M4	PO2	SH	0.9	0.0585	10	0.59
M5	SP7	S1	10.0	0.0213	10	0.21
M6	PO1	meadow[d]	1.8	0.1792	10	1.79
M7	KT	meadow	3.7	0.0709	10	0.71
M8	NT	S1[e]	13.0	0.0229	10	0.23

[a] Carbonate Production Rate, equal to standing crop (Eq. 20).

[b] Population turnover rate (see text).

[c] Sediment Production Rate (Eq. 18).

[d] Samples of *Halimeda* meadow analyzed as mollusc habitat.

[e] Dead coral colony analyzed as mollusc habitat.

Table 3-13. Sediment production by micromolluscs in Kailua Bay.

Zone	CPR[a] (kgm^{-2})	Turn.[b] (y^{-1})	SPR[c] ($kgm^{-2}y^{-1}$)	Habitat area ($x10^3 m^2$)	Non-coral substrate	Adjusted area[d] ($x10^3 m^2$)	ASP[e] ($x10^3 kgy^{-1}$)	Zone SPR[f] ($kgm^{-2}y^{-1}$)
N1	0.0213	10	0.21	1493.0	47%	701.2	149.2	0.10
N2	0.0052	10	0.05	764.0	91%	691.6	35.7	0.05
N2*	0.0052	10	0.05	546.7	88%	478.9	24.7	0.05
N3	0.0127	10	0.13	159.1	58%	92.1	11.7	0.07
N4	**0.0127**	10	0.13	71.5	80%	57.3	7.3	0.10
N5	0.0213	10	0.21	797.8	66%	524.4	111.6	0.14
NCG	0.0034	10	0.03	102.7	22%	22.1	0.8	0.01
NH	0.0585	10	0.59	608.9	100%	606.5	354.9	0.58
S1	**0.0213**	10	0.21	1096.7	38%	412.6	87.8	0.08
S2	0.0052	10	0.05	1116.8	92%	1023.0	52.8	0.05
S3	**0.0052**	10	0.05	518.6	65%	337.9	17.4	0.03
S4	0.0213	10	0.21	138.0	75%	103.9	22.1	0.16
SCG	**0.0034**	10	0.03	113.8	25%	28.8	1.0	0.01
SH	**0.0585**	10	0.59	838.5	100%	835.2	488.7	0.58
FRS	0.0585	10	0.59	4.0	100%	4.0	2.3	0.58
PO1 meadow[g]	**0.1792**	10	1.79	111.0	100%	110.5	198.1	1.79
KT meadow	**0.0709**	10	0.71	0.5	100%	0.5	0.4	0.71
				8481.7		6030.6	**1566.3**	
TOTAL Annual Sediment Production in Kailua Bay					**1566.3 ± 221.6 x 10^3 kgy^{-1}**			

[a] Carbonate Production Rate, equal to standing crop (Eq. 20). Values in **bold** are data collected from sites in this study. Other values were assigned based on proximity to those sites and on habitat similarity: the data for zone N4 was extrapolated to N3; SCG to NCG; S1 to N1, N5, and S4; SH to NH and FRS; and S3 to N2, N2*, and S2.

[b] Population turnover rate (see text).

[c] Sediment Production Rate (Eq. 18).

[d] The habitat area of each zone is adjusted for the percent non-coral substrate (median value in Table 3-2).

[e] Annual Sediment Production (Eq. 19).

[f] Sediment production rate for the zone = Zone ASP / Total area in zone.

[g] Only 30% of the area of PO1 meadow ($369.9x10^3 m^2$) is actually covered by *Halimeda* (Table 3-9).

Table 3-14. Standing crop of the articulated coralline alga *Porolithon gardineri* in Kailua Bay.

Sample	Site	Zone	Depth (m)	CPR[a] (kgm^{-2})	Turn.[b] (y^{-1})	SPR[c] ($kgm^{-2}y^{-1}$)
APG1	KY	N3	3.7	14.1	1	14.1
APG2	NP8	N2*	7.6	15.2	1	15.2
APG3	NP4	N2	5.0	8.5	1	8.5
APG4	NP4	N2	5.0	10.0	1	10.0
APG5	F7	N2	2.5	17.8	1	17.8

[a] Carbonate Production Rate, equal to standing crop (Eq. 20).

[b] Population turnover rate (see text).

[c] Sediment Production Rate (Eq. 18).

Table 3-15. Sediment production the articulated coralline alga *Porolithon gardineri* in Kailua Bay.

Zone	Map[a]	Site	CPR[b] (kgm^{-2})	Turn.[c] (y^{-1})	SPR[d] ($kgm^{-2}y^{-1}$)	Area[e] ($x10^3$ m^2)	Cover[f] (%)	Adj. area[h] ($x10^3$ m^2)	ASP[g] (kgy^{-1})	Zone ASP ($x10^3$ kgy^{-1})	Zone SPR[h] ($kgm^{-2}y^{-1}$)
N2	25	NP4	10.0	1	10.0	186.0	0.15	27.9	279.0	431.4	0.56
N2	26	NP5	10.0	1	10.0	186.0	0.06	11.2	111.6		
N2	36	NP10	10.0	1	10.0	372.0	0.01	3.7	37.2		
N2	43	F7	17.8	1	17.8	20.0	0.01	0.2	3.6		
N2*	34	NP8	15.2	1	15.2	546.7	0.04	21.9	332.4	332.4	0.61
N3	5	EB2	14.1	1	14.1	53.0	0.02	1.1	15.0	37.4	0.24
N3	39	F3	14.1	1	14.1	53.0	0.01	0.5	7.5		
N3	42	F6	14.1	1	14.1	53.0	0.02	1.1	15.0		
N5	33	NP7	15.2	1	15.2	797.8	0.02	16.0	242.5	242.5	0.30
NH	27	NP6	10.0	1	10.0	608.9	0.10	60.9	608.9	608.9	1.00
S2	49	SC	10.0	1	10.0	20.0	0.14	2.8	28.0	247.4	0.22
S2	50	BS	10.0	1	10.0	1096.8	0.02	21.9	219.4		
						3993.4		169.09	**1900.0**		
TOTAL Annual Sediment Production in Kailua Bay							**1900.0 ± 204.2 x 10^3 kgy^{-1}**				

[a] Refers to quantitative transect data in Appendix C (see text).

[b] Carbonate Production Rate, equal to standing crop (Eq. 22).

[c] Population turnover rate (see text).

[d] Sediment Production Rate (Eq. 18).

[e] See text for description of assigning total habitat area to multiple observations within a single zone.

[f] Based on quantitative transect data.

[g] Annual Sediment Production (Eq. 19).

[h] Sediment production rate for the zone = Zone ASP / Total area in zone.

articulated coralline algae production. Annual sediment production (ASP in kg, Eq. 19) by articulated algae is calculated only for those zones in which the transect-mapping data show the algae are present in the individual 'clump' form described. Results are presented in the following section.

RESULTS

Gross Framework Production

Table 3-16 lists the data, variables, equations, and results of framework production in the 14 physiographic zones that comprise the various benthic habitats of Kailua Bay. The calculations for each zone utilize benthic community data and physiographic characteristics that are zone-specific and based on field observations. Growth of hermatypic corals in this model is broken into morphological components: encrusting corals produce carbonate at a rate of 2.8 $kgm^{-2}y^{-1}$, massive corals at 8.4 $kgm^{-2}y^{-1}$, stoutly-branching *Pocillopora meandrina* at 6.7 $kgm^{-2}y^{-1}$, and finger-branching *Porites compressa* at 10.7 $kgm^{-2}y^{-1}$. Encrusting coralline algae produces carbonate at a rate of 2.6 $kgm^{-2}y^{-1}$. Gross production is the total mass of calcification accomplished by the skeletal growth of framework-building corals and coralline algae prior to any erosion or alteration.

Table 3-17 summarizes the gross annual production by corals, by encrusting algae, and in terms of total framework in each zone (first column). In zone N1, on the seaward

portion of the northern reef platform in water depths of 6.5–16 m, an extensive habitat area (A_h) of 1493.0 x 10^3 m^2 supports a moderately-diverse community of encrusting and massive corals (covering 42% and 9% of the reef surface, respectively). Gross production by encrusting corals (G_e) in this region is 1755.8 x 10^3 kgy^{-1}; the growth of massive corals (G_m) produces an additional 1128.7 x 10^3 kg of carbonate annually. Encrusting coralline algae cover 21% of the reef surface in this zone and contribute 815.2 x 10^3 kgy^{-1} (G_{ace}) to the reef edifice. Total framework production (G_F) in zone N1 is 3699.7 x 10^3 kgy^{-1}, the highest of all zones. When normalized to habitat area, the rate of gross framework production in this zone is 2.5 $kgm^{-2}y^{-1}$, a rate typical of 79% of the system (Table 3-18).

Owing to high species diversity, extensive coral cover, and rapid growth of dominantly massive and branching morphologies, gross annual production by corals is also very high in zones NCG and SCG (1934.2 x 10^3 kgy^{-1} and 2986 x 10^3 kgy^{-1}, respectively). Coralline algae contribute far less in this region (10.7 x 10^3 kgy^{-1} and 61.4 x 10^3 kgy^{-1}), but total framework production is still among the highest rates, particularly in zone SCG where G_F is 3047.4 x 10^3 kgy^{-1}, the second-highest in the system. When normalized to habitat area, the rate of gross framework production in these coral gardens exceeds that of all other zones (18.9 and 26.8 $kgm^{-2}y^{-1}$, respectively). These very high rates are characteristic of only 2% of the entire system.

A high rate of framework production exists in zone S1, owing to its extensive habitat area (1096.7 x 10^3 m^2) and moderately high coral cover (57%). Gross carbonate production in this zone is 2862.2 kgy^{-1}. Normalized framework production by corals and encrusting coralline algae in this zone is 2.6 $kgm^{-2}y^{-1}$.

Table 3-16. Variables, equations, and calculation results of framework production and bioerosion in Kailua Bay.

Section	Variable	Equation	Units	N1	N2	N2*	N3	N4
BENTHIC	A_s	area surface	m^2	1244193	587715	546717	132611	59601
COMMUNITY	R	rugosity	none	1.2	1.3	1.0	1.2	1.2
DATA	C_e	% cover of encrusting coral	decimal %	0.42	0.06	0.11	0.37	0.12
	GPR_e	GPR of encrusting coral	$kgm^{-2}y^{-1}$	2.8	2.8	2.8	2.8	2.8
	C_m	% cover of massive coral	decimal %	0.09	0.00	0.00	0.00	0.00
	GPR_m	GPR of massive coral	$kgm^{-2}y^{-1}$	8.4	8.4	8.4	8.4	8.4
	C_{sb}	% cover of stout-branching coral	decimal %	0.00	0.02	0.01	0.01	0.01
	GPR_{sb}	GPR of stout-branching coral	$kgm^{-2}y^{-1}$	6.7	6.7	6.7	6.7	6.7
	C_{fb}	% cover of finger-branching coral	decimal %	0.00	0.00	0.00	0.00	0.02
	GPR_{fb}	GPR of finger-branching coral	$kgm^{-2}y^{-1}$	10.7	10.7	10.7	10.7	10.7
	C_{ace}	% cover of encrust. coralline alg.	decimal %	0.21	0.86	0.05	0.33	0.74
	GPR_{ace}	GPR of encrust. coralline algae	$kgm^{-2}y^{-1}$	2.6	2.6	2.6	2.6	2.6
	B_K	Kailua bioerosion model	$kgm^{-2}y^{-1}$	0.50	0.30	0.30	0.90	0.90
	B_H	Hubbard bioerosion model	decimal %	0.23	0.23	0.23	0.23	0.23
	B_S	Spencer erosion model	$kgm^{-2}y^{-1}$	1.6	1.6	1.6	1.6	1.6
	t	time (Holocene)	y	5000	5000	5000	5000	5000
	d	approx. density	kgm^{-3}	1176	1176	1176	1176	1176
GROSS	A_h	$A_h = A_s \times R$	m^{-2}	1493032	764030	546717	159133	71521
ANNUAL	G_e	$G_e = C_e \times A_h \times GPR_e$	kgy^{-1}	1755805	128357	168389	164862	24632
FRAMEWORK	G_m	$G_m = C_m \times A_h \times GPR_m$	kgy^{-1}	1128732	0	0	0	0
PRODUCTION	G_{sb}	$G_{sb} = C_{sb} \times A_h \times GPR_{sb}$	kgy^{-1}	0	102380	36630	10662	4792
	G_{fb}	$G_{fb} = C_{fb} \times A_h \times GPR_{fb}$	kgy^{-1}	0	0	0	0	15306
	G_c	$G_c = G_e + G_m + G_{sb} + G_{fb}$	kgy^{-1}	2884537	230737	205019	175524	44729
	G_{ace}	$G_{ace} = C_{ace} \times A_h \times GPR_{ece}$	kgy^{-1}	815195	1708370	71073	136536	137402
	G_F	$G_F = G_c + G_{ace}$	kgy^{-1}	3699732	1939107	276092	312060	182132
	G_{Tc}	$G_{Tc} = \Sigma\, G_{c(z)}$	kgy^{-1}	12424507	± 745470	54%	coral	
	G_{Tace}	$G_{Tace} = \Sigma\, G_{ace(z)}$	kgy^{-1}	10765351	± 645922	46%	coralline algae	
	G_{TF}	$G_{TF} = G_{Tc} + G_{Tace}$	kgy^{-1}	23189858	± 1391392			
SEDIMENT	SB_K	$SB_K = A_h \times B_K$	kgy^{-1}	746516	229209	164015	143220	64369
BIOERODED/	SB_H	$SB_H = G_F \times B_H$	kgy^{-1}	850938	445995	63501	71774	41890
RELEASED	SB_S	$SB_S = A_h \times B_S$	kgy^{-1}	2388851	1222447	874747	254613	114434
	SB_{TK}	$SB_{TK} = \Sigma\, SB_{K(z)}$	kgy^{-1}	2982620	± 178957			
	SB_{TH}	$SB_{TH} = \Sigma\, SB_{H(z)}$	kgy^{-1}	5333667	± 320020			
	SB_{TS}	$SB_{TS} = \Sigma\, SB_{S(z)}$	kgy^{-1}	13392328	± 803540			
VOLUME	V_K	$V_K = SB_K \div d$	m^3y^{-1}	635	195	139	122	55
	V_H	$V_H = SB_H \div d$	m^3y^{-1}	724	379	54	61	36
	V_S	$V_S = SB_S \div d$	m^3y^{-1}	2031	1039	744	217	97
	V_{TK}	$V_{TK} = \Sigma\, V_{K(z)}$	m^3y^{-1}	2536	± 337			
	V_{TH}	$V_{TH} = \Sigma\, V_{H(z)}$	m^3y^{-1}	4535	± 603			
	V_{TS}	$V_{TS} = \Sigma\, V_{S(z)}$	m^3y^{-1}	11388	± 1515			
HOLOCENE	HV_K	$HV_K = V_K \times t$	m^3	3173962	974527	697343	608928	273678
	HV_H	$HV_H = V_H \times t$	m^3	3617936	1896235	269988	305161	178105
	HV_S	$HV_S = V_S \times t$	m^3	10156678	5197480	3719163	1082539	486539
	HV_{TK}	$HV_{TK} = \Sigma\, HV_K$	m^3	12681208	± 1686508			
	HV_{TH}	$HV_{TH} = \Sigma\, HV_H$	m^3	22677158	± 3015896			
	HV_{TS}	$HV_{TS} = \Sigma\, HV_S$	m^3	56940169	± 7572627			
RESULTS	HV_{TK}	$HV_{TK} = \Sigma\, HV_K$	$x10^5\ m^3$	**126.81**	± 16.87			
	HV_{TH}	$HV_{TH} = \Sigma\, HV_H$	$x10^5\ m^3$	**226.77**	± 30.16			
	HV_{TS}	$HV_{TS} = \Sigma\, HV_S$	$x10^5\ m^3$	**569.40**	± 75.73			

(Continued)

Table 3-16 (Continued). Variables, equations, and calculation results of framework production and bioerosion in Kailua Bay.

Section	Variable	Equation	Units	N5	NCG	NH	S1	S2
BENTHIC COMMUNITY DATA	A_s	area surface	m^2	797778	85600	608937	913881	698005
	R	rugosity	none	1.0	1.2	1.0	1.2	1.6
	C_e	% cover of encrusting coral	decimal %	0.30	0.61	0.00	0.52	0.08
	GPR_e	GPR of encrusting coral	$kgm^{-2}y^{-1}$	2.8	2.8	2.8	2.8	2.8
	C_m	% cover of massive coral	decimal %	0.00	0.14	0.00	0.04	0.00
	GPR_m	GPR of massive coral	$kgm^{-2}y^{-1}$	8.4	8.4	8.4	8.4	8.4
	C_{sb}	% cover of stout-branching coral	decimal %	0.01	0.00	0.00	0.01	0.00
	GPR_{sb}	GPR of stout-branching coral	$kgm^{-2}y^{-1}$	6.7	6.7	6.7	6.7	6.7
	C_{fb}	% cover of finger-branching coral	decimal %	0.00	0.00	0.00	0.00	0.00
	GPR_{fb}	GPR of finger-branching coral	$kgm^{-2}y^{-1}$	10.7	10.7	10.7	10.7	10.7
	C_{ace}	% cover of encrust. coralline alg.	decimal %	0.05	0.04	0.94	0.26	0.88
	GPR_{ace}	GPR of encrust. coralline algae	$kgm^{-2}y^{-1}$	2.6	2.6	2.6	2.6	2.6
	B_K	Kailua bioerosion model	decimal %	0.50	0.50	0.20	0.30	0.30
	B_H	Hubbard bioerosion model	decimal %	0.23	0.23	0.23	0.23	0.23
	B_S	Spencer erosion model	$kgm^{-2}y^{-1}$	1.6	1.6	1.6	1.6	1.6
	t	time	y	5000	5000	5000	5000	5000
	d	approx. density	kgm^{-3}	1176	1176	1176	1176	1176
GROSS ANNUAL FRAMEWORK PRODUCTION	A_h	$A_h = A_s \times R$	m^{-2}	797778	102720	608937	1096657	1116808
	G_e	$G_e = C_e \times A_h \times GPR_e$	kgy^{-1}	666133	175826	0	1581874	249540
	G_m	$G_m = C_m \times A_h \times GPR_m$	kgy^{-1}	0	1755805	0	472149	0
	G_{sb}	$G_{sb} = C_{sb} \times A_h \times GPR_{sb}$	kgy^{-1}	62884	2597	16000	56541	29930
	G_{fb}	$G_{fb} = C_{fb} \times A_h \times GPR_{fb}$	kgy^{-1}	0	0	0	0	0
	G_c	$G_c = G_e + G_m + G_{sb} + G_{fb}$	kgy^{-1}	729016	1934228	16000	2110564	279470
	G_{ace}	$G_{ace} = C_{ace} \times A_h \times GPR_{ace}$	kgy^{-1}	107856	10683	1483896	751683	2543642
	G_F	$G_F = G_c + G_{ace}$	kgy^{-1}	836873	1944911	1499895	2862248	2823112
SEDIMENT BIOERODED/ RELEASED	SB_K	$SB_K = G_F \times B_K$	kgy^{-1}	398889	51360	121787	328997	335042
	SB_H	$SB_H = G_F \times B_H$	kgy^{-1}	192481	447329	344976	658317	649316
	SB_S	$SB_S = A_S \times B_S$	kgy^{-1}	1276445	164352	974299	1754652	1786893
VOLUME	V_K	$V_K = SB_K \div d$	m^3y^{-1}	339	44	104	280	285
	V_H	$V_H = SB_H \div d$	m^3y^{-1}	164	380	293	560	552
	V_S	$V_S = SB_S \div d$	m^3y^{-1}	1085	140	828	1492	1519
HOLOCENE	HV_K	$HV_K = V_K \times t$	m^3	1695957	218367	517804	1398797	1424500
	HV_H	$HV_H = V_H \times t$	m^3	818370	1901911	1466734	2798967	2760696
	HV_S	$HV_S = V_S \times t$	m^3	5427061	698776	4142429	7460253	7597333

(Continued)

Table 3-16 (Continued). Variables, equations, and calculation results of framework production and bioerosion in Kailua Bay.

Section	Variable	Equation	Units	S3	S4	SCG	SH	FRS
BENTHIC	A_s	area surface	m^2	345730	125488	87511	838490	3986
COMMUNITY	R	rugosity	none	1.5	1.1	1.3	1.0	1.0
DATA	C_e	% cover of encrusting coral	decimal %	0.33	0.23	0.42	0.00	0.00
	GPR_e	GPR of encrusting coral	$kgm^{-2}y^{-1}$	2.8	2.8	2.8	2.8	2.8
	C_m	% cover of massive coral	decimal %	0.00	0.02	0.22	0.00	0.00
	GPR_m	GPR of massive coral	$kgm^{-2}y^{-1}$	8.4	8.4	8.4	8.4	8.4
	C_{sb}	% cover of stout-branching coral	decimal %	0.01	0.00	0.01	0.00	0.00
	GPR_{sb}	GPR of stout-branching coral	$kgm^{-2}y^{-1}$	6.7	6.7	6.7	6.7	6.7
	C_{fb}	% cover of finger-branching coral	decimal %	0.00	0.00	0.06	0.00	0.00
	GPR_{fb}	GPR of finger-branching coral	$kgm^{-2}y^{-1}$	10.7	10.7	10.7	10.7	10.7
	C_{ace}	% cover of encrust. coralline alg.	decimal %	0.46	0.75	0.21	0.94	0.73
	GPR_{ace}	GPR of encrust. coralline algae	$kgm^{-2}y^{-1}$	2.6	2.6	2.6	2.6	2.6
	B_K	Kailua bioerosion model	decimal %	0.30	0.30	0.30	0.20	0.10
	B_H	Hubbard bioerosion model	decimal %	0.23	0.23	0.23	0.23	0.23
	B_S	Spencer erosion model	$kgm^{-2}y^{-1}$	1.6	1.6	1.6	1.6	1.6
	t	time	y	5000	5000	5000	5000	5000
	d	approx. density	kgm^{-3}	1176	1176	1176	1176	1176
GROSS	A_h	$A_h = A_s \times R$	m^{-2}	518595	138037	113764	838490	3986
ANNUAL	G_e	$G_e = C_e \times A_h \times GPR_e$	kgy^{-1}	471921	89426	132194	0	0
FRAMEWORK	G_m	$G_m = C_m \times A_h \times GPR_m$	kgy^{-1}	0	196729	2775489	0	0
PRODUCTION	G_{sb}	$G_{sb} = C_{sb} \times A_h \times GPR_{sb}$	kgy^{-1}	48483	0	10223	22031	105
	G_{fb}	$G_{fb} = C_{fb} \times A_h \times GPR_{fb}$	kgy^{-1}	0	0	68082	0	0
	G_c	$G_c = G_e + G_m + G_{sb} + G_{fb}$	kgy^{-1}	520404	286155	2985988	22031	105
	G_{ace}	$G_{ace} = C_{ace} \times A_h \times GPR_{ace}$	kgy^{-1}	616477	270227	61460	2043285	7565
	G_F	$G_F = G_c + G_{ace}$	kgy^{-1}	1136881	556382	3047448	2065316	7670
SEDIMENT	SB_K	$SB_K = G_F \times B_K$	kgy^{-1}	155579	41411	34129	167698	399
BIOERODED	SB_H	$SB_H = G_F \times B_H$	kgy^{-1}	261483	127968	700913	475023	1764
	SB_S	$SB_S = A_S \times B_S$	kgy^{-1}	829752	220859	182023	1341584	6378
VOLUME	V_K	$V_K = SB_K \div d$	m^3y^{-1}	132	35	29	143	0
	V_H	$V_H = SB_H \div d$	m^3y^{-1}	222	109	596	404	2
	V_S	$V_S = SB_S \div d$	m^3y^{-1}	706	188	155	1141	5
HOLOCENE	HV_K	$HV_K = V_K \times t$	m^3	661473	176067	145108	713002	1695
	HV_H	$HV_H = V_H \times t$	m^3	1111746	544081	2980072	2019654	7501
	HV_S	$HV_S = V_S \times t$	m^3	3527857	939026	773907	5704014	27116

Table 3-17. Summary of gross framework and bioeroded sediment production in Kailua Bay. The first column summarizes the gross annual production by corals, by encrusting algae, and in terms of total framework in each zone. The second column summarizes the rates at which unconsolidated sediment is produced (and released from the edifice) during bioerosion of the reef framework (using the Kailua model of bioerosion, or SB_K). The third column presents the rates in terms of volume (see text for discussion of conversion).

GROSS PRODUCTION ($x10^3$ kgy^{-1})			
Zone	Coral (G_c)	Enc. coralg. (G_{ace})	Framework (G_F)
N1	2885	815	3700
N2	231	1708	1939
N2*	205	71	276
N3	176	137	312
N4	45	137	182
N5	729	108	837
NCG	1934	11	1945
NH	16	1484	1500
S1	2111	752	2862
S2	279	2544	2823
S3	520	616	1137
S4	286	270	556
SCG	2986	61	3047
SH	22	2043	2065
FRS	0	8	8
Total	12425	10765	23190
(±)[c]	745	646	1391
Cntrb.[d]	54%	46%	
G_{TF} = 23910 ± 1391 x 10^3 kgy^{-1}			

SEDIMENT PRODUCTION ($x10^3$ kgy^{-1})[a]			
Zone	Coral	Enc. coralg.	Framework (SB_K)
N1	403	347	747
N2	124	106	229
N2*	89	76	164
N3	77	66	143
N4	35	30	64
N5	215	185	399
NCG	28	24	51
NH	66	57	122
S1	178	153	329
S2	181	156	335
S3	84	72	156
S4	22	19	41
SCG	18	16	34
SH	91	78	168
FRS	0.2	0.2	0.4
Total	1611	1385	2983
(±)	97	83	179
SB_{TK} = 2983 ± 179 x 10^3 kgy^{-1}			

SEDIMENT PRODUCTION (m^3y^{-1})[b]			
Zone	Coral	Enc. coralg.	Framework (V_K)
N1	343	295	635
N2	105	90	195
N2*	75	65	139
N3	66	57	122
N4	30	25	55
N5	183	157	339
NCG	24	20	44
NH	56	48	104
S1	151	130	280
S2	154	132	285
S3	71	61	132
S4	19	16	35
SCG	16	13	29
SH	77	66	143
FRS	0.2	0.2	0.3
Total	1370	1177	2536
(±)[e]	182	157	337
V_{TK} = 2536 ± 337 m^3y^{-1}			

[a] Sediment derived from bioerosion of reef framework (Kailua model).

[b] Volume converted from mass using approximate density of 1176±80 kgm^{-3} (see text).

[c] Uncertainties on totals.

[d] Percent contribution of each component to total.

[e] Includes additional uncertainty of converting mass to volume.

Table 3-18. Gross framework productivity (by corals and encrusting coralline algae) normalized by habitat area in Kailua Bay reveals patterns of productivity over the entire system. Gross framework production over 81% of the total habitat area in Kailua Bay is between 1.9–4.0 $kgm^{-2}y^{-1}$ ('moderate'). Low rates (≤1 $kgm^{-2}y^{-1}$) are characteristic of 17% of the system. Very high productivity in 'coral gardens' (18.9–26.8 $kgm^{-2}y^{-1}$) is represented by only 2% of the entire habitat area. Framework-building corals and coralline algae produce carbonate at an average rate of 2.7 $kgm^{-2}y^{-1}$ over the entire reef system in Kailua Bay.

Zone	G_F/A_h[a] $kgm^{-2}y^{-1}$	A_h/A_{Th}[b] (%)
N1	2.5	18%
N2	2.5	9%
N2*	0.5	7%
N3	2.0	2%
N4	2.5	1%
N5	1.0	10%
NCG	18.9	1%
NH	2.5	7%
S1	2.6	13%
S2	2.5	13%
S3	2.2	6%
S4	4.0	2%
SCG	26.8	1%
SH	2.5	10%
FRS	1.9	0%
Mean[c]	**2.66**	

Productivity "mode"	Rate $kgm^{-2}y^{-1}$	% of system
Low	≤ 1	17%
Moderate	1.9–4.0	81%
High	18.9–26.8	2%

[a] Gross framework production ÷ Habitat area in each zone (data from Table 3-16).

[b] Percent of Kailua Bay system (Habitat area in zone ÷ Total habitat area).

[c] Mean of observations weighted by zone habitat area.

Moderate rates of production are calculated for zones N3 and N4 along the walls of the channel margin. Nearly equal contributions by coral and algae produce 312.1 x 10^3 kgy^{-1} (G_F) in zone N3, while coralline algae dominate zone N4 (74% cover) and contribute 137.4 x 10^3 kgy^{-1} (G_{ace}) of the zone's 182.1 x 10^3 kgy^{-1} (G_F) of total framework production. Normalized framework production rates for zones N3 and N4 are 2.0 and 2.5 $kgm^{-2}y^{-1}$, respectively.

Although coral cover is entirely absent in zone SH, its extensive habitat area and almost complete coverage by encrusting coralline algae (94%) results in a high rate of gross framework production (G_F) of 2043.3 x 10^3 kgy^{-1}. Gross production by encrusting coralline algae is also particularly high in zone S2 (G_{ace} = 2543.6 x 10^3 kgy^{-1}) where the coverage is 88%. Framework production normalized by habitat area in both of these zones is 2.5 $kgm^{-2}y^{-1}$.

Similarly, despite low coral cover, zones N2 and NH have relatively high framework production rates ($G_{F(N2)}$ = 1939.1 $kgm^{-2}y^{-1}$; $G_{F(NH)}$ = 1500 $kgm^{-2}y^{-1}$), contributed largely by encrusting coralline algae that covers 86% and 94% of the reef substrate, respectively ($G_{ace(N2)}$ = 1708.4 $kgm^{-2}y^{-1}$; $G_{ace(NH)}$ = 1483.9 $kgm^{-2}y^{-1}$). Framework production normalized by habitat area in both of these zones is also 2.5 $kgm^{-2}y^{-1}$.

The skeletal growth of both corals and encrusting algae contribute a significant amount of carbonate to the reef edifice. Total gross production by corals (G_{Tc}) over the entire reef system in Kailua Bay is 12425 ± 745 x 10^3 kgy^{-1} (Table 3-17). Total gross production by coralline algae (G_{Tace}) is nearly equal, contributing 10765 ± 646 x 10^3 kgy^{-1}. By these calculations, 54% of the total framework production in Kailua each year is contributed by corals; 46% is contributed by encrusting coralline

algae. Total gross carbonate framework production (G_{TF}) in Kailua Bay is $23190 \pm 1391 \times 10^3$ kgy^{-1}.

These results attest to the significance of calcifying rhodophytes in the construction of the reef edifice. They also illustrate the dependence of productivity on habitat area as well as the coverage of living corals and coralline algae in each zone. In Table 3-18, framework production rates for each zone are normalized by habitat area to reveal patterns of productivity over the entire system. Gross framework production over 81% of the total habitat area in Kailua Bay is between 1.9–4.0 $kgm^{-2}y^{-1}$. Low rates (≤1 $kgm^{-2}y^{-1}$) are characteristic of 17% of the system. Very high productivity in 'coral gardens' (18.9–26.8 $kgm^{-2}y^{-1}$) is represented by only 2% of the entire habitat area. Framework-building corals and coralline algae produce carbonate at an average rate of 2.7 $kgm^{-2}y^{-1}$ over the entire reef system in Kailua Bay.

Reef Bioerosion

To estimate the production of unconsolidated sediment in the reef edifice, a model of erosion to break down the framework structure must be applied. The processes of micritization and mechanical erosion have not been directly assessed in this study but will be discussed in a later section. In Table 3-16, three different methods of calculating sediment production by bioerosion of the reef framework are applied to the physiographic data for the reef complex: the Kailua model (B_K), the Hubbard et al. (1990) model (B_H), and Spencer's (1985) model of limestone erosion in shallow-marine environments (B_S).

The Kailua model applies a bioerosion rate (in $kgm^{-2}y^{-1}$) to the habitat area of each zone based on data gathered from analysis of drilled reef cores from the bay (0.1–1.0 $kgm^{-2}y^{-1}$, Tables 3-4 and 3-8). The Hubbard et al. model turns 23% of the annual gross framework production (G_F) in each zone into unconsolidated sediment, all of which is released from the edifice into channels. The Spencer model applies a uniform rate of bioerosion (1.6 $kgm^{-2}y^{-1}$) to every zone based on the average rate of subtidal limestone erosion (measured using micro-erosion meter techniques and weight-loss tablets) on fringing reefs of Grand Cayman. The mass of unconsolidated carbonate sediment derived from bioerosion (and released from the reef) is calculated for each zone using each of these three methods, then summed for all zones (Table 3-16). Each of the three totals is then used in separate assessments of total sediment production (i.e. each is added to the direct sediment production). In this manner, results of the model applied in this study (based on five reef cores collected in Kailua) can be directly compared to the data generated using two other approaches.

Extrapolation of bioerosion rates from Kailua cores

Estimates of bioerosion rates derived from the analysis of drilled reef cores from five sites (in four zones: N1, N4, S1, S3) in Kailua Bay range between 0.1–1.0 $kgm^{-2}y^{-1}$ (Table 3-4), consistent with published observations of subtidal erosion in reefal settings (Table 3-7). For those zones that did not have bioerosion data from cores, a rate was applied from a zone of similar physiographic setting that did have a rate associated with it. For zones N2, N2*, and S2, a bioerosion rate of 0.3 $kgm^{-2}y^{-1}$ derived from a zone S3 core was applied based on the physiographic similarity of these regions to that of zone

S3. These sites all lie within a mid-platform strip north and south of the channel in water depths of 4–8 m, situated between scoured nearshore hardgrounds and the deeper, coral-covered platform farther offshore. The proximity of N3 and N4 to one another along the channel margin of the northern platform (refer to Figure 3-8) allows for the extrapolation of N4's core bioerosion rate (0.9 $kgm^{-2}y^{-1}$) to N3. Since NCG is a small region of luxuriant coral growth within the northern seaward platform zone N1, the bioerosion rate determined from the N1 core (0.5 $kgm^{-2}y^{-1}$) is applied to NCG. Similarly, the bioerosion rate determined from the S1 core (0.3 $kgm^{-2}y^{-1}$) is applied to the southern coral garden zone SCG. The proximity and similar physiographic settings of zones N5 to N1 allow for the extrapolation of N1's bioerosion rate (0.5 $kgm^{-2}y^{-1}$) to N5. Both of these zones lie on the seaward portion of the northern platform (mean water depth is ~11 m). To the final three zones lying in shallow, nearshore regions of scoured fossil hardgrounds (NH, FRS, and SH) a conservative rate of 0.2 $kgm^{-2}y^{-1}$ is applied. Extrapolating the data from four zones to the remaining ten is a simplified quantification of complex processes, but it provides an estimate of framework destruction based on field observations and allows for variability in different physiographic settings.

Results of bioerosion calculations (comparing three models)

For each zone (vertical columns in Table 3-16), the assigned bioerosion rate (B_K in $kgm^{-2}y^{-1}$) is multiplied by the habitat area (A_h), resulting in an estimated mass of sediment derived annually from bioerosion of the reef framework in that zone (SB_K in kgy^{-1}, Table 3-16). The total amount of bioeroded sediment produced in the system is the sum of SB_K for all zones (SB_{TK}). (These and other equations are summarized in Table

3-6.) In general, offshore regions of the reef platform (e.g. zones N1, N3–5, and NCG) have higher rates of bioerosion (0.5–0.9 $kgm^{-2}y^{-1}$) than nearshore regions (e.g. 0.2–0.3 in NH, N2, SH, S2, and FRS). For example, in zone N1, the mass of unconsolidated coral and coralline algal sediment derived from bioerosion of the reef edifice at a rate of 0.5 $kgm^{-2}y^{-1}$ (B_K) is 746.5 x 10^3 kgy^{-1} (SB_K), the highest over the entire system. In this case, a high rate of sediment production is coincident with a high rate of gross framework production. In zones NCG and SCG where coral cover and diversity are quite high, but habitat area is relatively small, a bioerosion rate of 0.5 $kgm^{-2}y^{-1}$ yields only 51.3 and 34.1 x 10^3 kgy^{-1} of sediment. This illustrates the complex interplay between habitat extent, organism cover, morphology, growth rate, and bioerosion rate in determining the sediment yield from bioerosion in a reef setting.

Applying the Kailua model of bioerosion, the *total* mass of unconsolidated carbonate sediment produced by bioerosion and released from the reef framework in Kailua Bay is 2983 ± 179 x 10^3 kgy^{-1} (SB_{TK}) (Table 3-16). For comparison, the Hubbard et al. (1990) approach is also used to calculate the total mass of sediment produced by bioerosion of and subsequent release from the reef framework. Turning 23% of total gross framework production into loose sediment in channels via the Hubbard et al. model would yield 5333 ± 320 x 10^3 kgy^{-1} (SB_{TH}). Similarly, the Spencer (19883) approach is used to calculate the total mass of sediment produced. Applying a subtidal erosion rate of 1.6 $kgm^{-2}y^{-1}$ to the entire reef in Kailua would result in the production of 13392 ± 804 x 10^3 kg of unconsolidated carbonate sediment each year (SB_{TS}).

Sediment yield derived from bioerosion (in kgy^{-1}) is converted to volume using an average value of bulk sediment density determined from Kailua sediments (1176 ± 80

kgm^{-3}). This value is consistent with that used in the Hubbard et al. study (1.2 gcm^{-3} or 1200 kgm^{-3}). The volume of sediment produced by applying zone-specific bioerosion rates over the Kailua system yields an annual framework-derived sediment volume of 2536 ± 337 m^3 (V_{TK}). The Hubbard et al. model in Kailua yields 4535 ± 603 m^3 (V_{TH}), and the Spencer model yields 11388 ± 1515 m^3 (V_{TS}).

Summary of framework processes

Annual gross framework production and its subsequent bioerosion into unconsolidated sediment (using the Kailua model) are summarized for each physiographic zone in Kailua Bay (in vertical columns) and totaled in Table 3-17. Gross production by corals over the entire reef system (Total G_c) is 12425 ± 745 x 10^3 kgy^{-1} or 54% of total gross framework production. The growth of encrusting coralline algae adds 10765 ± 646 x 10^3 kgy^{-1} (Total G_{ace}) to bring the total gross framework production rate (Total G_F) up to 23190 ± 1391 x 10^3 kgy^{-1}. Assuming bioerosion of both corals and algae occurs without preference, the volume of coral sediment produced each year is estimated to be 1370 ± 182 m^3. Coralline algae contribute 1177 ± 156 m^3 to the total volume of framework-derived sediment produced annually (V_K = 2536 ± 337 m^3).

Framework-derived sediment production during the Holocene

Applying the annual volume of sediment produced by erosion of the reef edifice over the last 5000 years that Kailua Bay has been wholly inundated by post-glacial sea level (Fletcher and Jones 1996, Grossman and Fletcher 1998) results in an estimate of Holocene-aged, framework-derived sediment of 126.81 ± 16.87 x 10^5 m^3 (HV_{TK} in Table

3-16). By comparison, the Hubbard et al. model of bioerosion predicts $226.77 \pm 30.16 \times 10^5$ m^3 of framework-derived sediment would have been produced over that time (79% more than predicted by the Kailua model), and Spencer's predicts $569.40 \pm 75.73 \times 10^5$ m^3 (3.5 times more).

Direct Sediment Production

Halimeda

Table 3-9 summarizes the standing crop data and associated carbonate production of *Halimeda* at 14 sites in Kailua Bay. Dense meadows of lithophytic *Halimeda opuntia* flourish in 2–10 m water depths in Kailua Bay. Mature 'leaves' of this species contain up to 90% $CaCO_3$ by dry weight, and the flakes and fragments that result from organic tissue decomposition are common constituents of beach and submarine sediments in Kailua.

The term 'bioherm' has been used to describe *Halimeda* accumulations 5–50 m thick and hundreds of km in extent on the Great Barrier Reef (e.g. Davies and Marshall 1985). The term is used loosely here, as the features in Kailua are generally coalesced sandy mats of *H. opuntia* ~0.5 m in height with surface areas of several hundred m^2. Such a bioherm covers 100% of a bottom area of ~500 m^2 at site KT and has a standing crop biomass of 3.6 kgm^{-2}. Because carbonate content in the thalli is high (90%), carbonate production is 3.2 kgm^{-2}. Applying a turnover rate of twice per year, sediment production by this bioherm is estimated to be 6.4 $kgm^{-2}y^{-1}$, or 3224 kgy^{-1} based on its 100% cover of the 500 m^2 area.

The biomass of dense-growth *H. opuntia* meadows at sites SPX and T2 is 3.7 kgm^{-2}. Carbonate content is 90%, thus the rate of carbonate production is 3.3 kgm^{-2}. Biannual turnover of the meadows produces sediment at a rate of 6.7 $kgm^{-2}y^{-1}$. Annual sediment production at site SPX is thus 4829 kgy^{-1} and at site T2 is 3330 kgy^{-1} (owing to the 225 m^2 difference in areal extent between the two meadows). The combined rate of sediment production by these meadows is 11.4 x 10^3 kgy^{-1}.

Scattered clumps of highly-calcareous *Halimeda opuntia* grow in shallow, nearshore regions of the bay, covering up to 60% of the habitat area where fossil outcrops close to shore provide shallow, energetic habitats (OKLA3-1, 3-M, and 3-2). In the hardgrounds north of the triangular sand body (zone NH), sediment production by *Halimeda* occurs at a rate of 0.6–0.9 kgm^{-2}, yielding a total of 137.0 x 10^3 kg of calcareous sediment annually.

A portion of zone N3 supports significant *Halimeda* growth along the margins of the sand channel. At site F6, *H. opuntia* beds cover ~4% of the bottom in an area of ~16000 m^2. Sediment production is estimated to be 3.7 m^3y^{-1} in this region. In the central sandy region, outcrops of fossil reef to 1 m in relief supply substrate for lithophytic *Halimeda opuntia*. Three-quarters of the zone FRS is sparsely-covered by the algae (11% of the sea floor at site F8), but the large surface area of these outcrops support the production of 74.9 x 10^3 kgy^{-1} of *Halimeda* sediment annually. The remaining quarter of the region lies within the 200-m-wide band close to shore in which *H. opuntia* covers 60% of the rocky sea floor (similar to OKLA3 and OKLA5). In this area, sediment production by *Halimeda* is 33.4 x 10^3 kgy^{-1}. The combined total for zone FRS is thus 108.3 x 10^3 kgy^{-1}.

Halimeda discoidea is generally lower in carbonate content (50%) than *H. opuntia*. In Kailua Bay, *H. discoidea* is generally found in shallow waters of the extensive nearshore hardgrounds region and in the lee of Popoia Island (portions of the zone SH). In these settings (a total estimated surface area of 37 x 10^4 m^2), it grows in low, dispersed clumps covering ~30% of the rocky (PO1) or sandy (PO2) sea floor. Biomass is sparse for sand-dwelling forms (0.3 kgm^{-2}) and relatively dense for lithophytic forms (3.0 kgm^{-2}), thus the total seafloor area of this setting is equally 'divided' between the two growth forms (184.9 x 10^3 m^2 each in Table 3-9). Lithophytic forms produce sediment at a greater rate (164.6 x 10^3 kgy^{-1}) than do those plants anchored in sand (18.1 x 10^3 kgy^{-1}).

Halimeda opuntia also inhabits the nearshore hardgrounds area south of the central sand body. At sites JY2 and OKLA-5 (in zone SH), this species covers 20–60% of the sea floor, contains 72–76% $CaCO_3$, and produces sediment at rates of 43.9 x 10^3 kgy^{-1} and 79.5 x 10^3 kgy^{-1}, respectively.

Although *Halimeda* is a prolific inhabitant of shallow, well-lit, nearshore regions, it is generally rare to absent in the reef tracts offshore. Production by the algae is considered in budget calculations only for the zones (or portions thereof) listed above. The rate of sediment production by *Halimeda* is summarized for each zone in Table 3-9 ('Zone SPR' in $kgm^{-2}y^{-1}$). Total annual sediment production by *Halimeda* in Kailua Bay is 589.6 ± 70.2 x 10^3 kgy^{-1}.

These estimates of production in Kailua Bay are consistent with other rates of *Halimeda* production potential in subtropical populations. Standing crop biomass of *Halimeda* meadows on the Great Barrier Reef ranges between 0.5–4.6 $kgm^{-2}y^{-1}$ depending on the species, with mean carbonate content averaging 94% for *H. opuntia* and

73% for *H. discoidea* (Drew and Abel 1985). Drew (1983) determined reefal *Halimeda* production was 1.8–3.5 kgm^{-2} and that half of the standing crop was lost every 80 days (turnover = 2.3 y^{-1}), resulting in an annual sediment production rates between 4–8 $kgm^{-2}y^{-1}$. Modern *Halimeda* populations on the Great Barrier Reef produce calcareous sediment at rates of 2.2–2.5 $kgm^{-2}y^{-1}$ (Drew 1983, Drew and Abel 1985), in Tahiti at 2.3 $kgm^{-2}y^{-1}$ (Payri 1988), and in the Bahamas at 2.4 $kgm^{-2}y^{-1}$ (Freile et al. 1995). In an assessment of *Halimeda*'s role in global carbonate production, Hillis (1997) assigns *Halimeda* production rates to three different environmental settings: ~2 $kgm^{-2}y^{-1}$ for fore-reef and slope populations; ~3 $kgm^{-2}y^{-1}$ for populations of lagoons, banks, bays, and bioherms; and ~4 $kgm^{-2}y^{-1}$ for shallow regions of high physical disturbance.

Benthic foraminifera

Table 3-10 summarizes the sediment production rate of benthic foraminifera in Kailua Bay based on standing crop. This technique has proven valuable in assessing the density of field populations of reef-dwelling foraminifera (Hallock 1981, 1984; Hallock et al. 1995; Harney et al. 1999) and is here applied in assessing the contribution of the organisms to a reef budget. Sediment production rates estimated from the three samples analyzed in this study (0.02–0.14 $kgm^{-2}y^{-1}$) are consistent with those published for Oahu (38–500 $gm^{-2}y^{-1}$, Hallock 1981) and for Kailua Bay specifically (109–405 $gm^{-2}y^{-1}$, Harney et al. 1999). These rates are applied to available (non-coral) habitat area in each physiographic zone across the reef platform in Kailua Bay, yielding rates of annual sediment production in kgy^{-1} (Table 3-11).

Sediment production rates (SPR) are highest in zones N1 and S1 (0.13 $kgm^{-2}y^{-1}$) and N4 (0.14 $kgm^{-2}y^{-1}$) (Table 3-11). Owing to the availability of large areas of suitable substrate, annual sediment production (ASP) is highest in zones N1 (91 kgy^{-1}) and S2 (82 kgy^{-1}). Rates of 37–55 kgy^{-1} are typical over most of the reef system (zones N2, N2*, N5, S1, and S3). Low sediment production by forams (ASPs of 6.1–10.4 x 10^3 kgy^{-1}) is found in nearshore hardgrounds (NH and SH) and in zones N4 and S4. Zones NCG and SCG are regions of high coral cover and thus low sediment production rates for foraminifera (0.2 and 0.5 x 10^3 kgy^{-1}, respectively). Only 3986 m^2 of suitable (consolidated) substrate are found in zone FRS, thus annual sediment production in this zone is very low (0.04 x 10^3 kgy^{-1}), despite equitable standing crop.

The rate of sediment production by benthic foraminifera is summarized for each zone in Table 3-11 ('Zone SPR' in $kgm^{-2}y^{-1}$). Total annual sediment production by benthic foraminifera in Kailua Bay is 442.3 ± 69.6 x 10^3 kgy^{-1}.

Molluscs

Tables 3-12 and 3-13 summarize the standing crop and associated sediment production of micromolluscs in Kailua Bay. Sediment production rates (SPR) are highest in *Halimeda* meadows where small bivalves and gastropods live in high numbers. In the rocky meadow at site PO1, these organisms produce sediment at a rate of 1.79 $kgm^{-2}y^{-1}$; in the 'bioherm' at site KT, the SPR is 0.71 $kgm^{-2}y^{-1}$.

Shallow depths in the hardgrounds near shore (NH, FRS, and SH) are host to micromollusc populations producing sediment at a rate of 0.59 $kgm^{-2}y^{-1}$.

Over most of the seaward reef platform (zones N1, N5, S1, and S4), mollusc SPRs are 0.21–0.23 $kgm^{-2}y^{-1}$; on the landward reef platform (zones N2, N2*, S2, and S3) production rates fall to 0.13 $kgm^{-2}y^{-1}$. Owing to high coverage of living coral, mollusc sediment production rates are <0.05 $kgm^{-2}y^{-1}$ in zones NCG and SCG. These rates are applied to available habitat area in each physiographic zone across the reef platform in Kailua Bay, yielding rates of annual sediment production in kgy^{-1} (Table 3-13).

Annual sediment production (ASP) by micromolluscs in Kailua Bay is highest in the northern and southern hardgrounds regions (zones NH and SH). Owing to large areas of consolidated (non-coral) substrate in these areas, ASPs are 354.9 x 10^3 kgy^{-1} and 488.7 x 10^3 kgy^{-1}, respectively. Zones N1, N5, and S1 also have high ASPs (149.2, 111.6, and 87.8 x 10^3 kgy^{-1}, respectively). Owing to the dense population of micromolluscs living in *Halimeda* meadows, the combined ASP of sites PO1 and KT is 198.5 x 10^3 kgy^{-1}. Low cover of non-coral substrate in zones NCG and SCG results in ASP estimates of ≤1.0 x 10^3 kgy^{-1}. Elsewhere in Kailua Bay, the mass of sediments of micromollusc origin produced annually is 17.4–52.8 x 10^3 kgy^{-1}.

The rate of sediment production by micromolluscs is summarized for each zone in Table 3-13 ('Zone SPR' in $kgm^{-2}y^{-1}$). Total annual sediment production by micromolluscs in Kailua Bay is 1566.3 ± 221.6 x 10^3 kgy^{-1}.

Articulated coralline algae

Table 3-14 summarizes the standing crop data and associated sediment production rate of the articulated coralline alga *Porolithon gardineri* at four sites in Kailua Bay. The rather simple method of estimating this alga's carbonate production based on its standing

crop provides results that are consistent with data collected in detailed growth-rate studies (~20 $kgm^{-2}y^{-1}$, Agegian 1985). Carbonate production ranges between 8.5–17.8 kgm^{-2} depending on the degree of ramification of the skeleton and on the energetic setting of the sampling site. Once-yearly turnover of the population will produce sediment at rates (SPR) of 17–35.6 $kgm^{-2}y^{-1}$. These rates are applied to zones in which the algae were quantitatively mapped (12 sites total in zones N2, N3, N5, NH, and S2; Table 3-15). Assigning a rate to a zone is based on general habitat similarity to the four sites where production data was actually collected. The high rate of production found at site F7 (17.8 $kgm^{-2}y^{-1}$) is applied only to site F7 and its immediate area (estimated at 20 x 10^3 m^2 using image analysis); while the rest of that zone (N2) is assigned a more conservative rate of 10.0 $kgm^{-2}y^{-1}$. A rate of 14.1 $kgm^{-2}y^{-1}$ was applied to zone N3 based on the sample collected at KY in that zone. Similarly, a rate of 15.2 $kgm^{-2}y^{-1}$ is assigned at site NP8 where it was collected and at site NP7 based on the habitat similarity between zones N2* and N5. Since no samples were collected from the southern part of the reef platform, a conservative estimate of 10 $kgm^{-2}y^{-1}$ is applied in zone S2, the only one in which *P. gardineri* was mapped.

Individual clumps of the articulated coralline algae *P. gardineri* were present on 12 of the 51 transect-mapping sites, ranging in cover from 1 to 15%. Annual sediment production (ASP) for each region is thus a function of the production rate, habitat area, and percent articulated algae cover.

For zones in which several observations of percent cover exist, the total habitat area is divided among the observations of percent cover. For example, the total habitat area of zone N2 (764 x 10^3 m^2) is apportioned to regions within it based on the abundance of

coralline algae at mapped sites: a 20,000 m^2 area is reserved for the high rate of production around site F7; of the remainder, half was applied to algal coverage of 1%; a quarter to coverage of 8%, and a quarter to 15%. Resultant estimates of ASP for each region are presented in Table 3-15.

Direct sediment production by articulated coralline algae is high compared to other direct producers. In zones N2 and N2* annual sediment production (ASP) is 431.4 x 10^3 kgy^{-1} and 332.4 x 10^3 kgy^{-1}, respectively. Owing to a smaller habitat area and generally sparse cover of articulated algae in zone N3, annual sediment production rates are fairly low (31.2 x 10^3 kgy^{-1}). In zone N5, ASP is 242.5 x 10^3 kgy^{-1}. In the hardgrounds near shore (zone NH), annual sediment production by the algae is very high, estimated at 608.9 x 10^3 kg each year. On the southern portion of the reef platform, the alga was mapped in only one zone (S2); its sediment productivity in that region is also among the highest rates, estimated at 247.4 x 10^3 kgy^{-1}.

The rate of sediment production by these algae is summarized for each zone in Table 3-15 ('Zone SPR' in $kgm^{-2}y^{-1}$). Total annual sediment production by articulated coralline algae in Kailua Bay is 1900.0 ± 204.2 x 10^3 kgy^{-1}.

Total direct sediment production

The total annual sediment production of *Halimeda*, forams, molluscs, and articulated coralline algae in various physiographic zones in Kailua Bay are summarized in Table 3-19. Total annual direct sediment productivity over the system is 4498.2 ± 565.0 x 10^3 kgy^{-1}. To this annual mass, *Halimeda* contributes 13%, forams 10%, molluscs 35%, and articulated coralline algae 42%. These results are converted to sediment volumes using an

approximation for sediment density determined from sediment samples collected in Kailua (1176 ± 80 kgm^{-3}). *Halimeda* sediments are far less dense than the 'average' sediment assemblage, thus a conversion factors of 500 kgm^{-3} (*Halimeda* sediment, Drew and Abel 1985) is applied to convert the alga's annual rate of sediment production into annual volume. The total volume of sediment produced directly by the biological activities of these organisms in Kailua Bay is 4502.8 ± 835.0 m^3y^{-1}. To this volume, *Halimeda* contributes 26%, forams 8%, molluscs 30%, and articulated algae 36%.

Direct sediment production during the Holocene

Applying the volume of sediment produced annually by direct means (4502.8 ± 835.0 m^3y^{-1}) to the last 5000 years that Kailua Bay has been wholly inundated by post-glacial sea level results in an estimate of Holocene-aged, directly-derived sediment of 225.1 ± 41.8 x 10^5 m^3 (Table 3-20). This volume of direct sediment production by calcareous and coralline algae, molluscs, and forams constitutes 64% of the total volume of unconsolidated calcareous sediment produced in Kailua Bay since 5000 yr BP (349.15 ± 58.62 x 10^5 m^3, Table 3-20).

Table 3-19. Summary of direct sediment production in Kailua Bay.

ANNUAL SEDIMENT PRODUCTION (ASP, x10^3 kgy^{-1}					ANNUAL SEDIMENT VOLUME (m^{3}y^{-1})[a]				
Zone	*Halimeda*	Forams	Molluscs	Articul. cor. algae	Zone	*Halimeda*	Forams	Molluscs	Articul. cor. algae
N1	–	91.1	149.2	–	N1	–	77.5	126.9	–
N2	–	55.3	35.7	431.4	N2	–	47.0	30.3	366.8
N2*	–	38.3	24.7	332.4	N2*	–	32.6	21.0	282.7
N3	1.9	9.2	11.7	37.4	N3	3.7	7.8	9.9	31.8
N4	–	8.0	7.3	–	N4	–	6.8	6.2	–
N5	–	42.0	111.6	242.5	N5	–	35.7	94.9	206.2
NCG	–	0.2	0.8	–	NCG	–	0.2	0.6	–
NH	137.0	6.1	354.9	608.9	NH	274.0	5.2	301.8	517.8
S1	–	53.6	87.8	–	S1	–	45.6	74.7	–
S2	–	81.8	52.8	247.4	S2	–	69.6	44.9	210.3
S3	–	37.2	17.4	–	S3	–	31.6	14.8	–
S4	–	10.4	22.1	–	S4	–	8.8	18.8	–
SCG	–	0.5	1.0	–	SCG	–	0.4	0.8	–
SH	331.0	8.4	488.7	–	SH	662.1	7.1	415.5	–
FRS	108.3	0.0	2.3	–	FRS	216.7	0.0	2.0	–
Meadows[b]	11.4	–	198.4	–	Meadows	22.8	–	168.7	–
Sum	589.6	442.3	1566.3	1900.0	Sum	1179.2	376.1	1331.9	1615.6
(±)[c]	70.2	69.6	221.6	204.2	(±)[e]	140.4	91.0	299.4	304.2
Total	**4498.2 ± 565.0 x 10^3 kgy^{-1}**				Total[e]	**4502.8 ± 835.0 m^{3}y^{-1}**			
Contrib.[d]	13%	10%	35%	42%	Contrib.[f]	26%	8%	30%	36%

[a] Volume converted from mass using density: *Halimeda* sediment = 500 kgm^{-3} (Drew and Abel 1985); others = 1176±80 kgm^{-3} "average" sediment density (see text).

[b] Combined result of all *Halimeda* meadows sampled.

[c] Uncertainty of annual production rate by each organism.

[d] Percent contribution of each organism to the total mass of directly-produced sediments.

[e] Includes additional uncertainty of converting mass to volume.

[f] Percent contribution of *Halimeda* is greater due to lower density.

Table 3-20. Identifying sediment source from budget calculations. Applying the volume of sediment produced annually by direct means (4502.8 ± 835.0 m^3y^{-1}) to the last 5000 years that Kailua Bay has been wholly inundated by post-glacial sea level results in an estimate of Holocene-aged, directly-derived sediment of 225.1 ± 41.8 x 10^5 m^3. This volume of direct sediment production by calcareous and coralline algae, molluscs, and forams constitutes 64% of the total volume of unconsolidated calcareous sediment produced in Kailua Bay since 5000 yr BP. Dividing the estimated volume of calcareous sediment produced by each organism over the last 5000 years *by* the total volume produced in the Holocene (351.96 ± 58.62 x 10^5 m^3) reveals the carbonate sediment contribution made by each organism.

Total Holocene volume produced			351.96 ± 58.62 x 10^5 m^3
Source	Annual	Holocene	% of total Holocene
Framework production (m^3)	2536 ± 337	126.8 ± 16.9	36%
Direct (m^3)	4503 ± 835	225.1 ± 41.8	64%
Organism	Annual	Holocene	%
Coral	1359 ± 61	67.9 ± 3.1	19%
Encrusting coralline algae	1177 ± 276	58.9 ± 13.8	17%
Halimeda	1179 ± 140	59.0 ± 7.0	17%
Foraminifera	376 ± 91	18.8 ± 4.5	5%
Molluscs	1332 ± 299	66.6 ± 15.0	19%
Articulated coralline algae	1616 ± 304	80.8 ± 15.2	23%

DISCUSSION

PART I: Sediment Storage

Submarine reservoirs

Table 3-21 summarizes the volume of biogenic sediments in various Kailua reservoirs. All sediment volumes in the table and text have been corrected for 40% porosity (after Friedman et al. 1992). Submarine reservoirs are divided into five general deposits (Figure 3-10). The shore-normal paleo-channel bisecting the fringing reef is the most significant submarine sand reservoir and is a large conduit for its transport. Based on limited jet-probings (Casciano 1979), the channel is estimated to contain at least $2220 \pm 185 \times 10^3$ m^3 of sand. The surface area of reef-top sand bodies are multiplied by sediment thicknesses (measured by jet-probing or inferred from the depths of adjacent bodies) to estimate their total sediment volume ($145 \pm 15 \times 10^3$ m^3 and $604 \pm 60 \times 10^3$ m^3 for the north and south portions of the reef platform, respectively). The volume of sediment in the triangular nearshore sand field landward of the channel body is estimated to be $285 \pm 29 \times 10^3$ m^3 (based on jet-probings in the region). A seismic line along the reef front in 25 m water depth (Ericksen et al. 1997) reveals sub-bottom characteristics at the sand channel's seaward mouth, suggesting the fossil reef margins converge gradually and asymmetrically 12–15 m below the sea floor to form the channel basement. The volume of sediment at the seaward mouth of the channel (extending out 500 m from the reef front in a sub-circular shape) is estimated to be $471 \pm 47 \times 10^3$ m^3. The total volume of sediment stored in submarine reservoirs of Kailua Bay is $3726 \pm 336 \times 10^3$ m^3.

Subaerial reservoirs – beach face and coastal plain

Figure 3-11 illustrates a generalized beach profile based on survey data collected from the central portion of Kailua beach. Using profile data, Norcross et al. (1998) calculated the volume of sand stored in the beach face (from the berm crest to the sand-rock interface offshore) to be $600 \pm 30 \times 10^3$ m^3.

Coastal plain deposits contain a significant volume of carbonate sand and silt in both low-lying Kawainui Marsh and in the sandy Kailua Accretion Barrier (KAB) on which the town is built (Figure 3-12). The locations of sediment cores from the marsh and KAB (collected over the last six decades by researchers, Honolulu geotechnical firms, and the Army Corps of Engineers) are illustrated in Figure 3-13. The numbered transects X1 and X2 in this figure correspond to the cross-section diagrams in Figures 3-14 and 3-15, respectively. Graphical reconstructions of the carbonate sand and silt underlying the marsh and KAB are modified from Kraft (1984) in conjunction with sediment core logs from additional sources (see figure legend for references).

Figure 3-14 is a NW–SE cross-section of Kawainui Marsh and the sandy KAB along transect line X1–X1'. The location and depth of 12 sediment cores along this transect are illustrated to scale in the figure. Arrows point to radiocarbon ages of bulk sediments collected offshore (a, from Harney et al. 2000) and skeletal fragments in lagoonal mud (b, from Kraft 1984). Radiocarbon ages and core lithologies (Kraft 1982, 1984; Athens and Ward 1991) indicate Kawainui Marsh was a marine embayment during the mid- to late Holocene sea-level high stand and became an entirely terrestrial wetland ca. 2200 yr BP due to a fall in relative sea level. This resulted in the abandonment of lagoonal

sediments in the marsh and stranded a thick berm of calcareous sand (the KAB) just landward of the new shoreline position.

Cores in the marsh penetrate 15 m down through layers of peat, terrestrial mud, and lagoonal sediment. Two radiocarbon ages of carbonate skeletal material found 7 m and 15 m below the marsh surface (Kraft 1984) indicate these sediments were deposited in the last 5000 years. Sediment cores in the KAB suggest that a deposit of medium- to coarse-grained calcareous sand 3–10 m thick underlies Kailua town. One core (#417, from Stearns 1941) penetrated more than 10 m of marine sand underlain by another 40 m lagoonal silt. None of the cores reached fossil reef or basalt basement. Submarine jet-probings of nearshore sand bodies performed in this study (c, Figure 3-14) indicate sediment thickness reaches 7 m in places.

Figure 3-15 is an enlarged cross-section along the SE–NE transect line X2–X2'. The location and depth of 10 sediment cores along this transect are illustrated to scale in the figure. The thickness of the central portion of the berm suggests it is the onshore expression of the meandering paleostream channel bisecting the fringing reef offshore. No sediment cores have been found that penetrate alluvium or basalt basement beneath the Kailua coastal plain, suggesting a long and complex carbonate sedimentation history.

Sediment core logs and the graphical interpretations illustrated in Figures 3-14 and 3-15 were used to estimate the volume of marine sediment stored in the coastal plain. Image analysis of these graphics provided an estimate of the surface area and thickness of the sediment deposits. Volume was calculated along each transect and extrapolated over the length of the marsh and berm. Approximately $10049 \pm 1809 \times 10^3$ m^3 of Holocene-aged marine sediment is stored in the Kailua coastal plain.

Table 3-21. Sediment storage in submarine and subaerial reservoirs of Kailua, Oahu.

Submarine reservoirs	Area[a] ($x10^3$ m^2)	Storage volume[b] ($x10^3$ m^3)	Sediment volume[c] ($x10^3$ m^3)	% of total storage	% of Holocene production
Channel[d]	300	3700	**2220** ± 185	15%	6%
Reef sand bodies (north)	132	242	**145** ± 15	1%	0%
Reef sand bodies (south)	295	1007	**604** ± 60	4%	2%
Nearshore triangle	1000	475	**285** ± 29	2%	1%
Offshore mouth	163	785	**471** ± 47	3%	1%
Total submarine storage	1890	6210	**3726** ± 336	26%	11%

Subaerial reservoirs	Storage volume $x10^3$ m^3	Sediment volume[c] ($x10^3$ m^3)	% of total storage	% of Holocene production
Beach[e]	1000	**600** ± 30	4%	2%
Kailua Accretion Barrier (KAB)[f]	16749	**10049** ± 1809	70%	29%
Total subaerial storage	17749	**10649** ± 1839	74%	31%

TOTAL sediment storage	**14375** ± 2174	**41%**

[a] Surface area measured in image analysis.

[b] Raw storage volume of reservoir.

[c] Volume of sediment stored in reservoir (40% porosity; Friedman et al. 1992).

[d] Channel volume estimate converted from yd^3 data in Casciano (1979).

[e] Estimated from beach profile data (Norcross et al. 1998; see Figure 3-12).

[f] Estimated using core logs (see Figures 3-14, 3-15, and 3-16 and Appendix C).

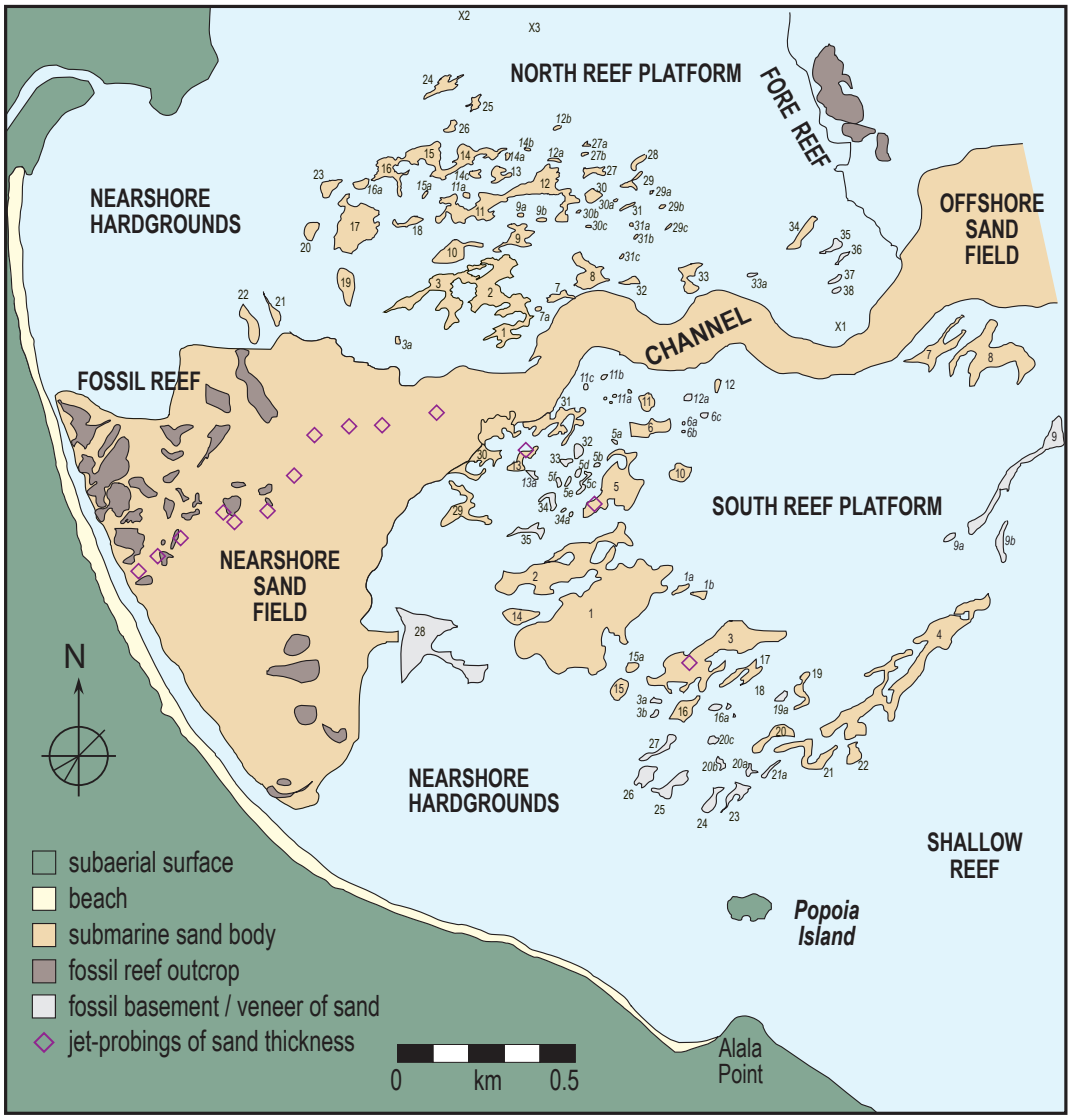


Figure 3-10. Submarine sediment storage in Kailua Bay. Sediment volume was calculated using the areas of numbered sand bodies (measured in image analysis) and their respective thicknesses (measured by jet-probing, inferred from adjacent bodies, or cited in Casciano 1979).

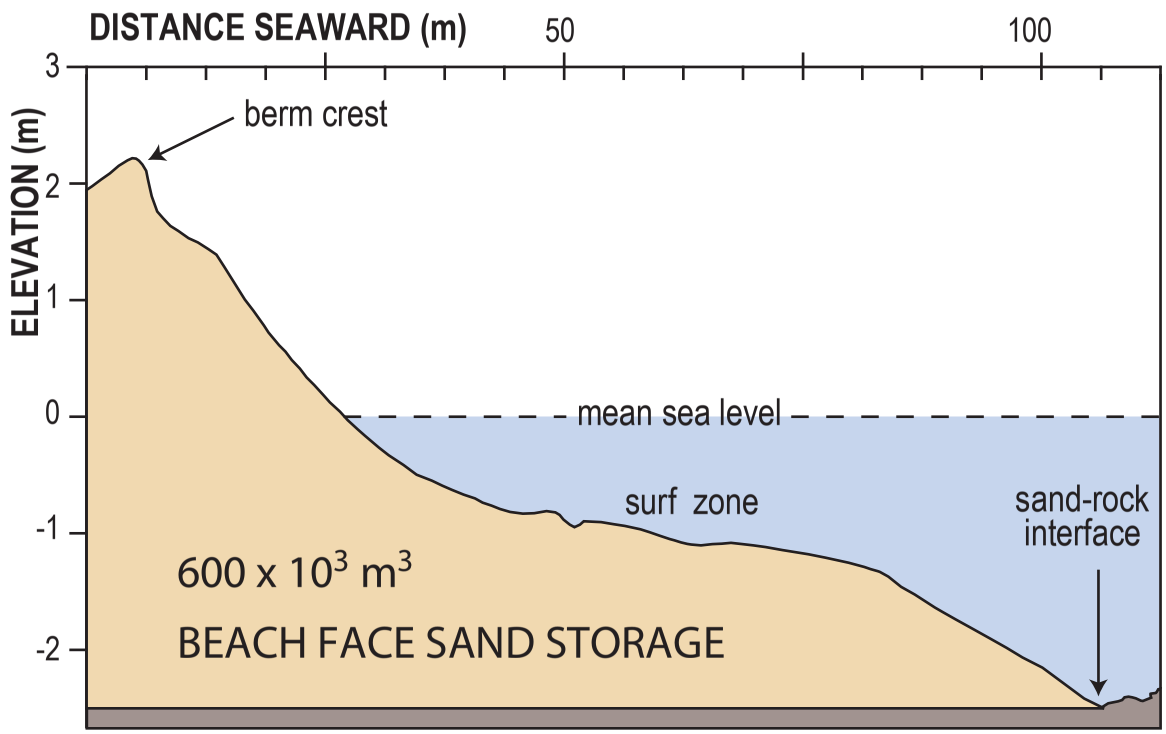


Figure 3-11. Idealized beach profile in Kailua. Sedimentvolume under the profile is calculated from the berm crest (the landward extent of the beach) to the "depth of closure" at the sand-rock interface offshore (Norcross et al. 1998).

Figure 3-12. Kawainui Marsh (green region at center and left), Kailua town (center), and Bay (right).

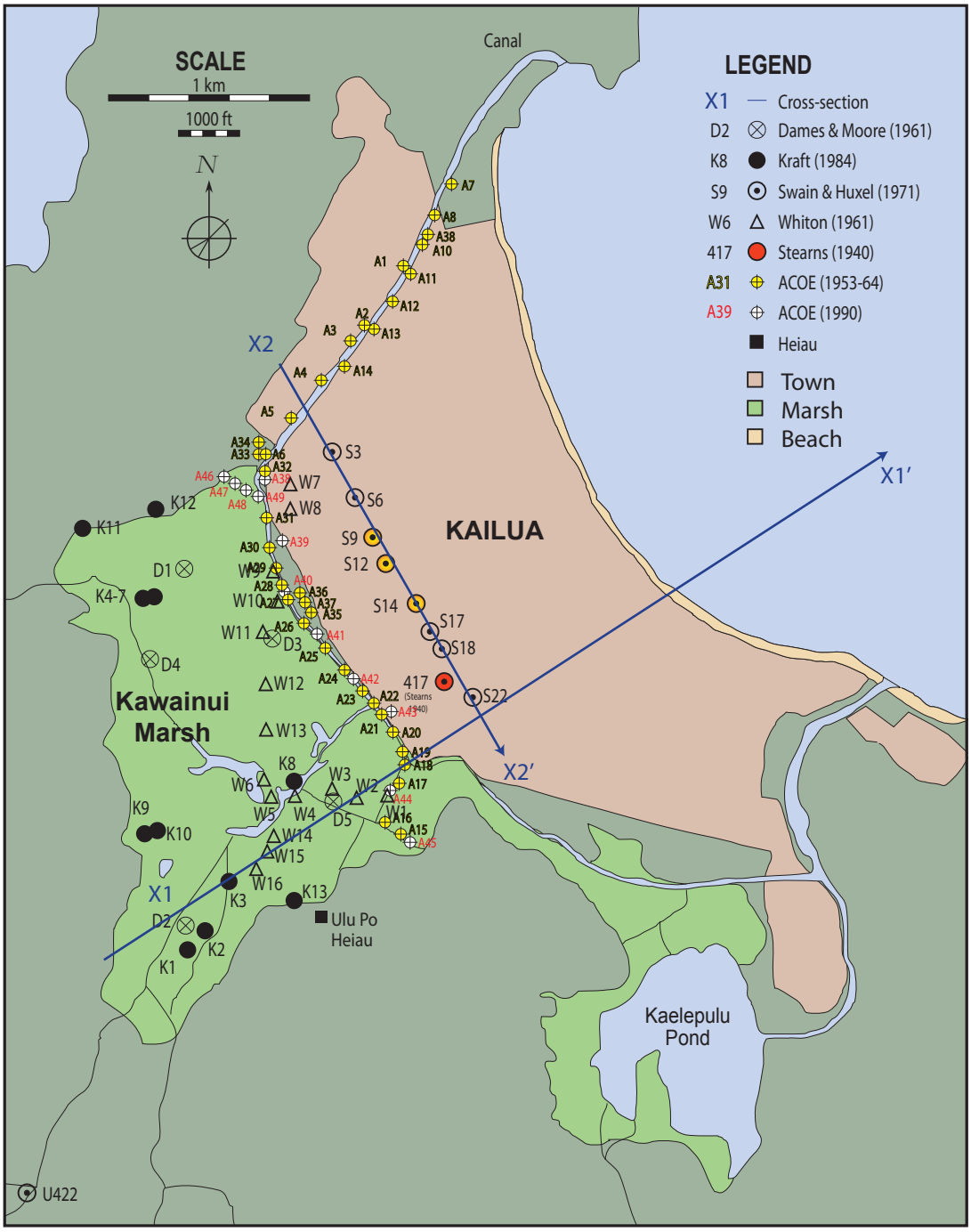


Figure 3-13. Location of sediment cores in Kawainui Marsh and Kailua town used in this study. Numbered transects X1 and X2 correspond to the cross-sections in Figures 3-14 and 3-15.

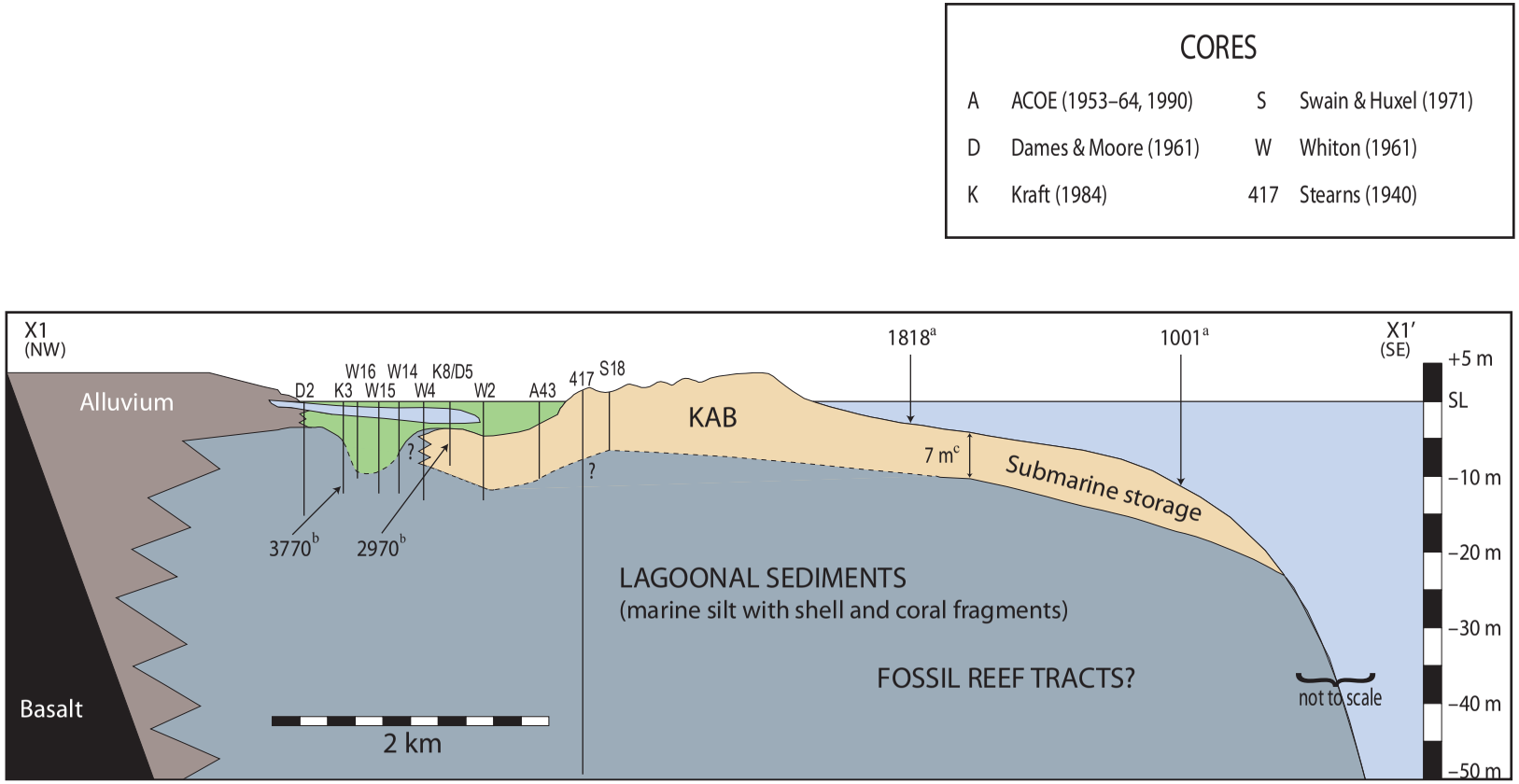


Figure 3-14. Cross-section of Kawainui Marsh and the sandy Kailua Accretion Barrier (KAB) along transect X1. Arrows point to radiocarbon ages of bulk sediments (a, from Harney et al. 2000) and skeletal fragments in lagoonal mud (b, from Kraft 1984). One core (417, from Stearns 1941) penetrated nearly 50 m of marine sediment. Jet-probing of nearshore submarine sand bodies indicates sediment is up to 7 m thick in places (c). Section modified from Kraft 1984).

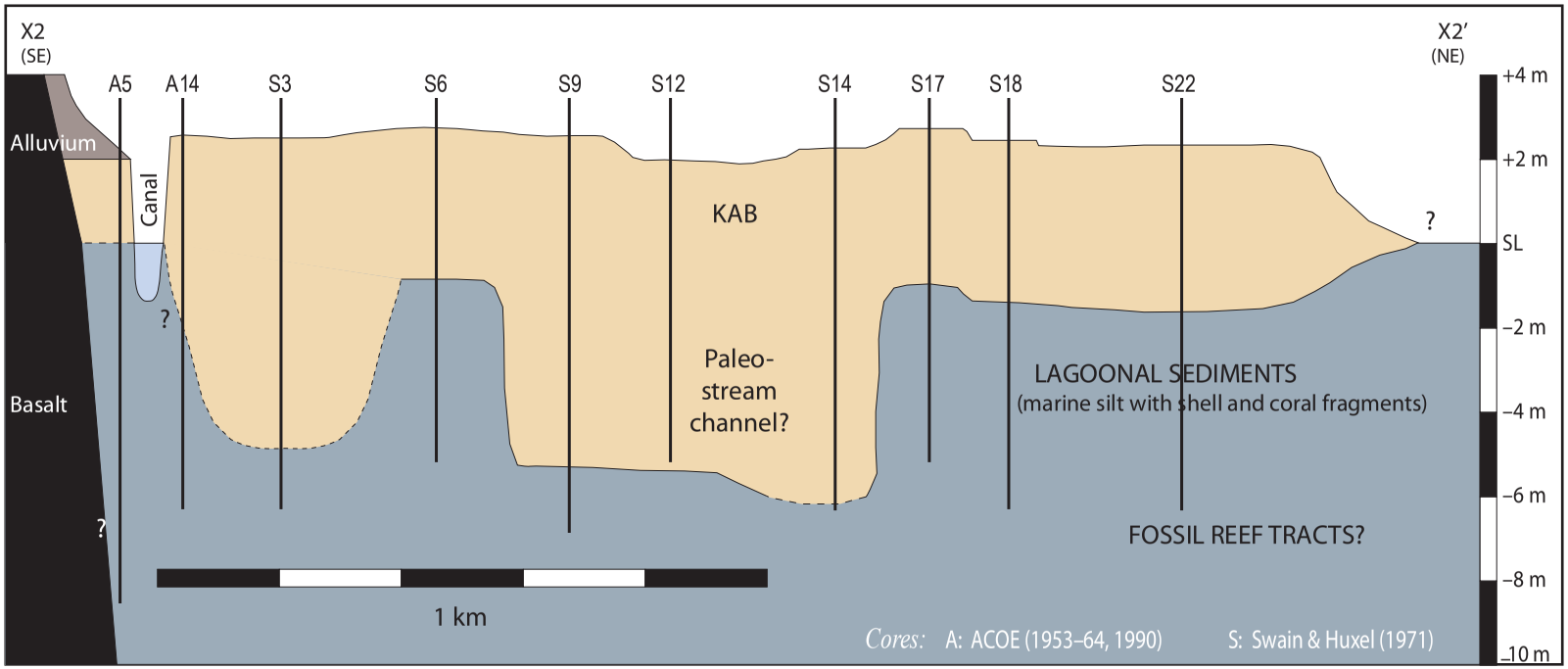


Figure 3-15. Transect section X2 across the Kailua Accretion Barrier (KAB, composed of fine- and medium-grained calcaerous sand) illustrating sediment thickness and lithology. Section modified from Kraft (1984).

Total storage

The total volume of Holocene-aged calcareous sediment stored in submarine and subaerial reservoirs of the bay, beach, and coastal plain in Kailua is estimated to be 14375 ± 2174 x 10^3 m^3. Of that total volume, 26% is stored in submarine reservoirs (15% in the meandering paleostream channel bisecting the reef platform; 5% in sand bodies in the reef; 2% in the 1-km^2 triangular deposit at the landward mouth of the channel, and 3% in the deposit spilling from the channel's seaward mouth). The beach face contains 4% of the total storage, while the coastal plain accounts for 70% of the total storage.

Balancing the Budget: Production vs. Storage

Applying a total sediment production rate of 7039 ± 1172 m^3y^{-1} (2536 ± 337 m^3y^{-1} from framework bioerosion [Table 3-17] and 4503 ± 835 m^3y^{-1} by direct production [Table 3-19]) over the last 5000 years estimates a total volume of 351.95 ± 58.62 x 10^5 m^3 of calcareous sediment has been produced in Kailua Bay since 5000 yr BP. Submarine and subaerial reservoirs in the bay and coastal plain currently store 143.75 ± 21.74 x 10^5 m^3 of Holocene-aged marine sediment. By these calculations, 41% (±7%) of sediments produced in the 5000-year Kailua model are currently stored in the system (Table 3-21). More than half of the sediment produced in the model is unaccounted for. This imbalance may represent sediment loss due to dissolution, abrasion, and/or transport offshore; it may arise from the inaccuracy of some model parameters (e.g. annual carbonate production rates); or it may be due to the application of modern production rates over a 5000-year period.

PART II: Analyzing Production and Comparing to Previous Studies

Gross Framework Production

Average gross framework production by zone in Kailua Bay is summarized in Table 3-22. Although total framework production is highest in zone N1 (3700 x 10^3 kgy^{-1}), when normalized to habitat area, productivity in N1 (2.48 $kgm^{-2}y^{-1}$) is close to the mean for the entire system (2.66 $kgm^{-2}y^{-1}$). Similarly, zones S1 and S2 produce framework at rates of 2862 and 2823 x 10^3 kgy^{-1}, respectively; when this rate is normalized over their large habitat area, productivity averages 2.61 and 2.53 $kgm^{-2}y^{-1}$, respectively. The highest carbonate productivity per unit area exists in the coral garden zones NCG and SCG, where normalized rates of framework production are 18.93 and 26.79 $kgm^{-2}y^{-1}$, respectively. These high productivities are representative of only 2% of the system (Table 3-18). Gross framework production over 81% of the total habitat area in Kailua Bay is between 1.9–4.0 $kgm^{-2}y^{-1}$. Lower rates (≤1 $kgm^{-2}y^{-1}$) are characteristic of 17% of the system. The distribution of productivity in this reef budget demonstrates a pattern that is consistent with the partitioning of reef environments into 'modes' of low, moderate, and high rates of carbonate production, where 90% of reef environments calcify at low rates, generally <4 $kgm^{-2}y^{-1}$ (Chave et al. 1972, Smith and Kinsey 1976, Smith 1978b, Kinsey 1983a).

Average gross framework production over the entire study area in Kailua Bay is 2.66 $kgm^{-2}y^{-1}$, with 1.44 $kgm^{-2}y^{-1}$ contributed by corals (54%) and 1.22 $kgm^{-2}y^{-1}$ contributed by encrusting coralline algae (46%) (Table 3-23). Bioerosion of the reef framework

occurs at an average rate of 0.35 $kgm^{-2}y^{-1}$ and results in the production of 1.24 $kgm^{-2}y^{-1}$ of sediment (SB_{TK} in Table 3-23). Direct production averages 0.52 $kgm^{-2}y^{-1}$, with 0.30 $kgm^{-2}y^{-1}$ contributed by *Halimeda*, molluscs, and benthic foraminifera (combined) and 0.22 $kgm^{-2}y^{-1}$ contributed by articulated coralline algae. The contribution of direct sediment producers in Kailua Bay is significant, accounting for 64% of annual sediment production.

Gross framework production in Cane Bay (Hubbard et al. 1990) averaged 1.15 $kgm^{-2}y^{-1}$ over the reef (1.13 $kgm^{-2}y^{-1}$ contributed by corals, 0.02 $kgm^{-2}y^{-1}$ by coralline algae). Direct production by 'accessory organisms' (primarily molluscs, forams, and echinoderms) contributed an average of 0.06 $kgm^{-2}y^{-1}$. The calcareous green alga *Halimeda*, usually characteristic of such Caribbean settings, was entirely absent from Cane Bay, and no mention of articulated coralline algae was made. This system is coral-dominated, with coralline algae contributing <2% of the annual gross framework production. Although coral productivity is comparable between Cane Bay and Kailua Bay, the prevalence of coralline algae in the windward Kailua system drives up the gross framework productivity, contributing 46% of the total. Higher bioerosion rates were used in the Cane Bay study, converting 23% of gross production to unconsolidated sediment annually.

In the study at Bellairs reef in Barbados (Stearn and Scoffin 1977), gross carbonate productivity was 8.90 $kgm^{-2}y^{-1}$ (6.35 $kgm^{-2}y^{-1}$ for corals and 2.55 $kgm^{-2}y^{-1}$ for encrusting coralline algae). Boring organisms eroded 0.80–3.85 $kgm^{-2}y^{-1}$, a total of 25 x 10^3 kgy^{-1} over the whole reef, or ~15% of the gross carbonate production by corals and coralline algae. The authors attribute an additional bioerosion quantity of 189 x 10^3 kgy^{-1} to large,

grazing parrotfish and abundant *Diadema antillarum* sea urchins. Both gross productivity and sediment productivity are considerably higher in the Bellairs study than in the Kailua budget. Diversity and growth rates are higher in the coral-dominated Bellairs system. Extremely high rates of bioerosion in the Bellairs study result in the calculation of a budget deficit where more sediment is produced than reef framework. Neither of the principal bioeroding organisms in the Bellairs study exists in Kailua Bay in significant size or number to warrant such weighty consideration.

Land (1979) determined average gross carbonate productivity by corals over the reef in Discovery Bay, Jamaica, was 3.1 $kgm^{-2}y^{-1}$. Lacking data on green and red algae production, he added in 'non-coral' productivity of 2.1 $kgm^{-2}y^{-1}$ (based on their relative abundance in sediments), bringing gross productivity to 5.2 $kgm^{-2}y^{-1}$. This figure is higher than that estimated for Kailua, yet it does not include the carbonate productivity of *Halimeda* or articulated coralline algae. Net production (reef accretion) in Discovery Bay averaged 1.1 $kgm^{-2}y^{-1}$, or 21% of gross production. Land considers the remaining carbonate (79% of gross production) to be loose sediment that is transported out of the system or lost in solution.

Reef Bioerosion

The carbonate budgets discussed in Part I of the Introduction ('Previous Work') demonstrate that constructive and destructive processes are nearly balanced on most reefs, with net accumulation barely keeping ahead of net loss (Glynn 1997). The significant role of bioerosion in reef budgets is illustrated by comparing results of this

model to those predicted by applying the bioerosion methodologies of Hubbard et al. (1990) and Spencer (1985) to the Kailua system (Table 3-24).

If the results of the Hubbard et al. model of bioeroded sediment production in Kailua (4535 ± 603 m^3y^{-1}) are combined with direct production (4503 ± 835 m^3y^{-1}) and the resultant annual volume of sediments produced (9038 ± 1438 m^3y^{-1}) are extrapolated over 5000 years, the total volume of Holocene sediment yield predicted is $451.91 \pm 71.91 \times 10^5$ m^3. Of this volume predicted to be produced, 32% (±5%) remains stored in the Kailua system. A similar exercise with Spencer's model reveals 18% (±3%) of the $794.54 \pm 117.48 \times 10^5$ m^3 predicted remains stored in the system.

The results of all three bioerosion models are comparable within an order of magnitude, but neither the Hubbard et al. or Spencer models is more effective at 'balancing' the budget in terms of the percent of sediment produced that remains stored in the system (Table 3-24). Both models predict a greater volume of annual sediment production (and therefore a lower rate of reef accretion) than does the Kailua model, owing to their use of higher rates of framework bioerosion.

Table 3-25 summarizes the results of several models of bioerosion applied in Kailua are normalized. To compare the Hubbard et al. bioerosion parameter directly with those from Kailua cores, the 23% factor is multiplied by the normalized rates of gross framework productivity in Kailua Bay, and individual bioerosion rates for each zone are calculated. The rates are thus in a comparable format ($kgm^{-2}y^{-1}$). Spencer's (1985) uniform rate of average subtidal limestone erosion is also listed for reference. Hubbard et al. reduce 23% of the reef's gross production to unconsolidated sediment released from the framework annually. Because this bioerosion factor is a function of gross framework

Table 3-22. Total and mean carbonate productivity by zone in Kailua Bay.

Zone	Habitat area ($x10^3$ m^2)	$CaCO_3$ Production[a] ($x10^3$ kgy^{-1})		Normalized $CaCO_3$ Prod.[b] ($kgm^{-2}y^{-1}$)		
	A_h	Framework	Direct	Framework	Direct	**Total**
N1	1493	3700	240	2.48	0.16	2.64
N2	764	1939	522	2.54	0.68	3.22
N2*	547	276	395	0.51	0.72	1.23
N3	159	312	60	1.96	0.38	2.34
N4	72	182	15	2.55	0.21	2.76
N5	798	837	396	1.05	0.50	1.55
NCG	103	1945	1	18.93	0.01	18.94
NH	609	1500	1107	2.46	1.82	4.28
S1	1097	2862	141	2.61	0.13	2.74
S2	1117	2823	382	2.53	0.34	2.87
S3	519	1137	55	2.19	0.11	2.30
S4	138	556	33	4.03	0.24	4.27
SCG	114	3047	1	26.79	0.01	26.80
SH	838	2065	828	2.46	0.99	3.45
FRS	350	8	111	0.02	0.32	0.34
Meadows	–	0	210	–	–	–
Total	8717	23190	4498	–	–	–
Mean[c]	–	–	–	2.66	0.52	**3.18**

[a] The production of $CaCO_3$ by all calcifying organisms in Kailua Bay.

[b] Carbonate production (kgy^{-1}) normalized by the habitat area (m^2) of each zone.

[c] Mean of productivities weighted by total habitat area.

Table 3-23. Summary of carbonate productivity in Kailua Bay (total and normalized to habitat area).

Whole-reef $CaCO_3$ productivity		Total[a] ($x10^3$ kgy^{-1})	Mean[b] ($kgm^{-2}y^{-1}$)
Coral	(G_{Tc})	12425	1.43
Encrusting cor. algae	(G_{Tace})	10765	1.24
Total framework	(G_{TF})	23190	2.66
Direct - *Halimeda,* mollusc, foram		2598	0.30
Direct - articulated coralline algae		1900	0.22
Direct - total		4498	0.52

Whole-reef sediment productivity		Total ($x10^3$ kgy^{-1})	Mean ($kgm^{-2}y^{-1}$)
Framework bioerosion	(SB_{TK})	10765	1.24
Direct		4498	0.52

[a] The production of $CaCO_3$ by all calcifying organisms in Kailua Bay.

[b] Carbonate production (kgy^{-1}) normalized by the total habitat area (m^2) in Kailua Bay.

Table 3-24. Balancing the sediment budget in Kailua Bay.

Balancing the Kailua budget		V_T m^3y^{-1}	HV_T $x10^5$ m^3 m^3
Framework bioerosion (Kailua model)		2536 ± 337	126.81 ± 16.87
Direct:	*Halimeda*	1179 ± 140	58.96 ± 7.02
	forams	376 ± 91	18.80 ± 4.55
	molluscs	1332 ± 299	66.60 ± 14.97
	articulated coralline algae	1616 ± 304	80.78 ± 15.21
Total sediment production		7039 ± 1172	**351.95** ± 58.62
Sediment storage (±21.74 x105 m3)			**143.75** ± 21.74
Percentage of production that is stored (±7%)			**41%**
Percentage of production that has been lost (±7%)			**59%**

Balancing with other bioerosion models	V_T m^3y^{-1}	HV_T $x10^5$ m^3
Hubbard et al. (1990) (23% of gross)	4535 ± 603	226.77 ± 30.16
Total sed. prod. (Hubbard + direct)	9038 ± 1438	451.91 ± 71.91
Percentage stored (±5%)		32%
Percentage lost (±5%)		68%
Spencer (1985) (1.6 kgm $^{-2}y^{-1}$)	11388 ± 1515	569.40 ± 75.73
Total sed. prod. (Spender + direct)	15891 ± 2350	794.54 ± 117.48
Percentage stored (±3%)		18%
Percentage lost (±3%)		82%

Table 3-25. Comparison of bioerosion rates of various models normalized to habitat area in Kailua Bay.

Zone	Normalized framework prod. G_F/A_h [a] ($kgm^{-2}y^{-1}$)	Hubbard's 23% bioerosion rate[b] ($kgm^{-2}y^{-1}$)	Kailua bioerosion rate[c] (B_K) ($kgm^{-2}y^{-1}$)	Spencer bioerosion rate[d] (B_S) ($kgm^{-2}y^{-1}$)
N1	2.5	0.57	**0.5**	1.6
N2	2.5	0.58	0.3	1.6
N2*	0.5	0.12	0.3	1.6
N3	2.0	0.45	0.9	1.6
N4	2.5	0.59	**0.9**	1.6
N5	1.0	0.24	0.5	1.6
NCG	18.9	4.35	0.5	1.6
NH	2.5	0.57	0.2	1.6
S1	2.6	0.60	**0.3**	1.6
S2	2.5	0.58	0.3	1.6
S3	2.2	0.50	**0.3**	1.6
S4	4.0	0.93	0.3	1.6
SCG	26.8	6.16	0.3	1.6
SH	2.5	0.57	0.2	1.6
FRS	1.9	0.44	0.2	1.6
Mean[e]	2.66	0.63	0.35	1.6

[a] Normalized gross production in Kailua Bay (from Table 3-18).

[b] Bioerosion rate required by Hubbard model = 0.23 x Normalized gross production rate.

[c] Bioerosion rates applied in the Kailua model (from Table 3-8).

[d] Uniform rate of average subtidal limestone erosion.

[e] Mean of observations weighted by zone habitat area.

production, the bioerosion rate is highest in coral gardens (4.35 and 6.16 $kgm^{-2}y^{-1}$ in NCG and SCG, respectively) and lowest in fossil-dominated regions (0.12 in zone N2*, 0.24 in zone N5), a consequence that is not necessarily accurate. The mean of the Hubbard et al. rates is 1.2 $kgm^{-2}y^{-1}$; the mean of those used in Kailua is 0.4 $kgm^{-2}y^{-1}$. This suggests bioerosion in Kailua may be underestimated in the model, at least in certain zones.

In some cases, the differences between the bioerosion models applied are quite high. For example, in zones NCG and SCG where coral cover and diversity are high, but habitat area is relatively small, a bioerosion rate of 0.5 $kgm^{-2}y^{-1}$ (in the Kailua model) yields only 51.3 x 10^3 kgy^{-1} and 34.1 x 10^3 kgy^{-1} of sediment, respectively. Applying the Hubbard et al. model in these zones (rates of 4.35 and 6.16 $kgm^{-2}y^{-1}$, respectively) would yield sediment at rates of 447.3 x 10^3 kgy^{-1} and 700.9 x 10^3 kgy^{-1}, respectively. This illustrates the complex interplay between habitat extent, organism cover, morphology, framework construction rate, and bioerosion rate in determining the sediment yield in any reef setting.

Bioerosion rates applied in this study may also be minimum estimates because they were collected from the upper portions of recent framework material. Bioerosion that occurs deep within the edifice or in very fossilized portions was not assessed. Bioerosion rates were determined from reef cores drilled at five sites (in four zones) and were extrapolated to the entire reef platform, a necessary simplification but one that introduces a margin of uncertainty.

Utilizing drilled cores is an excellent method of defining the rates and processes by which reef framework is altered or destroyed in a particular system. Unlike a bioerosion

rate that is a function of gross production, it is a quantity based directly on reef samples collected in the study area. The method employed here is independent of the rate of coral and algal growth and of their distribution over the reef yet still allows for variability in different physiographic settings. In addition, estimating bioerosion directly from reef samples is not dependent on error-prone assessments of the abundance and activities of cryptic bioeroding organisms.

Direct Sediment Production

The assessment of direct carbonate sediment production with field-based measurements on the standing crop and distribution of *Halimeda*, molluscs, benthic foraminifera, and articulated coralline algae is a unique aspect of this model. In no other reef systems has the contribution of all sediment components been quantitatively assessed. Uncertainties in the standing crop approach are primarily due to the patchy nature of these organisms' distributions in different physiographic settings (and even within the same setting). Organism populations are inherently dynamic, and variations in population turnover rates can affect the estimated production potential.

Halimeda has proven to be a productive, ubiquitous inhabitant of both energetic and protected settings over a range of depths in Kailua. Although its carbonate content, standing crop, growth rate, and sediment production capability vary with species, habitat, depth, and life cycle stage, these aspects are relatively easy to quantify with field and laboratory observations. Researchers agree that *Halimeda* should no longer be

considered a predominantly lagoonal alga, and its importance in a variety of tropical and temperate shallow-marine settings is unmistakable.

Molluscs contribute significantly to the carbonate budget of Kailua Bay and are likely important producers of sediment in all reef settings. Except for this study, little is known about the carbonate productivity of molluscs of various size and life habit. Reef budgets in general would benefit from more information on the distribution and production potential of these ubiquitous creatures. Benthic foraminifera are also an important piece of the puzzle, although their contribution is not as great as that of other sediment producers. The ubiquity of reef-dwelling benthic forams in a variety of shallow-marine settings, intertidal to deep fore-reef, is a testament to their important role in sediment budgets.

The articulated coralline algae are generally absent from other carbonate budgets, either overlooked, considered unimportant, or lumped in with encrusting algae. Encrusting coralline algae have long been appreciated as binders and cementers of reef framework and rubble, while the importance of articulated forms has gone generally unmentioned. The voluminous production by these rhodophytes observed in the Kailua system suggests their roles in Hawaiian reef systems are significant, consistent with observations by Littler and Doty (1975) and Adey et al. (1982). Their large contribution to coastal sediments in Kailua is an important factor in a budget in which accretion dominates over erosion.

Part III: Sources of Uncertainty

Estimates of uncertainty around data and sediment budget calculations have been provided in the text and tables throughout. These quantitative uncertainties arise primarily from assessing the distribution of sediment producers over the 10 km^2 carbonate reef complex (i.e. limitations of image analysis and field mapping; refer to Methods section) and from converting sediment mass to volume using an average density (1175 ± 76 kgm^{-3}). These uncertainties were calculated using the 'Monte Carlo' method in which the lowest and highest possible results were determined for each calculation, summed at the end of each string of calculations, divided in half, and reported as a '±' uncertainty around the result. Additional sources of uncertainty exist that could not be similarly quantified, as they were beyond the scope of this study and were not rigorously assessed. Such uncertainties include sediment loss (e.g. transport in bedload and in suspension, abrasion and dissolution of carbonate particles), the extent and nature of Holocene reef accretion in Kailua, the effect of reef diagenesis (cementation and micritization), the effect of storms and mechanical erosion, and the assumptions involved in calculating 5000 years of processes based only on modern rates. These sources of uncertainty are discussed in detail in the following sections.

Sediment Loss

The possible means by which sediment has been removed from the Kailua system over the last 5000 years are discussed below, based both on data collected in Kailua and

on research findings from other studies. Of those discussed, the most significant and likely means of sediment loss (bedform migration, suspended sediment transport, and dissolution) and their cumulative effects over 5000 years are summarized in Table 3-26.

Bedload sediment transport in Kailua Bay

Video observations and bottom velocity data collected by a seafloor instrument tripod reveal aspects of bottom circulation and bedload transport through the central sand channel in Kailua Bay (Cacchione et al. 1999). The channel is floored by calcareous sand of medium size formed into large, long-crested symmetric ripples with wavelengths 0.75–1.0 m and heights of 6–12 cm. The ripples are oriented approximately normal to the channel walls and extend across the total width of the channel body. Oscillatory bottom currents move the sediment at the tops of the ripples. Current measurements showed that grain motion was correlated closely with bottom wave speeds.

Under summer trade wind conditions, ripples migrate in the onshore direction at a rate of 0.5 m per day; under winter north swell conditions, migration is in the offshore direction at a comparable rate. Onshore transport would simply move the sediment between reservoirs and would not represent 'loss' from the system. Lateral movement of sediment in the northward direction is prevented by Mokapu Peninsula. Sediment 'leakage' south toward Lanikai is considered insignificant, an assumption supported by beach profile data and by the absence of sand on the shallow reef flat between the two systems.

Sediment is therefore only 'lost' when transported offshore far enough that it effectively 'exits' the region of storage at the channel's seaward mouth. This distance is

~700 m from the site where the instrument tripod observed ripple migration. At a migration rate of 0.5 m per day, it would take the average ripple almost four years of continuous, unidirectional migration to exit the system. Since offshore bedload transport was observed only during winter swell conditions that exist less than half the year, effective removal of this sediment is more likely on a decadal time scale.

Applying the formula for the volume of a triangular prism to sand ripples with wavelengths of 1 m and heights of 10 cm that are continuous across the 100-m width of the channel, the volume per ripple is estimated to be ~5 m^3. Correcting this volume for 40% porosity, ~3 m^3 of sand is contained in each ripple. The length of the offshore portion of the sand channel (lying in water depths similar to those of the instrument) is ~500 m. If 500 bedforms in this region transport 3 m^3 of sand each, then ~1500 m^3 of sand is being transported during bedform migration. If this 1500 m^3 of sand exits the system every ten years, the average annual rate of sediment removal in this manner is 150 m^3y^{-1}, or just over 2% of the volume of sediment produced annually in Kailua Bay. Applying this rate of bedload export over the last 5000 years results in the loss of 7.5×10^5 m^3 of sediment (Table 3-26). This volume represents 4% of the sediments that are 'unaccounted for' in the budget.

Suspended sediment transport in Kailua Bay

The concentration of suspended sediments in waters of Kailua Bay was determined from water samples collected during moderate (10–20 kts) and sustained heavy (>20 kts) trade winds (Table 3-27). Samples were collected offshore (from waters over the channel) and nearshore (from waters over the sand triangle and in and near the surf zone)

using a Niskin sampler. Water samples were sieved and vacuum-filtered over an 11-µm filter to determine the concentration of carbonate particles. The concentration of sediment in suspension is greatest near shore where bottom sediments are disturbed by breaking waves (e.g. 24.6 and 68.3 mgL^{-1} in the surf zone; 1.4–5.6 mgL^{-1} in nearshore regions). Offshore, in waters over the sand channel, suspended sediment concentration is 0–1.8 mgL^{-1}. Scanning electron micrographs of suspended sediments are provided in Appendix B.

Although somewhat limited, the data can provide a basic, order-of-magnitude estimate of annual sediment loss via transport out of the system in suspension. During moderate trade wind conditions (15–20 kts), the upper 2 m of the water column in the area over the channel (3×10^5 m^2) contains ~6×10^5 L of water carrying a conservative estimate of 0.5 mgL^{-1} of sediment in suspension, or a total of 3×10^5 kg of suspended sediment. If these conditions prevail for two months per year and only 10% of the suspended sediment is actually transported offshore far enough to be removed from the system, the volume of sediment lost annually would be ~5000 m^3. Over 5000 years, this amounts to 2.5 x 1047 m^3 of sediment, or 120% of the sediments that are unaccounted for in the budget.

Sediment loss in other systems (and applications to Kailua Bay)

Using sediment trap data, Hubbard et al. (1990) estimated the annual rate of sediment export over the Cane Bay shelf edge to be 65 kgm^{-1} in fair weather and 1130 kgm^{-1} during annual storms. Assuming 30 stormy days per year, the authors calculated an

Table 3-26. Primary modes and rates of estimated sediment loss from Kailua Bay budget.

Mode and rate of loss	Effect over 5000 years	Portion of budget 'unaccounted for'
Channel bedform migration ~150 m^3y^{-1}	750 x 10^3 m^3	4%
Suspended sediment transport Of 0.5 mgL^{-1} in upper 2 m of water column above channel in 20 kt trades, lose 10%	25000 x 10^3 m^3	120%
Land's (1979) dissolution 56% of production	19700 x 10^3 m^3	95%

Table 3-27. Suspended sediment concentration in offshore waters of Kailua Bay.

Date and conditions		Site / setting	Water depth (m)	Sample depth (m)	Suspended sediment concentration [Total] (mgL^{-1}) [a]
September 1998		Sand channel	70	22	0.5
Wind speed:	10-15 kts	Sand channel	42	11	1.8
Wave height:	1 m	Nearshore triangle	14	3	3.1
		Outside surf zone	9	2	5.6
		Surf zone	4	1	68.3
October 1998		Sand channel	70	20	0.0
Wind speed:	>20 kts	Sand channel	45	11	0.5
Wave height:	to 3 m	Nearshore triangle	11	2	1.4
		Surf zone	9	2	24.6

Date and conditions		Site	Setting	Nearshore suspended sediment concentration [Fine] (mgL^{-1}) [b]	[Coarse] (gL^{-1}) [c]
March 1999		OKLA-5	impact [d]	9.5	0.6
Wind speed:	10–20 kts	OKLA-5	RSI (2 m)[e]	0.0	0.0
Wave height:	1 m	OKLA-4	impact	13.7	1.6
		OKLA-4	RSI (2 m)	5.9	0.0
		OKLA-1	impact	0.0	13.3
		OKLA-1	RSI (2 m)	6.8	0.0
		OKLA-3-1	beach toe[f]	4.5	6.4
		OKLA3-1	impact	13.8	0.4
		OKLA3-1	RSI (2 m)	0.2	0.0
		OKLA-3-2	impact	25.4	0.3
		OKLA-3-2	RSI (2 m)	4.0	0.0
		OHAN	beach toe	17.9	6.6
		OHAN	impact	9.5	1.8
		OHAN	RSI (2 m)	10.1	0.0
		OKLA-2	impact	8.1	0.8
		OKLA-2	RSI (2 m)	6.7	0.0

[a] Total concentration of suspended sediment without size classification (all particles were <63 um)

[b] [Fine] suspended sediment is <63 μm in size.

[c] Coarse suspended sediment is >63 μm in size.

[d] Impact zone is the region of breaking waves in the surf zone.

[e] Rock-sand interface in 2 m water depth.

[f] Beach toe is the approximate position of sea level.

average of 153 kgm^{-1} moved off-shelf through channels along the shelf margin. Export channels represented 25% of the 1140-m shelf margin, thus the total sediment export over the Cane Bay shelf edge was ~55,100 kgy^{-1}. Applying the average rate of sediment export over the *entire* length of the fore-reef in Kailua Bay (3698 ± 195 m) would result in the loss of 565.8 x 10^3 kg of sediment each year, or just over 7% of annual sediment production (framework and direct). Extrapolated over 5000 years, the rate of loss would total 28289.7 ± 1491.8 x 10^5 kg and represent 4% of the sediments that are 'unaccounted for' by the storage model (59%). Aside from the main channel, few sand chutes exist along the reef-front in Kailua. In addition, the oceanographic settings of Cane Bay and Kailua Bay are quite different. Cane Bay is a small, protected, leeward setting, while Kailua Bay is positioned windward to trades and also receives north swell in the winter. Thus, applying the Hubbard et al. rate of sediment export over the fore-reef in Kailua is a useful exercise but likely does not adequately estimate sediment removal from the system.

Land (1979) estimated an off-reef sediment transport rate of 1.2 $kgm^{-2}y^{-1}$. As a simple exercise, applying this rate to the planimetric surface area of Kailua Bay suggests 85 x 10^5 kg of carbonate sediment could be lost from the system annually, or 114% of the total annual mass of sediments produced. To satisfy his mass-balance equation, Land (1979) estimated that sediment loss through *dissolution* occurred at a rate of 2.9 $kgm^{-2}y^{-1}$ in Discovery Bay. Applying this loss parameter to Kailua Bay (again, as a simple exercise) results in the additional removal of 205 x 10^5 kg of carbonate sediment from the system each year. Taken together, both types of loss predict the annual removal of a quantity of sediment from Kailua Bay (290 x 10^5 kg) that is nearly *four times* the total

annual sediment production rate for the entire reef system. This is clearly not the case in Kailua, at least partially owing to the system's unique capacity for sediment storage within the channels and bodies of the reef platform.

Land (1979) derived the rate of dissolution (2.9 $kgm^{-2}y^{-1}$) derived from his mass-balance equation and discovered this process removes 59% of the estimated reef productivity in Discovery Bay. Applying a rate of dissolution (here meaning the eventual 'disappearance' of silt-sized carbonate particles) that is 59% of gross reef productivity in Kailua Bay (instead of the 2.9 $kgm^{-2}y^{-1}$ rate) results in an estimate of 19700 x 10^3 m^3 over 5000 years, or 95% of the sediment volume that is unaccounted for in the model. Although this estimate is not based on a study of dissolution in Kailua Bay, carbonate particles have certainly been dissolved over the 5000 year budget, and this estimate is not unreasonable. It serves only to suggest that a portion of the 'loss' term in the sediment can likely be attributed to this dissolution.

Hughes (1999) estimates the off-reef transport of coral fragments at Lizard Island, Australia, averages 1.87 kgy^{-1} per meter of reef front. Applying this transport rate to the 3698 ± 195 m of reef front in Kailua Bay, the loss of sediment per year is 6915 ± 365 kgy^{-1} (0.1% of the 7481 ± 744 x 10^3 kgy^{-1} of sediment produced annually). Over 5000 years, this amounts to 345.8 ± 18.2 x 10^5 kg, or <1% of the sediment budget that remains unaccounted for.

In Driscoll's (1967) experimental field study of shell abrasion, mollusc shells in the surf zone lost 0.5–2% of their initial mass after 100 hours of exposure. On gravelly beaches, this rate increased to 2–3.5% after 24 hours. Shells left under water at 30' depth for one year experienced weight *gain* due to encrustation by other organisms, and no

decrease in shell weight due to abrasion could be detected. If 0.5% of the initial weight of skeletal sediment is lost every 100 hours due to abrasion in the surf zone, and there are 8760 hours in a year, or ~87 segments of 0.5% loss each, this amounts to a loss equal to 35% of the initial weight after one year.

This abrasion factor is applied in Kailua in the following manner: if only 5% of the total beach volume is exposed to surf conditions in any given year (based on a two-decade turnover estimated from Kailua's beach profile data), then 30 x 10^3 m^3 of beach sand can be treated with Driscoll's abrasion parameter each year. By this method, surf abrasion results in the loss of 10500 m^3 of sediment annually. Extrapolated over 5000 years, this figure leaps to a total loss of 525 x 10^5 m^3, or nearly *twice* the total volume of sediments *produced* in the Holocene model.

If beach sand composition is considered such that 40% of the volume is easily-abraded shell material (molluscs, forams, and *Halimeda*) and 60% is more durable coral and coralline algae fragments that abrade half as quickly, the volume lost over the Holocene is 246 x 10^5 m^3, which is 77% of total Holocene sediment production but still 1.3 times greater than the amount of sediments that are 'unaccounted for' in the model.

Sediment export rates from Hubbard et al. (1990) allow for the removal of 8% of total sediment production and explain 4% of the 'lost' 59% of sediments produced over the Holocene that are no longer stored in Kailua. The off-shelf movement of coral fragments observed by Hughes (1999) calls for the removal of <1% of sediment production; Land's (1979) observations allow for the loss of *four times* the amount of sediment production; and Driscoll's (1967) abrasion model allows for the loss of 77% of sediment production. These examples are instructive in illustrating the great quantities of sediment that are lost

from any 'reef budget.' They also suggest that the 'loss' term of this study (59% of the sediments produced over the Holocene that are no longer present in the system) is reasonable. Table 3-26 summarizes the three most probable modes of sediment loss from the system and their cumulative effect over the 5000-year budget. If reasonable rates of bedform migration, suspended sediment transport, and dissolution are applied to the system, they can account for the removal of a volume of sediment that is twice that 'lost' in the Kailua model. This exercise addresses the possible modes and rates of loss in discussion and in reference to other studies. Individual rates of loss (e.g. transport in bedload and suspension, abrasion, dissolution) can be examined in detail with further study of sediment transport and carbonate cycling in Kailua Bay.

Holocene Reef Accretion

Rearranging Land's (1979) simple equation *Gross = Net + Sediment removed* to *Net = Gross – Sediment removed* offers the opportunity to quantify the volume of reef framework this model predicts to have accreted over the last 5000 years in Kailua Bay. Converting total gross framework productivity in the system (G_{TF} = 23190 ± 1391 x 10^3 kgy^{-1}) to volume (using a density of 1.4 gcm^{-3}) predicts ~16564 m^3y^{-1} of gross reef framework is constructed annually in Kailua Bay. If the total volume of sediment produced by bioerosion of the reef framework annually is 2536 m^3y^{-1} (V_{TK}) as calculated in the model, net annual reef accretion is 14028 m^3y^{-1}. Dividing this volume by the total area of consolidated substrate in Kailua (sum of A_s for all zones without rugosity correction = 7076 x 10^3 m^2) yields an accretion rate of 1.98 mmy^{-1}. This rate is slightly

lower than the 3 mmy^{-1} accretion rate characteristic of most Holocene 'margin reefs' (Smith 1983) and within the 1–4 mmy^{-1} accretion range suggested for fringing reef systems (Davies and Hopley 1983), and while it is reasonable, it predicts 9.9 m of net reef accretion would have occurred in the last 5000 years over the study area.

Observations of Holocene reef accretion in Kailua Bay suggest this is not the case and that reef accretion has been limited to scattered packages in protected or wave-shadowed subregions of the bay. For example, no significant Holocene accretion has been found in zone N2*, while portions of the reef front boast nearly 10 m of Holocene accretion (Grossman and Fletcher 1999). This estimate predicts reef accretion in the vertical direction only and does not account for lateral accretion, which may have resulted in seaward progradation along part or all of the 3.7-km length of the fore-reef slope and 3.1-km length of the channel margin's reef walls. Lateral accretion of the enclosing walls of more than 100 reef-top sand bodies may also have occurred. However, this exercise suggests that bioerosion alone does not account for enough framework destruction and that the role of mechanical erosion by storms, winter swell, and frequent sustained tradewind disturbance must be significant.

Reef Diagenesis

Micritization and cementation are common post-depositional (diagenetic) processes that occur in shallow-marine carbonate reefs at low latitudes. These processes affect the fabric, porosity, and consolidation of reef components and thus likely play a role in reef productivity in the carbonate complex of Kailua Bay. Micritization is a widespread form

of shallow-marine diagenesis in which original fabrics and microstructures are progressively altered to micro- and cryptocrystalline carbonate textures by changing the size and arrangement of carbonate crystals (Reid and Macintyre 1998), often aided by microbial activity in low-energy settings such as back-reef lagoons (Tucker 1991). This form of 'recrystallization' can take place with or without a change in mineralogy and can occur syndepositionally (Macintyre and Reid 1995). The formation of lime mud is also linked to the processes of bioerosion, mechanical attrition of carbonate particles, and inorganic as well as biochemical precipitation (Tucker 1991b). The production of lime mud is an important aspect of budgets in calm-water settings, such as the Bight of Abaco where Neuman and Land (1975) did their classic study. Kailua Bay is a windward, well-circulated embayment that lacks a restricted mouth and a true back-reef lagoon. The fate of silt- and mud-sized particles in such a setting is probably to be carried offshore in suspension or to be cemented within subsurface reef cavities.

Cementation is common in high-energy areas where seawater is pumped through the reef and sediments. Precipitation of marine cements in reefs leads to solidification and consolidation of the reef framework as well as the filling of internal voids. Little evidence of marine cementation is found in petrographic analysis of sediments (see Chapter 2). Isopachous fringes and fibrous crystals are far less common features in individual carbonate particles than are micritic textures of peloids and infills observed in skeletal grains ('intraclastic' nonskeletal particles that are up to 17% of reef sediments [Harney et al. 2000]). Cementation is more a concern in the analysis of Holocene reef accretion than in unconsolidated sediment production, because the process of bioerosion effectively breaks down even well-cemented substrates. The assumption is thus made that

cementation would have a minor effect on the production of unconsolidated sediments, which result from the bioerosion of reef framework, whether well-cemented or unaltered.

Fine and silt-sized 'internal sediments' resulting from bioerosion may become cemented in reef cavities and thus remain within the framework. The relative importance of this process on the overall budget has not been assessed. The model assumes that sediment generated by bioerosion in the upper half-meter of the reef edifice will be released from the framework owing to scouring by waves and currents, as well as frequent trade wind events. Subsurface bioerosion likely leads to internal sedimentation and cementation within the edifice. The impact of such internal processes has not been assessed in this study. However, the particles produced during micritization and internal sedimentation are so fine in size that they are not likely to be important in the production of sand-sized particles that are the primary focus of this quantitative budget.

Storms and Mechanical Erosion

To test the importance of episodic sediment production by storms, the 'destruction' of stands of the branching coral *Porites compressa* in Kailua Bay by 100-year storm events can be added into the Holocene sediment production model. Grigg (1995) suggests that destruction of branching corals is the most common result of storm events, while massive and encrusting corals are more resistant to even major disturbance. Transect mapping reveals *P. compressa* has an average cover of 1% in zones NCG and S1, 2% in zones N2 and N4, and 6% in zone SCG. The sum of gross production at 10.7 $kgm^{-2}y^{-1}$ over the habitat areas of these zones is 2299.1 x 10^3 kgy^{-1}. Destroying the entire population of

branching corals once every 100 years would yield ~16.4 x 10^3 m^3 of sediment (or an average rate of 164.2 m^3y^{-1}). This reduces the annual reef accretion volume to 13864 m^3, or 1.96 mmy^{-1} over the reef. Over 5000 years, this change is relatively insignificant, and 9.8 m of reef accretion is still predicted for the platform. This suggests that infrequent (albeit severe) storms may be *less* effective compared to bioerosion in producing sediment from well-consolidated material, particularly in a windward reef system dominated by encrusting and massive growth forms.

A similar exercise can be performed on direct sediment producers to estimate the volume of sediment added by episodic destruction of standing crops. The estimated standing crop of *Halimeda* at any one time in Kailua Bay is one-half of its annual production shown in Table 3-19 (owing to two turnovers per year), or 294.8 x10^3 kg. The equivalent volume of this standing crop mass is ~590 m^3 (using 500 kgm^{-3}, after Drew and Abel 1985). Destruction of all *Halimeda* beds (which exist only in shallow waters and would likely be severely impacted) every 100 years would result in the addition of ~29.5 x 10^3 m^3 of sediment to the Holocene budget over 5000 years.

The estimated standing crop of foraminifera at any one time in Kailua Bay is ~376 m^3 (which is 442.3 x 10^3 kg [from Table 3-11] converted to volume using 1176 kgm^{-3}). If the population is wiped out every 100 years by a severe storm, ~18.8 x 10^3 m^3 of foram tests would be added to the Holocene budget over 5000 years.

The estimated standing crop of micromolluscs at any one time in Kailua Bay is one-tenth of their annual production shown in Table 3-13 (owing to ten turnovers per year), or 156.6 x10^3 kg. The volume of this standing crop (using 1176 kgm^{-3}) is ~133 m^3.

Destruction of the total micromollusc population every 100 years would result in the addition of ~6.6 x 10^3 m^3 of shells to the Holocene budget over 5000 years.

The estimated standing crop of articulated coralline algae at any one time in Kailua Bay is ~1616 m^3 (which is 1900.0 x 10^3 kg [from Table 3-15] converted to volume using 1176 kgm^{-3}). If all shallow-dwelling articulated coralline algae were destroyed by storms every 100 years, an additional ~80.8 x 10^3 m^3 of sediment would be provided to the Holocene budget over 5000 years.

The total addition of sediment owing to the complete destruction of *Halimeda*, foram, micromollusc, and articulated coralline algae populations by severe storms every 100 years since the mid-Holocene is ~135.7 x 10^3 m^3. Adding this to the volume produced by destruction of *Porites compressa* corals (~16.4 x 10^3 m^3) would result in the contribution of ~152.1 x 10^3 m^3 of unconsolidated calcareous sediment (or 1.5 x 10^5 m^3) to the Holocene total of 351.96 ± 58.62 x 10^5 m^3, or less than 1%.

These exercises reinforce that mechanical erosion during episodic storms may be less effective in producing unconsolidated calcareous sediment than the continuous, natural processes of population growth and turnover. In addition, the likelihood of complete destruction of these populations, even by a severe storm, is limited. Unfortunately, the true effect of large ocean swells and sustained tradewind events on the reef framework remains unknown. Quantitative measurements of the frequency and magnitude of mechanical erosion under significant swell and trade conditions are required to assess their relative impact on the reef and its associated sediment budget.

The 5000-year Budget

This model looks in detail at the structure and function of modern benthic communities in Kailua Bay. It utilizes data and information on quantifiable, modern processes to elucidate the carbonate history of an extensive, complex, dynamic system. It makes the assumption that the present is an efficient and accurate means to explore the past, and it extrapolates a brief 'snapshot' of the reef system into recent geologic time.

Unique to this model is the 5000-year period over which the budget is examined. The high rate of reef accretion discussed in Part III may arise from over-predicting gross framework production over this long period. Applying quantitative data collected from modern reef communities to those in the last 5000 years is certainly a simplification. In truth, the distribution and productivity of reef communities in Kailua Bay probably changed with time, sea level, and in response to constantly-evolving antecedent topography (i.e. the accreting reef would itself alter the habitat area and accommodation space). These changes and their relative significance remain unexplored and are beyond the scope of this study.

However, there also exists the possibility that gross framework production in Kailua Bay has been *under*-estimated over the last 5000 years. Certainly not all of the highly-productive 'coral gardens' on the platform have been discovered and mapped. Other small but possibly important 'zones' in the bay have been largely ignored for lack of data. For example, a region in the lee of Popoia Island on the southern reef platform is characterized by patch reefs 1–4 m in diameter composed of a variety of living and recently dead corals, fossil substrates, and fleshy, calcareous, and encrusting algae. The

gross carbonate productivity of patch reefs has been suggested to be as high 13 $kgm^{-2}y^{-1}$ (Chave et al. 1972). These patch reef communities in Kailua Bay are randomly scattered over a 0.5 km^2 area of sandy or limestone seafloor (a portion of zone SH) and may represent a significant amount of framework production that is not included in the model.

The uncertainties in its assumptions are tested by estimates of sediment still present in the system – a sand record. Unlike many other reef systems, Kailua has an immense capacity for storage in both submarine and subaerial reservoirs. Extensive sand deposits exist that are many meters thick and still receiving sediment. The 'balancing' of the budget would benefit from a more detailed analysis of sediment storage. The current storage model relies heavily on data collected by other researchers (both published and unpublished) and on basic field observations (e.g. jet-probing of sand bodies). Sub-bottom profiling of the sand channels and fields within the fringing reef would provide a more accurate measurement of their sediment thickness. Vibracoring of submarine sand deposits would provide samples that could be radiocarbon-dated and analyzed sedimentologically to confirm the assumption that they are calcareous and of Holocene age. Cores collected from the subaerial Kailua Accretion Barrier would provide much-needed data on the volume, age, and composition of the sand in the large berm. Similarly, additional cores from the coastal plain would augment the minimal amount of data currently being used to assess the nature of the sediment beneath the modern terrestrial marsh. Improving estimates of sediment storage may refine the 'balance' and elucidate terms of sediment loss over the Holocene.

The age and subaerial distribution of calcareous sediment in Kailua reflect aspects of an antecedent system, possibly one that operated during the mid- to late Holocene under a

+1–2 m sea-level high stand (Grossman and Fletcher 1998). Paleoenvironmental reconstructions (Kraft 1984, Athens and Ward 1991) suggest the terrestrial marsh land behind Kailua today was a flooded marine lagoon under a 1–2 m relative sea-level high stand in the mid- to late Holocene. Flooding the broad, low coastal plain may have resulted in significant expansion of shallow, nearshore areas and in the temporary deepening of the fringing reef, and perhaps these conditions moderated the rates and processes of gross production and sediment generation in the bay. Data is lacking on the evolution of this complex shoreface, and it is not yet known what effect the high stand had on benthic communities or to what degree it may have moderated the carbonate budget.

Although environmental and ecological changes have certainly occurred in Kailua over five millennia, and some may have had a significant impact on the carbonate budget, the validity of the 5000-year model is argued by its general consistency: measured storage and reasonable rates of loss are able to account for the volume of sediment predicted by the production model.

PART IV: Significance

Oceanic Islands

In Hawaii and on other oceanic islands lacking a continental sand source, where coastal sediments are largely calcareous, reef productivity is the primary control on sediment supply. Analysis of carbonate sediment supply is valuable in assessing the progradational history of an area, in predicting the response of a coastline to changes in sea level, in accounting for sand volume in coastal deposits, and in understanding shoreface evolution. The Kailua budget is the first such quantitative analysis of shallow-marine carbonate sediment dynamics in Hawaii. The methodology involved in estimating annual sediment production can be applied to other coastal and reef systems on oceanic islands in Hawaii and elsewhere. Sediment budgets derived from such quantitative observations in reef systems provide a better understanding of carbonate dynamics, reef ecology and development, benthic diversity, and coastal processes. Sediment budgets also offer practical opportunities to improve coastal and resource management practices.

Coastal Dynamics

Kailua's length of sandy beach is one of the few sites on Oahu experiencing net long-term beach accretion. This study suggests the key to accretion along a coastal segment lies in sediment availability, i.e. a constant source of sediment to replenish eroded beaches following seasonal changes and episodic events. The voluminous storage

capacity of the channel and reef system of Kailua Bay is unique and illustrates the important relationship between reef development and beach stability. The balanced nature of this relationship suggests that perturbation (e.g. in the form of mining sediments stored in reefs) may have profound, long-term effects on a 'stable' system.

The results of this study illustrate a significant difference exists between the rates of sediment production and shoreline change. The average rate of calcareous sediment production in Kailua Bay (normalized over the entire study area of 10 km^2) is 0.86 $kgm^{-2}y^{-1}$. This indicates that each square meter of consolidated substrate in Kailua Bay produces a volume of ~0.0007 m^3 of sediment each year. The net rate of seasonal shoreline change along Kailua Beach is 43 m^3 per meter of beach length, which is equal to an annual flux of 172,000 m^3 of sand along the beach (Gibbs et al. 2000). This suggests that sediment production occurs at a rate that is *eight* orders of magnitude slower than the rate of *seasonal* shoreline change (which does not even include severe storms and erosion events). This relationship has implications for coastal erosion measures and beach sand mining issues, particularly along Hawaiian coasts troubled by chronic shoreline retreat and beach loss. Removing what seems an insignificant volume of sand from an accreting or 'healthy' beach may result in its destabilization. The rate at which an adjacent reef can supply sediment to replace that which was removed will be insufficient to re-establish a healthy equilibrium on time scales of human need.

Carbonate Dynamics

Offshore transport of particulate carbonates of shallow-water origin are an important source of sediment accumulating on offshore terraces and on the upper slopes of banks. In addition, Agegian et al. (1988) suggested that the production of reactive carbonates (Mg-calcite and aragonite) by shoal-water and mid-depth benthic communities may be important to the regional carbonate budget of the central North Pacific gyre. The distribution of alkalinity excess at intermediate depths in the Pacific could not be accounted for by the dissolution of pelagic carbonates alone and required ~0.35 g $CaCO_3$ $m^{-2}d^{-1}$ from other sources be dissolved at intermediate depths. The authors suggested that up to 25% of this requirement could be met by the dissolution and transport of reactive carbonates derived from benthic communities at depths of 0–100 m.

Loss of 59% of the carbonate sediments produced in Kailua over the last 5000 years may have resulted in the flux of $220.69 \pm 59.15 \times 10^8$ kg $CaCO_3$, which, through dissolution and transport, may contribute to the observed alkalinity excess at mid-depth in the North Pacific. Although the proportion of reef-derived sediment that is dissolved and transported to the open ocean remains unknown, it is a factor that could be significant in the alkalinity balance of the open ocean.

Importance of Coralline Algae in Hawaiian Reef Ecology

Pacific reefs in trade wind belts possess well-described algal ridges and shallow-water pavements constructed primarily of the genus *Porolithon* (see review in Macintyre

1997). In his reevaluation of the role of crustose coralline algae in the construction of coral reefs, Macintyre (1997) concludes their contribution to reef framework is significant only in shallow, high-energy conditions and is most likely to occur in the latter stages of Holocene reef development when there is little accommodation space left.

The carbonate budget of Kailua Bay demonstrates the significance of coralline algae in both reef construction and sediment production. Total gross production by corals (G_{Tc}) over the entire reef system in Kailua Bay is $12425 \pm 745 \times 10^3$ kgy^{-1}; total gross production by encrusting coralline algae (GT_{ace}) is nearly equal, contributing $10765 \pm 646 \times 10^3$ kgy^{-1}. By these calculations, 54% of the total framework production in Kailua each year is contributed by corals; 46% is the result of encrusting coralline algae.

This budget is unique in also quantifying the direct contribution of articulated coralline algae, a ubiquitous inhabitant of Hawaiian reefs (Littler and Doty 1975, Adey et al. 1982), based on their distribution and abundance in shallow, energetic habitats. The results of this study help explain the dominance of coralline algae in sediments of Kailua Bay and beach (Harney et al. 2000). Table 3-28 illustrates the comparison of the 'average' sand composition in Kailua to the composition predicted by the production rates in this model. The prevalence of coralline algae (40%) in both observed and predicted sediment assemblages is demonstrated. The paucity of coral fragments in Kailua sand that was so surprising in earlier studies (Harney et al. 2000) is consistent with its abundance predicted by the sediment production model in this study (19%). The relatively equal contributions of *Halimeda* and molluscs are suggested, as well as the rather low contribution by benthic foraminifera.

Table 3-28. Predicting sediment composition based on carbonate production in Kailua Bay.

Composition	"Average"[a]	Predicted by production model		
	Kailua sediment	Kailua	Spencer	Hubbard
Coral	15%	19%	26%	36%
Coralline algae[b]	40%	40%	42%	43%
Halimeda	20%	17%	11%	7%
Foraminifera	5%	5%	6%	4%
Molluscs	20%	19%	14%	9%

[a] After Harney et al. 2000.

[b] Encrusting and articulated coralline algae.

CONCLUSIONS

Carbonate dynamics in the Kailua Bay system are controlled by physiographic setting (e.g. depth, substrate type, and hydrodynamics), structure and function of the carbonate-producing community, and changing environmental regimes. This comprehensive model of sediment production in various habitats of Kailua Bay quantifies the modern processes of gross carbonate framework construction (by corals and encrusting coralline algae), the subsequent degradation of consolidated reefal substrates into loose sediment, and the direct addition of carbonate sediment through the biologic activities of the calcareous green alga *Halimeda*, molluscs, benthic foraminifera, and the articulated coralline alga *Porolithon gardineri*. Quantitative results of the sediment budget include:

1. Carbonate sediments are produced at a rate of ~7039 ± 1172 m^3y^{-1}. Bioerosion of the reef framework accounts for 2536 ± 337 m^3y^{-1} of the total, with 1359 ± 61 m^3y^{-1} contributed by coral and 177 ± 276 m^3y^{-1} contributed by encrusting coralline algae. The calcifying activities of direct sediment producers account for 4503 ± 835 m^3y^{-1} of the total sediment produced annually. To this volume, the green alga *Halimeda* contributes 1179 ± 140 m^3y^{-1}, benthic forams contribute 376 ± 91 m^3y^{-1}, molluscs contribute 1332 ± 299 m^3y^{-1}, and the articulated coralline alga *Porolithon gardineri* contributes 1616 ± 304 m^3y^{-1}.
2. Average gross framework production normalized over the entire study area in Kailua Bay is 2.77 $kgm^{-2}y^{-1}$, with 1.49 $kgm^{-2}y^{-1}$ contributed by corals and 1.29 $kgm^{-2}y^{-1}$ contributed by encrusting coralline algae. Bioerosion of the reef

framework occurs at an average rate of 0.36 $kgm^{-2}y^{-1}$ and results in the production of 1.29 $kgm^{-2}y^{-1}$ of sediment.

3. Average direct production normalized over the entire study area in Kailua Bay is 0.54 $kgm^{-2}y^{-1}$, with 0.31 $kgm^{-2}y^{-1}$ contributed by *Halimeda*, molluscs, and benthic foraminifera (combined) and 0.23 $kgm^{-2}y^{-1}$ contributed by articulated coralline algae. The contribution of direct sediment producers in Kailua Bay is significant, accounting for 64% of annual sediment production.
4. Extrapolating these modern rates of production back in time over the 5000 years that Kailua Bay has been wholly inundated by post-glacial sea level predicts $351.95 \pm 58.62 \times 10^5$ m^3 of unconsolidated calcareous sediment would have been produced in the system.
5. Cumulative production over 5000 years is compared to the estimated volume of Holocene-aged calcareous sediments currently stored in submarine ($3726 \pm 336 \times 10^3$ m^3) and subaerial ($10649 \pm 1839 \times 10^3$ m^3) reservoirs of Kailua. By these calculations, 41 ± 7% of the sediments produced since 5000 yr BP remain stored in the system.
6. Although transport and other means of loss are not directly assessed in this model, it is reasonable to suggest a significant portion of the 'missing' 59 ± 7% of Holocene sediment production is the result of loss owing to particle transport out of the system, dissolution, and attrition.

The study in Kailua Bay demonstrates that the collection of detailed field observations over a range of spatial scales offers a high-resolution look at carbonate dynamics in a natural, complex system. An interdisciplinary approach provides the

opportunity to study a suite of biogeological processes and products in both the present and over the last several thousand years. The multispectral image of Kailua Bay is a unique and beneficial aspect of this study, enabling the characterization of reef environments over a range of spatial scales with a resolution far greater than aerial photography can provide. This work contributes to an understanding of the rates of natural processes governing shoreface evolution, an important issue during current and predicted trends of climate change, sea level rise, and human impact to coastal regions.

Table A-1. Quantitative benthic substrate data collected in Kailua Bay. (Continued on following pages.)

Site	Site number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
information	Site name	T4-7	LR1	LR2	EB1	EB2	JE1a	JE1b	JE2	EM1	EM2	EM3	EM4	EM5	RS1	RS2	OM	KC
	Date collected	06.13.99	08.03.99	08.03.99	08.21.99	08.21.99	09.22.99	09.22.99	09.22.99	10.15.99	10.15.99	10.15.99	10.15.99	10.15.99	10.18.99	10.18.99	10.18.99	10.18.99
	Site name	T4-7	LR1	LR2	EB1	EB2	JE1a	JE1b	JE2	EM1	EM2	EM3	EM4	EM5	RS1	RS2	OM	KC
	Longitude	-157.72333	-157.71260	-157.71258	-157.72517	-157.72528	-157.72272	-157.72272	-157.72583	-157.71328	-157.71593	-157.72002	-157.72405	-157.72643	-157.71620	-157.71733	-157.71885	-157.71827
	Latitude	21.41073	21.41542	21.41242	21.41887	21.41972	21.42347	21.42347	21.42400	21.41805	21.41572	21.41393	21.42973	21.41965	21.42102	21.42037	21.42033	21.41775
	EPE (m)	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
	Bearing	45	170	330	330	0	270	45	45	150	345	180	240	270	190	90	270	270
	Depth_min	4.0	13.7	9.0	6.4	6.0	12.2	12.0	7.6	12.0	12.0	8.0	6.4	5.2	14.0	15.2	10.7	10.0
	Depth_max	5.5	13.7	9.0	13.7	7.0	12.2	13.0	7.6	15.0	15.0	8.0	6.4	5.2	17.0	15.2	10.7	11.0
	Depth_mean	5.0	13.7	9.0	10.0	6.4	12.2	12.5	7.6	13.5	13.5	8.0	6.4	5.2	15.5	15.2	10.7	10.5
	Rugosity	1.7	1.2	1.2	1.2	1.2	1.2	1.2	1.5	1.4	1.3	1.2	1.3	1.5	1.3	1.2	1.5	1.2
	Zone	S3	SCG	S1	N3	N3	NCG	NCG	N1	SCG	S1	S1	S3	N2	N1	N1	N3	N4
General	Fossil reef	0.60	0.15	0.20	0.36	0.35	0.12	0.19	0.17	0.05	0.30	0.39	0.57	0.41	0.11	0.24	0.42	0.37
substrate	Living coral	0.36	0.76	0.62	0.41	0.38	0.82	0.74	0.49	0.73	0.54	0.44	0.34	0.12	0.53	0.73	0.42	0.16
type	Dead coral	0.04	0.07	0.18	0.01	0.20	0.02	0.05	0.29	0.21	0.16	0.15	0.07	0.45	0.30	0.03	0.16	0.45
	Coralline algae	0.64	0.15	0.29	0.28	0.57	0.04	0.02	0.16	0.27	0.46	0.54	0.27	0.86	0.21	0.14	0.33	0.76
	Sand	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00
	Rubble	0.00	0.02	0.00	0.04	0.01	0.04	0.02	0.05	0.00	0.00	0.00	0.02	0.00	0.06	0.00	0.00	0.00
Substrate	Fossil reef - bare	0.00	0.00	0.00	0.08	0.00	0.08	0.17	0.15	0.00	0.00	0.00	0.37	0.00	0.05	0.10	0.25	0.06
type	FR w/ encrusting coralg	0.60	0.15	0.20	0.28	0.35	0.04	0.02	0.02	0.05	0.30	0.39	0.20	0.41	0.06	0.14	0.17	0.31
	FR w/ branching coralg	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Coral - living	0.36	0.76	0.62	0.41	0.38	0.82	0.74	0.49	0.73	0.54	0.44	0.34	0.12	0.53	0.73	0.42	0.16
	Coral - dead / bare	0.00	0.07	0.09	0.01	0.00	0.02	0.05	0.15	0.00	0.00	0.00	0.00	0.00	0.15	0.03	0.00	0.00
	Coral - dead w/ encrust alg	0.04	0.00	0.09	0.00	0.12	0.00	0.00	0.14	0.21	0.16	0.15	0.07	0.39	0.15	0.00	0.16	0.45
	Coral - dead w/ branch alg	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00
	Coralline algae - encrust	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Coralline algae - branch	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Rubble	0.00	0.02	0.00	0.04	0.01	0.04	0.02	0.05	0.00	0.00	0.00	0.02	0.00	0.06	0.00	0.00	0.00
	Rubble w/ encrust coralg	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Sand	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00
	Zoanthid	0.00	0.00	0.00	0.18	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.02
	Other	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Living	Total	0.36	0.76	0.62	0.41	0.38	0.82	0.74	0.49	0.73	0.54	0.44	0.34	0.12	0.53	0.73	0.42	0.16
coral	Porites lobata - sum of all	0.00	0.44	0.14	0.00	0.18	0.18	0.14	0.27	0.31	0.07	0.09	0.19	0.00	0.15	0.20	0.11	0.02
cover	Montipora verrucosa - sum	0.00	0.15	0.09	0.00	0.02	0.26	0.27	0.06	0.08	0.12	0.06	0.02	0.00	0.16	0.21	0.01	0.00
	Montipora patula - sum	0.34	0.16	0.28	0.36	0.17	0.31	0.32	0.16	0.21	0.28	0.29	0.10	0.05	0.11	0.32	0.27	0.06
	Porites lobata - encrusting	0.00	0.17	0.10	0.00	0.18	0.04	0.01	0.05	0.06	0.01	0.08	0.19	0.00	0.08	0.02	0.08	0.03
	Porites lobata - massive	0.00	0.27	0.04	0.00	0.00	0.14	0.13	0.11	0.23	0.06	0.01	0.00	0.00	0.05	0.16	0.03	0.00
	Porites lobata - plate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.02	0.02	0.00	0.00
	Porites compressa	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.12	0.01	0.00	0.00	0.00	0.10	0.00	0.00	0.04
	Montipora verrucosa - encr	0.00	0.15	0.09	0.00	0.02	0.26	0.27	0.06	0.08	0.12	0.06	0.02	0.00	0.12	0.21	0.01	0.00
	Montipora verrucosa - plate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00
	Montipora patula - encrust	0.34	0.16	0.28	0.36	0.17	0.31	0.32	0.16	0.21	0.28	0.29	0.10	0.05	0.10	0.32	0.27	0.06
	Montipora patula - plate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00
	Montipora flabellata - encrust	0.00	0.00	0.03	0.00	0.00	0.02	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.01	0.00	0.00	0.00
	Pocillopora meandrina	0.00	0.00	0.08	0.00	0.01	0.00	0.01	0.00	0.02	0.03	0.00	0.03	0.06	0.00	0.00	0.03	0.02
	Pocillopora eydouxi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Pavona varians	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Pavona duerdeni	0.02	0.00	0.00	0.01	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
	Leptastrea purpurea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
	Cyphastrea ocellina	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Other	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coral	Encrusting	0.34	0.48	0.50	0.39	0.37	0.63	0.60	0.27	0.35	0.43	0.43	0.31	0.06	0.31	0.55	0.36	0.09
morphology	Massive	0.00	0.27	0.04	0.00	0.00	0.14	0.13	0.11	0.23	0.06	0.01	0.00	0.00	0.05	0.16	0.03	0.00
	Plate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.07	0.02	0.00	0.00
	Stoutly-branched	0.00	0.00	0.08	0.00	0.01	0.00	0.01	0.00	0.02	0.03	0.00	0.03	0.06	0.00	0.00	0.03	0.02
	Finger-branched	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.12	0.01	0.00	0.00	0.00	0.10	0.00	0.00	0.04
	Bladed	0.02	0.00	0.00	0.01	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
	Other	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coral	Porites lobata - sum of all	0.00	0.58	0.24	0.00	0.46	0.23	0.19	0.55	0.41	0.13	0.21	0.19	0.00	0.28	0.27	0.27	0.16
community	Montipora verrucosa - sum	0.00	0.19	0.14	0.00	0.06	0.32	0.36	0.12	0.11	0.23	0.12	0.02	0.00	0.32	0.29	0.02	0.00
composition	Montipora patula - sum	0.98	0.21	0.45	0.88	0.44	0.37	0.44	0.33	0.28	0.52	0.67	0.10	0.05	0.21	0.44	0.64	0.36
(normalized	Porites lobata - encrusting	0.00	0.23	0.16	0.00	0.46	0.07	0.01	0.11	0.08	0.02	0.19	0.19	0.00	0.15	0.03	0.20	0.16
to coral cover)	Porites lobata - massive	0.00	0.35	0.08	0.00	0.00	0.16	0.18	0.44	0.30	0.11	0.02	0.00	0.00	0.09	0.22	0.07	0.00
	Porites lobata - plate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.04	0.03	0.00	0.00
	Porites compressa	0.00	0.01	0.00	0.00	0.00	0.05	0.00	0.00	0.17	0.02	0.00	0.00	0.00	0.19	0.00	0.00	0.24
	Montipora verrucosa - encr	0.00	0.19	0.14	0.00	0.06	0.32	0.36	0.12	0.11	0.23	0.12	0.02	0.00	0.23	0.29	0.02	0.00
(continued)	Montipora verrucosa - plate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00

Table A-1. (Continued) Quantitative benthic substrate data collected in Kailua Bay.

Site	Site number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
information	Site name	T4-7	LR1	LR2	EB1	EB2	JE1a	JE1b	JE2	EM1	EM2	EM3	EM4	EM5	RS1	RS2	OM	KC
Coral	Montipora patula - encrust	0.98	0.21	0.45	0.88	0.44	0.37	0.44	0.33	0.28	0.52	0.67	0.10	0.05	0.19	0.44	0.64	0.36
community	Montipora patula - plate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00
composition	Montipora flabellata - encrust	0.00	0.00	0.05	0.00	0.00	0.02	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00
(normalized	Pocillopora meandrina	0.00	0.01	0.12	0.00	0.04	0.00	0.01	0.00	0.03	0.06	0.00	0.03	0.06	0.00	0.00	0.07	0.13
to coral cover)	Pocillopora eydouxi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
(continued)	Pavona varians	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Pavona duerdeni	0.02	0.00	0.00	0.03	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.11
	Leptastrea purpurea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Cyphastrea ocellina	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Other	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coral	Encrusting	0.98	0.63	0.80	0.97	0.96	0.77	0.81	0.56	0.47	0.81	0.98	0.31	0.06	0.58	0.75	0.86	0.52
community	Mound, lobate, head	0.00	0.35	0.08	0.00	0.00	0.17	0.18	0.44	0.30	0.11	0.02	0.00	0.00	0.09	0.22	0.07	0.00
morphology	Plate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.15	0.03	0.00	0.00
(normalized	Stoutly-branched	0.00	0.01	0.12	0.00	0.04	0.00	0.01	0.00	0.03	0.06	0.00	0.03	0.06	0.00	0.00	0.07	0.13
to coral cover)	Finger-branched	0.00	0.01	0.00	0.00	0.00	0.05	0.00	0.00	0.17	0.02	0.00	0.00	0.00	0.19	0.00	0.00	0.24
	Bladed	0.02	0.00	0.00	0.03	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11
	Other	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coralline	Total	0.64	0.15	0.29	0.28	0.57	0.04	0.02	0.16	0.27	0.46	0.54	0.27	0.86	0.21	0.14	0.33	0.76
algae	encrusting on FR	0.60	0.15	0.20	0.28	0.35	0.04	0.02	0.02	0.05	0.30	0.39	0.20	0.41	0.06	0.14	0.17	0.31
cover	branching on FR	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	encrusting on DC	0.04	0.00	0.09	0.00	0.12	0.00	0.00	0.14	0.21	0.16	0.15	0.07	0.39	0.15	0.00	0.16	0.45
	branching on DC	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00
	encrusting algae substrate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	branching algae substrate	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	on rubble	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Site	Site number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
information	Site name	T4-7	LR1	LR2	EB1	EB2	JE1a	JE1b	JE2	EM1	EM2	EM3	EM4	EM5	RS1	RS2	OM	KC
Dead	Total	0.04	0.07	0.19	0.01	0.20	0.02	0.05	0.29	0.21	0.16	0.15	0.07	0.45	0.30	0.03	0.16	0.45
coral	Porites lobata	0.00	0.02	0.01	0.00	0.00	0.00	0.04	0.26	0.02	0.08	0.07	0.00	0.00	0.04	0.01	0.07	0.00
	Porites compressa	0.00	0.04	0.01	0.00	0.00	0.00	0.00	0.03	0.19	0.07	0.00	0.00	0.00	0.26	0.02	0.05	0.43
	Montipora verrucosa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Montipora patula	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Pocillopora meandrina	0.04	0.01	0.15	0.01	0.20	0.02	0.00	0.00	0.00	0.01	0.08	0.07	0.45	0.00	0.00	0.05	0.02
	Pocillopora eydouxi	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Pavona duerdeni	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Other	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dead coral	Porites lobata	0.00	0.29	0.05	0.00	0.00	0.00	0.92	0.90	0.07	0.50	0.47	0.00	0.00	0.13	0.34	0.44	0.00
community	Porites compressa	0.00	0.57	0.05	0.00	0.00	0.00	0.00	0.10	0.86	0.43	0.00	0.00	0.00	0.87	0.66	0.28	0.95
composition	Montipora verrucosa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
(normalized	Montipora patula	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
to dead	Pocillopora meandrina	1.00	0.14	0.80	1.00	1.00	1.00	0.00	0.00	0.00	0.07	0.53	1.00	1.00	0.00	0.00	0.28	0.05
coral cover)	Pocillopora eydouxi	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Pavona duerdeni	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Other	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coral colony	Total	10	37	37	14	20	19	17	23	35	31	28	17	15	32	21	27	17
counts	Porites lobata - sum of all	0	16	9	0	9	7	4	15	12	7	8	4	0	11	9	8	3
	Montipora verrucosa - sum	0	8	4	0	2	3	6	4	5	6	3	2	0	7	6	1	0
	Montipora patula - sum	9	9	15	11	7	5	5	4	12	12	17	8	7	7	6	14	6
	Porites lobata - encrusting	0	9	8	0	9	2	1	2	4	3	6	4	0	5	3	6	3
	Porites lobata - massive	0	7	1	0	0	5	3	13	7	4	2	0	0	4	5	2	0
	Porites lobata - plate	0	0	0	0	0	0	0	0	1	0	0	0	0	2	1	0	0
	Porites compressa	0	3	0	0	0	1	0	0	5	1	0	0	0	7	0	0	2
	Montipora verrucosa - encr	0	8	4	0	2	3	6	4	5	6	3	2	0	6	6	1	0
	Montipora verrucosa - plate	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
	Montipora patula - encrust	9	9	15	11	7	5	5	4	12	12	17	8	7	6	6	14	6
	Montipora patula - plate	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
	Montipora flabellata - encrust	0	0	2	0	0	2	0	0	0	2	0	0	0	0	0	0	0
	Pocillopora meandrina	0	1	7	0	2	0	1	0	1	3	0	3	7	0	0	4	2
	Pocillopora eydouxi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Pavona varians	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
	Pavona duerdeni	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	4
	Leptastrea purpurea	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
	Cyphastrea ocellina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Other	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Diversity	H'c	0.45	0.98	1.16	0.52	0.73	1.28	1.04	0.82	1.21	1.03	0.74	0.73	0.36	1.10	1.01	0.75	0.53

Table A-1. (Continued) Quantitative benthic substrate data collected in Kailua Bay.

Site	Site number	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
information	Site name	SP1	SP2	SP3	SP4	NP1	NP2	NP3	NP4	NP5	NP6	NT	NTEW	SP5	SP6	SP7	NP7
	Date collected	1.24.00	01.24.00	01.24.00	01.24.00	01.25.00	01.25.00	01.25.00	01.25.00	01.25.00	01.25.00	02.02.00	02.03.00	02.06.00	02.06.00	02.06.00	02.06.00
	Site name	SP1	SP2	SP3	SP4	NP1	NP2	NP3	NP4	NP5	NP6	NT	NTEW	SP5	SP6	SP7	NP7
	Longitude	-157.71777	-157.71961	-157.72156	-157.71667	-157.71864	-157.72250	-157.72944	-157.73478	-157.73089	-157.73706	-157.71353	-157.71353	-157.71319	-157.70856	-157.71700	-157.73078
	Latitude	21.41265	21.41117	21.40650	21.40833	21.42475	21.42781	21.42689	21.42642	21.42153	21.42061	21.41782	21.41782	21.40650	21.41236	21.41631	21.42894
	EPE (m)	7	9	6	8	11	8	9	8	9	9	7	7	14	14	14	14
	Bearing	330	30	310	0	330	310	270	330	310	0	225	315	315	315	180	0
	Depth_min	8.2	8	4	8	15	13	6	5.0	5	3	12	12	9	13	9	6
	Depth_max	10.1	9	6	9	17	13	7	5.0	5	3	13	18	11	14	17	6
	Depth_mean	10.0	8	5	8.5	16	13	6.5	5.0	5	3	13	12	10	13	10	6
	Rugosity	1.1	1.1	1.7	1.2	1.3	1.2	1.5	1.0	1.5	1.0	1.2	1.5	1.2	1.1	1.6	1.0
	Zone	S1	S1	S2	S1	N1	NCG	N1	N2	N2	NH	SCG	SCG	S1	S4	S1	N5
General	Fossil reef	0.24	0.32	0.77	0.11	0.39	0.21	0.34	0.79	0.75	0.88	0.04	0.13	0.27	0.73	0.26	0.51
substrate	Living coral	0.74	0.53	0.08	0.74	0.40	0.78	0.59	0.05	0.03	0.00	0.85	0.70	0.59	0.25	0.61	0.35
type	Dead coral	0.02	0.15	0.15	0.16	0.19	0.01	0.07	0.00	0.17	0.01	0.11	0.16	0.14	0.02	0.04	0.12
	Coralline algae	0.24	0.34	0.49	0.11	0.53	0.11	0.11	0.15	0.84	0.94	0.08	0.29	0.36	0.75	0.35	0.10
	Sand	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Rubble	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.09	0.00
Substrate	Fossil reef - bare	0.02	0.05	0.36	0.08	0.02	0.11	0.23	0.79	0.08	0.05	0.00	0.00	0.05	0.00	0.00	0.49
type	FR w/ encrusting coralg	0.23	0.27	0.41	0.03	0.37	0.10	0.11	0.00	0.60	0.84	0.04	0.13	0.22	0.73	0.26	0.00
	FR w/ branching coralg	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.02
	Coral - living	0.74	0.53	0.08	0.74	0.40	0.78	0.59	0.05	0.03	0.00	0.85	0.70	0.59	0.25	0.61	0.35
	Coral - dead / bare	0.01	0.09	0.07	0.08	0.03	0.00	0.07	0.00	0.05	0.01	0.08	0.00	0.00	0.00	0.01	0.07
	Coral - dead w/ encrust alg	0.01	0.06	0.00	0.08	0.16	0.01	0.00	0.00	0.09	0.00	0.03	0.15	0.14	0.02	0.03	0.00
	Coral - dead w/ branch alg	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.05
	Coralline algae - encrust	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Coralline algae - branch	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.06	0.10	0.00	0.00	0.00	0.00	0.00	0.02
	Rubble	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00
	Rubble w/ encrust coralg	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.06	0.00
	Sand	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Zoanthid	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Other	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Living	Total	0.74	0.53	0.08	0.74	0.40	0.78	0.59	0.05	0.03	0.00	0.85	0.70	0.59	0.25	0.61	0.35
coral	Porites lobata - sum of all	0.09	0.01	0.04	0.20	0.16	0.24	0.11	0.04	0.00	0.00	0.18	0.27	0.05	0.07	0.11	0.07
cover	Montipora verrucosa - sum	0.05	0.05	0.01	0.04	0.05	0.21	0.04	0.01	0.00	0.00	0.09	0.13	0.18	0.10	0.16	0.04
	Montipora patula - sum	0.59	0.46	0.03	0.47	0.16	0.33	0.42	0.00	0.01	0.00	0.47	0.24	0.32	0.07	0.31	0.17
	Porites lobata - encrusting	0.05	0.01	0.04	0.10	0.01	0.07	0.07	0.04	0.00	0.00	0.02	0.01	0.03	0.06	0.02	0.07
	Porites lobata - massive	0.04	0.00	0.00	0.10	0.14	0.17	0.05	0.00	0.00	0.00	0.15	0.21	0.03	0.02	0.07	0.00
	Porites lobata - plate	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.01	0.05	0.00	0.00	0.02	0.00
	Porites compressa	0.00	0.00	0.00	0.02	0.03	0.00	0.00	0.00	0.00	0.00	0.08	0.03	0.00	0.00	0.00	0.00
	Montipora verrucosa - encr	0.05	0.05	0.01	0.04	0.05	0.21	0.04	0.01	0.00	0.00	0.09	0.13	0.18	0.10	0.13	0.04
	Montipora verrucosa - plate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00
	Montipora patula - encrust	0.59	0.46	0.03	0.47	0.13	0.33	0.42	0.00	0.01	0.00	0.47	0.17	0.32	0.07	0.26	0.17
	Montipora patula - plate	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.05	0.00
	Montipora flabellata - encrust	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00
	Pocillopora meandrina	0.00	0.01	0.00	0.01	0.00	0.00	0.01	0.00	0.02	0.00	0.03	0.01	0.04	0.00	0.02	0.00
	Pocillopora eydouxi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Pavona varians	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Pavona duerdeni	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00
	Leptastrea purpurea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Cyphastrea ocellina	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Other	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07
Coral	Encrusting	0.70	0.52	0.08	0.61	0.19	0.61	0.53	0.05	0.01	0.00	0.57	0.31	0.53	0.23	0.42	0.28
morphology	Massive	0.04	0.00	0.00	0.10	0.14	0.17	0.05	0.00	0.00	0.00	0.15	0.21	0.03	0.02	0.07	0.00
	Plate	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.01	0.11	0.00	0.00	0.09	0.00
	Stoutly-branched	0.00	0.01	0.00	0.01	0.00	0.00	0.01	0.00	0.02	0.00	0.03	0.01	0.04	0.00	0.02	0.00
	Finger-branched	0.00	0.00	0.00	0.02	0.03	0.00	0.00	0.00	0.00	0.00	0.08	0.03	0.00	0.00	0.00	0.00
	Bladed	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00
	Other	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07
Coral	Porites lobata - sum of all	0.12	0.03	0.51	0.27	0.39	0.30	0.19	0.83	0.00	0.00	0.21	0.39	0.09	0.30	0.18	0.21
community	Montipora verrucosa - sum	0.07	0.09	0.08	0.05	0.13	0.27	0.08	0.17	0.00	0.00	0.10	0.18	0.30	0.41	0.27	0.11
composition	Montipora patula - sum	0.80	0.87	0.37	0.64	0.39	0.42	0.72	0.00	0.29	0.00	0.55	0.34	0.55	0.26	0.51	0.48
(normalized	Porites lobata - encrusting	0.07	0.03	0.51	0.13	0.01	0.09	0.11	0.83	0.00	0.00	0.02	0.02	0.05	0.23	0.03	0.21
to coral cover)	Porites lobata - massive	0.05	0.00	0.00	0.14	0.36	0.22	0.08	0.00	0.00	0.00	0.18	0.30	0.05	0.06	0.12	0.00
	Porites lobata - plate	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.01	0.07	0.00	0.00	0.03	0.00
	Porites compressa	0.00	0.00	0.00	0.03	0.07	0.00	0.00	0.00	0.00	0.00	0.10	0.04	0.00	0.00	0.00	0.00
	Montipora verrucosa - encr	0.07	0.09	0.08	0.05	0.13	0.27	0.08	0.17	0.00	0.00	0.10	0.18	0.30	0.41	0.22	0.11
(continued)	Montipora verrucosa - plate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00

Table A-1. (Continued) Quantitative benthic substrate data collected in Kailua Bay.

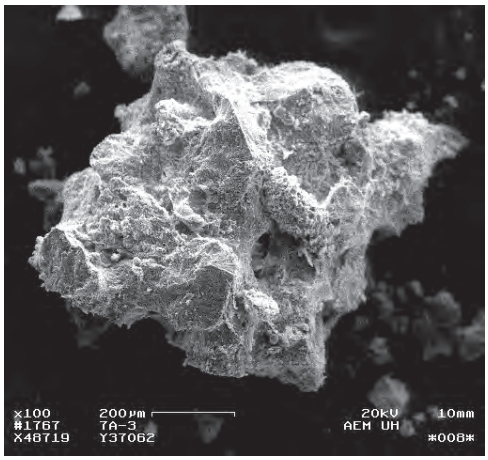
Site	Site number	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
information	Site name	SP1	SP2	SP3	SP4	NP1	NP2	NP3	NP4	NP5	NP6	NT	NTEW	SP5	SP6	SP7	NP7
Coral	Montipora patula - encrust	0.80	0.87	0.37	0.64	0.33	0.42	0.72	0.00	0.29	0.00	0.55	0.25	0.55	0.26	0.44	0.48
community	Montipora patula - plate	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.08	0.00
composition	Montipora flabellata - encrust	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.01
(normalized	Pocillopora meandrina	0.01	0.01	0.05	0.01	0.00	0.00	0.01	0.00	0.71	1.00	0.03	0.02	0.06	0.00	0.03	0.00
to coral cover)	Pocillopora eydouxi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
(continued)	Pavona varians	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Pavona duerdeni	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00
	Leptastrea purpurea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Cyphastrea ocellina	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Other	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.19
Coral	Encrusting	0.95	0.99	0.95	0.83	0.48	0.78	0.91	1.00	0.29	0.00	0.68	0.45	0.89	0.94	0.69	0.81
community	Mound, lobate, head	0.05	0.00	0.00	0.14	0.36	0.22	0.08	0.00	0.00	0.00	0.18	0.30	0.05	0.06	0.12	0.00
morphology	Plate	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.01	0.16	0.00	0.00	0.15	0.00
(normalized	Stoutly-branched	0.01	0.01	0.05	0.01	0.00	0.00	0.01	0.00	0.71	1.00	0.03	0.02	0.06	0.00	0.03	0.00
to coral cover)	Finger-branched	0.00	0.00	0.00	0.03	0.07	0.00	0.00	0.00	0.00	0.00	0.10	0.04	0.00	0.00	0.00	0.00
	Bladed	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00
	Other	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.19
Coralline	Total	0.24	0.34	0.49	0.11	0.53	0.11	0.11	0.15	0.84	0.94	0.08	0.29	0.36	0.75	0.35	0.10
algae	encrusting on FR	0.23	0.27	0.41	0.03	0.37	0.10	0.11	0.00	0.60	0.84	0.04	0.13	0.22	0.73	0.26	0.00
cover	branching on FR	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.02
	encrusting on DC	0.01	0.06	0.00	0.08	0.16	0.01	0.00	0.00	0.09	0.00	0.03	0.15	0.14	0.02	0.03	0.00
	branching on DC	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.05
	encrusting algae substrate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	branching algae substrate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.06	0.10	0.00	0.00	0.00	0.00	0.00	0.02
	on rubble	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.06	0.00
Site	Site number	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
information	Site name	SP1	SP2	SP3	SP4	NP1	NP2	NP3	NP4	NP5	NP6	NT	NTEW	SP5	SP6	SP7	NP7
Dead	Total	0.02	0.15	0.15	0.16	0.18	0.01	0.07	0.00	0.17	0.01	0.11	0.16	0.14	0.02	0.04	0.12
coral	Porites lobata	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.01	0.02	0.00
	Porites compressa	0.00	0.00	0.00	0.10	0.12	0.01	0.02	0.00	0.00	0.00	0.10	0.13	0.04	0.00	0.01	0.07
	Montipora verrucosa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Montipora patula	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Pocillopora meandrina	0.01	0.15	0.15	0.06	0.00	0.00	0.03	0.00	0.00	0.01	0.01	0.01	0.06	0.01	0.01	0.00
	Pocillopora eydouxi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Pavona duerdeni	0.00	0.00	0.00	0.00	0.01	0.00	0.02	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
	Other	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05
Dead coral	Porites lobata	0.00	0.00	0.00	0.00	0.31	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.25	0.50	0.43	0.00
community	Porites compressa	0.18	0.00	0.00	0.60	0.64	1.00	0.33	0.00	0.00	0.00	0.90	0.84	0.29	0.00	0.29	0.55
composition	Montipora verrucosa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
(normalized	Montipora patula	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
to dead	Pocillopora meandrina	0.55	1.00	1.00	0.40	0.00	0.00	0.47	0.00	1.00	1.00	0.10	0.09	0.45	0.50	0.29	0.00
coral cover)	Pocillopora eydouxi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Pavona duerdeni	0.00	0.00	0.00	0.00	0.05	0.00	0.21	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00
	Other	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.45
Coral colony	Total	32	29	8	26	28	32	30	6	4	1	45	54	35	31	32	20
counts	Porites lobata - sum of all	7	2	3	8	8	11	0	4	0	0	0	17	7	11	7	5
	Montipora verrucosa - sum	6	4	1	3	5	9	3	2	0	0	2	9	10	14	7	4
	Montipora patula - sum	16	20	3	13	11	11	4	0	2	0	6	18	14	5	15	9
	Porites lobata - encrusting	4	2	3	5	2	5	0	4	0	0	0	1	5	9	2	5
	Porites lobata - massive	3	0	0	3	5	6	0	0	0	0	0	11	2	2	4	0
	Porites lobata - plate	0	0	0	0	1	0	0	0	0	0	0	5	0	0	1	0
	Porites compressa	1	0	0	0	3	0	6	0	0	0	0	6	0	0	0	0
	Montipora verrucosa - encr	6	4	1	3	5	9	3	2	0	0	0	9	10	14	6	4
	Montipora verrucosa - plate	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0
	Montipora patula - encrust	16	20	3	13	10	10	1	0	2	0	5	14	14	5	13	8
	Montipora patula - plate	0	0	0	0	1	1	3	0	0	0	1	4	0	0	2	1
	Montipora flabellata - encrust	0	0	0	0	0	0	0	0	0	0	9	0	0	1	0	0
	Pocillopora meandrina	1	2	1	2	0	1	16	0	2	1	6	2	4	0	3	0
	Pocillopora eydouxi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Pavona varians	1	1	0	0	0	0	0	0	0	0	18	0	0	0	0	0
	Pavona duerdeni	0	0	0	0	1	0	1	0	0	0	0	2	0	0	0	0
	Leptastrea purpurea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Cyphastrea ocellina	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0
	Other	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Diversity	H'c	0.72	0.60	0.30	0.91	0.88	1.06	0.79	0.17	0.11	0.00	1.18	1.19	0.96	0.64	0.97	0.82

Table A-1. (Continued) Quantitative benthic substrate data collected in Kailua Bay.

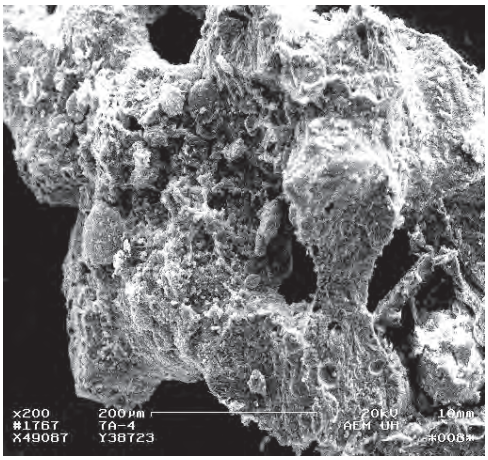
Site	Site number	34	35	36	37	38	39	40	41	42	43	44	47	48	49	50	51
information	Site name	NP8	NP9	NP10	F1	F2	F3	F4	F5	F6	F7	F8	KA	BR	SC	BS	LA
	Date collected	02.06.00	02.06.00	02.06.00	02.16.00	02.16.00	02.16.00	02.16.00	02.16.00	02.16.00	02.16.00	02.16.00	03.12.00	03.12.00	03.12.00	03.12.00	03.12.00
	Site name	NP8	NP9	NP10	F1	F2	F3	F4	F5	F6	F7	F8	KA	BR	SC	BS	LA
	Longitude	-157.72894	-157.72486	-157.72547	-157.72161	-157.72161	-157.72294	-157.72108	-157.72297	-157.72967	-157.73078	-157.73628	-157.71022	-157.72208	-157.72822	-157.72486	-157.70778
	Latitude	21.44106	21.44047	21.42228	21.41653	21.41653	21.41803	21.41917	21.42122	22.41717	23.41847	24.41497	21.41364	21.43297	21.41411	21.40747	21.40650
	EPE (m)	14	14	14	19	19	19	19	19	19	19	19	14	19	19	19	19
	Bearing	0	0	90	165	225	45	180	225	0	255	0	315	225	135	45	315
	Depth_min	7.6	15	6	9	8	6	7	7	8	2	3	11.6	12	3.6	2.7	12
	Depth_max	7.6	15	8	13	10	6	14	9	8	3	3	15	12	4.2	4	12
	Depth_mean	7.6	15	6	11	9	6	11	8	8	2.5	3	11.6	12	4	3	12
	Rugosity	1.0	1.0	1.2	1.5	1.2	1.2	1.2	1.2	1.1	1.4	1.0	1.5	1.0	1.2	2.0	1.1
	Zone	N2	N5	N2	S1	S1	N3	N4	N1	N3	N2	FRS	S1	N1	S2	S2	S1
General	Fossil reef	0.83	0.65	0.59	0.15	0.33	0.35	0.67	0.28	0.42	0.81	0.73	0.13	0.47	0.74	0.77	0.31
substrate	Living coral	0.12	0.34	0.12	0.72	0.64	0.42	0.24	0.57	0.47	0.09	0.00	0.66	0.51	0.10	0.03	0.63
type	Dead coral	0.00	0.01	0.27	0.10	0.03	0.22	0.07	0.14	0.00	0.08	0.00	0.21	0.02	0.01	0.17	0.07
	Coralline algae	0.05	0.01	0.88	0.07	0.15	0.57	0.72	0.40	0.26	0.91	0.73	0.23	0.47	0.88	0.97	0.15
	Sand	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.00
	Rubble	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Substrate	Fossil reef - bare	0.83	0.65	0.00	0.12	0.21	0.00	0.02	0.02	0.20	0.00	0.00	0.00	0.00	0.02	0.00	0.20
type	FR w/ encrusting coralg	0.00	0.00	0.59	0.03	0.12	0.35	0.60	0.26	0.17	0.59	0.73	0.13	0.47	0.72	0.77	0.11
	FR w/ branching coralg	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.05	0.23	0.00	0.00	0.00	0.00	0.00	0.00
	Coral - living	0.12	0.34	0.12	0.72	0.64	0.42	0.24	0.57	0.47	0.09	0.00	0.66	0.51	0.10	0.03	0.63
	Coral - dead / bare	0.00	0.00	0.00	0.06	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.11	0.02	0.00	0.00	0.02
	Coral - dead w/ encrust alg	0.00	0.01	0.24	0.04	0.03	0.21	0.07	0.14	0.00	0.08	0.00	0.10	0.00	0.01	0.15	0.04
	Coral - dead w/ branch alg	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00
	Coralline algae - encrust	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Coralline algae - branch	0.04	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.02	0.01	0.00	0.00	0.00	0.14	0.02	0.00
	Rubble	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Rubble w/ encrust coralg	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Sand	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.00
	Zoanthid	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Other	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.11	0.00	0.00	0.00	0.00	0.00
Living	Total	0.12	0.34	0.12	0.72	0.64	0.42	0.24	0.57	0.47	0.09	0.00	0.66	0.51	0.10	0.03	0.63
coral	Porites lobata - sum of all	0.04	0.05	0.00	0.01	0.01	0.01	0.02	0.14	0.00	0.01	0.00	0.18	0.16	0.03	0.00	0.19
cover	Montipora verrucosa - sum	0.06	0.08	0.01	0.10	0.10	0.03	0.00	0.02	0.29	0.00	0.00	0.10	0.11	0.00	0.00	0.31
	Montipora patula - sum	0.00	0.17	0.07	0.60	0.54	0.28	0.10	0.38	0.17	0.07	0.00	0.34	0.17	0.07	0.00	0.11
	Porites lobata - encrusting	0.04	0.05	0.00	0.00	0.01	0.01	0.00	0.04	0.00	0.01	0.00	0.01	0.10	0.03	0.00	0.14
	Porites lobata - massive	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.17	0.06	0.00	0.00	0.05
	Porites lobata - plate	0.00	0.00	0.00	0.01	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Porites compressa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00
	Montipora verrucosa - encr	0.06	0.08	0.01	0.01	0.10	0.03	0.00	0.02	0.29	0.00	0.00	0.10	0.11	0.00	0.00	0.31
	Montipora verrucosa - plate	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Montipora patula - encrust	0.00	0.17	0.07	0.50	0.54	0.28	0.08	0.38	0.17	0.07	0.00	0.34	0.17	0.07	0.00	0.11
	Montipora patula - plate	0.00	0.00	0.00	0.11	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Montipora flabellata - encrust	0.01	0.02	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.02
	Pocillopora meandrina	0.02	0.02	0.04	0.00	0.00	0.06	0.00	0.02	0.01	0.02	0.00	0.00	0.03	0.00	0.03	0.01
	Pocillopora eydouxi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Pavona varians	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Pavona duerdeni	0.00	0.00	0.00	0.00	0.00	0.03	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Leptastrea purpurea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Cyphastrea ocellina	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Other	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coral	Encrusting	0.11	0.31	0.08	0.51	0.64	0.33	0.16	0.46	0.46	0.08	0.00	0.45	0.42	0.10	0.00	0.57
morphology	Massive	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.17	0.06	0.00	0.00	0.05
	Plate	0.00	0.00	0.00	0.21	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Stoutly-branched	0.02	0.02	0.04	0.00	0.00	0.06	0.00	0.02	0.01	0.02	0.00	0.00	0.03	0.00	0.03	0.01
	Finger-branched	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00
	Bladed	0.00	0.00	0.00	0.00	0.00	0.03	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Other	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coral	Porites lobata - sum of all	0.29	0.15	0.00	0.02	0.01	0.03	0.07	0.24	0.00	0.08	0.00	0.27	0.32	0.31	0.00	0.30
community	Montipora verrucosa - sum	0.45	0.24	0.07	0.14	0.16	0.08	0.00	0.03	0.61	0.03	0.00	0.16	0.22	0.04	0.00	0.49
composition	Montipora patula - sum	0.03	0.49	0.63	0.84	0.83	0.67	0.43	0.67	0.36	0.71	0.00	0.52	0.33	0.65	0.00	0.17
(normalized	Porites lobata - encrusting	0.29	0.15	0.00	0.00	0.01	0.03	0.00	0.07	0.00	0.08	0.00	0.02	0.19	0.31	0.00	0.23
to coral cover)	Porites lobata - massive	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.16	0.00	0.00	0.00	0.26	0.12	0.00	0.00	0.08
	Porites lobata - plate	0.00	0.00	0.00	0.02	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Porites compressa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00
	Montipora verrucosa - encr	0.45	0.24	0.07	0.02	0.16	0.08	0.00	0.03	0.61	0.03	0.00	0.16	0.22	0.04	0.00	0.49
(continued)	Montipora verrucosa - plate	0.00	0.00	0.00	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table A-1. (Continued) Quantitative benthic substrate data collected in Kailua Bay.

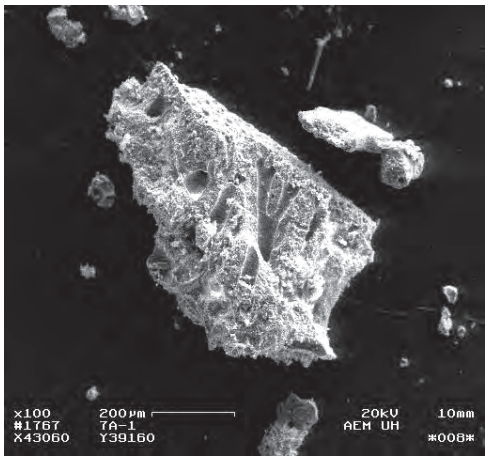
Site	Site number	34	35	36	37	38	39	40	41	42	43	44	47	48	49	50	51
information	Site name	NP8	NP9	NP10	F1	F2	F3	F4	F5	F6	F7	F8	KA	BR	SC	BS	LA
Coral	Montipora patula - encrust	0.03	0.49	0.63	0.69	0.83	0.67	0.34	0.67	0.36	0.71	0.00	0.52	0.33	0.65	0.00	0.17
community	Montipora patula - plate	0.00	0.00	0.00	0.15	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
composition	Montipora flabellata - encrust	0.10	0.05	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.03
(normalized	Pocillopora meandrina	0.13	0.07	0.31	0.00	0.00	0.15	0.00	0.03	0.02	0.17	0.00	0.01	0.06	0.00	1.00	0.01
to coral cover)	Pocillopora eydouxi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
(continued)	Pavona varians	0.00	0.00	0.00	0.00	0.00	0.00	0.32	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Pavona duerdeni	0.00	0.00	0.00	0.00	0.00	0.06	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Leptastrea purpurea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Cyphastrea ocellina	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Other	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coral	Encrusting	0.87	0.93	0.69	0.71	1.00	0.79	0.66	0.79	0.97	0.83	0.00	0.69	0.82	1.00	0.00	0.91
community	Mound, lobate, head	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.16	0.00	0.00	0.00	0.26	0.12	0.00	0.00	0.08
morphology	Plate	0.00	0.00	0.00	0.29	0.00	0.00	0.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
(normalized	Stoutly-branched	0.13	0.07	0.31	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00
to coral cover)	Finger-branched	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.03	0.02	0.17	0.00	0.01	0.06	0.00	1.00	0.01
	Bladed	0.00	0.00	0.00	0.00	0.00	0.06	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Other	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coralline	Total	0.05	0.01	0.88	0.07	0.15	0.57	0.72	0.40	0.26	0.91	0.73	0.23	0.47	0.88	0.97	0.15
algae	encrusting on FR	0.00	0.00	0.59	0.03	0.12	0.35	0.60	0.26	0.17	0.59	0.73	0.13	0.47	0.72	0.77	0.11
cover	branching on FR	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.05	0.23	0.00	0.00	0.00	0.00	0.00	0.00
	encrusting on DC	0.00	0.01	0.24	0.04	0.03	0.21	0.07	0.14	0.00	0.08	0.00	0.10	0.00	0.01	0.15	0.04
	branching on DC	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00
	encrusting algae substrate	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	branching algae substrate	0.04	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.02	0.01	0.00	0.00	0.00	0.14	0.02	0.00
	on rubble	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Site	Site number	34	35	36	37	38	39	40	41	42	43	44	47	48	49	50	51
	Site name	NP8	NP9	NP10	F1	F2	F3	F4	F5	F6	F7	F8	KA	BR	SC	BS	LA
Dead	Total	0.00	0.01	0.27	0.10	0.00	0.22	0.00	0.14	0.00	0.08	0.00	0.21	0.02	0.01	0.17	0.07
coral	Porites lobata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.03	0.02	0.00	0.00	0.07
	Porites compressa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00
	Montipora verrucosa	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Montipora patula	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Pocillopora meandrina	0.00	0.01	0.27	0.04	0.03	0.14	0.00	0.13	0.00	0.08	0.00	0.02	0.00	0.01	0.17	0.00
	Pocillopora eydouxi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Pavona duerdeni	0.00	0.00	0.00	0.00	0.00	0.08	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Other	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dead coral	Porites lobata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.80	0.00	0.00	1.00
community	Porites compressa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.31	0.00	0.00	0.00	0.00
composition	Montipora verrucosa	0.00	0.00	0.00	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
(normalized	Montipora patula	0.00	0.00	0.00	0.36	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
to dead	Pocillopora meandrina	1.00	1.00	1.00	0.43	1.00	0.62	0.00	0.96	0.00	1.00	0.00	0.08	0.20	1.00	1.00	0.00
coral cover)	Pocillopora eydouxi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Pavona duerdeni	0.00	0.00	0.00	0.00	0.00	0.38	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Other	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coral colony	Total	17	26	12	22	19	33	12	36	30	10	0	36	37	8	4	35
counts	Porites lobata - sum of all	5	6	0	1	1	1	1	7	0	1	0	12	11	2	0	10
	Montipora verrucosa - sum	4	7	1	7	4	4	0	3	13	1	0	6	11	1	0	14
	Montipora patula - sum	1	6	6	14	14	19	5	19	15	7	0	15	11	5	0	8
	Porites lobata - encrusting	5	6	0	1	1	1	0	4	0	1	0	1	9	2	0	8
	Porites lobata - massive	0	0	0	0	0	0	0	3	0	0	0	11	2	0	0	2
	Porites lobata - plate	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	Porites compressa	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0
	Montipora verrucosa - encr	4	7	1	7	4	4	0	3	13	1	0	6	11	1	0	14
	Montipora verrucosa - plate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Montipora patula - encrust	1	6	6	14	14	19	4	19	15	7	0	15	11	5	0	8
	Montipora patula - plate	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	Montipora flabellata - encrust	3	2	0	0	0	0	0	3	0	0	0	0	1	0	0	1
	Pocillopora meandrina	4	5	5	0	0	6	0	3	1	1	0	1	3	0	4	2
	Pocillopora eydouxi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Pavona varians	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0
	Pavona duerdeni	0	0	0	0	0	3	3	0	0	0	0	0	0	0	0	0
	Leptastrea purpurea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Cyphastrea ocellina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Other	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Diversity	H'c	0.42	0.81	0.35	0.60	0.59	0.80	0.63	0.87	0.72	0.31	0.00	1.04	1.06	0.32	0.11	1.02



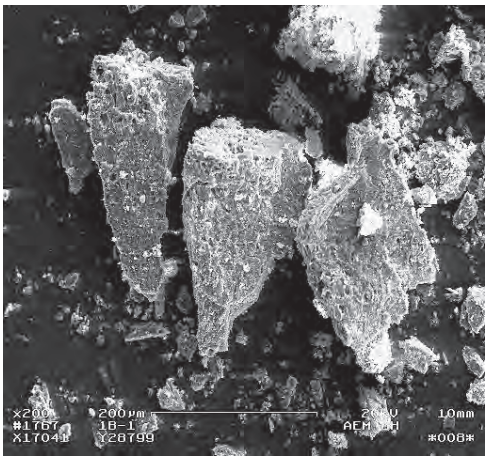
(a) coral fragment (x100)



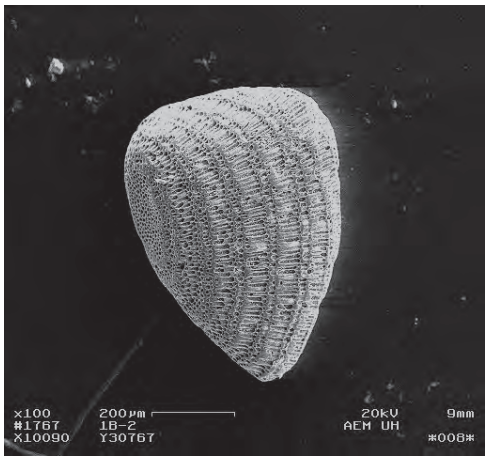
(b) coral fragment (x200)



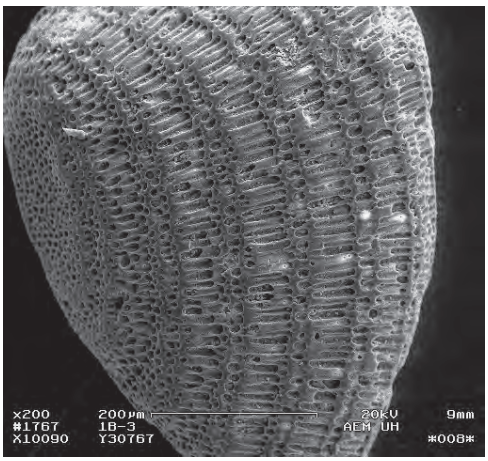
(c) Halimeda fragment (x100)



(d) coralline algae fragments (x200)

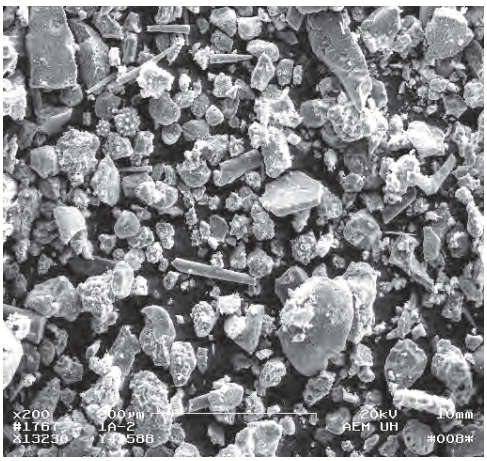


(e) coralline algae fragment (x100)

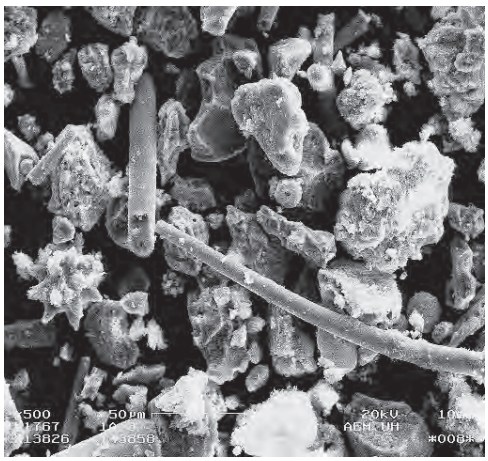


(f) coralline algae fragment (x200)

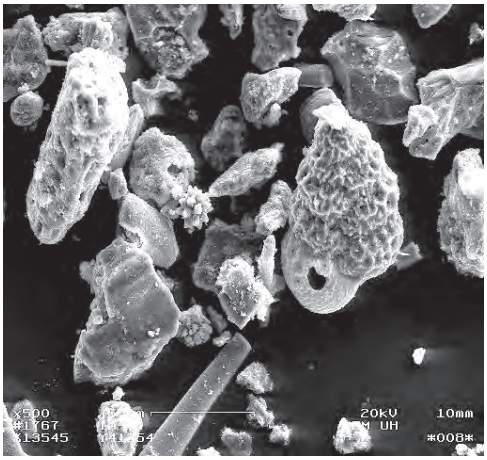
Figure B-1. SEM (scanning electron microscopy) images of calcareous sediment components.



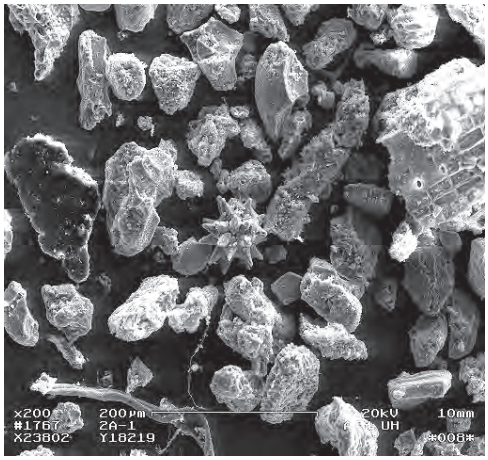
(a) internal sediment (from core)



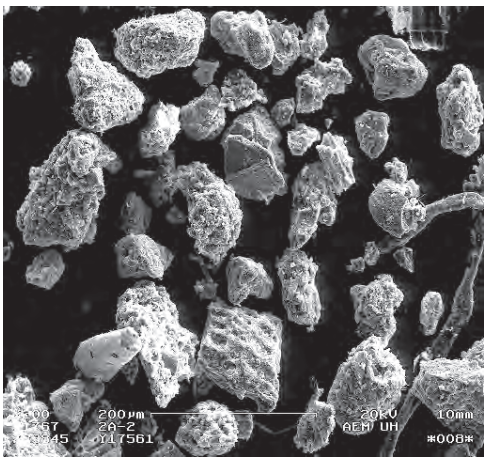
(b) internal sediment (from core)



(c) internal sediment (from core)



(d) suspended sediment



(e) suspended sediment

(f) suspended sediment

Figure B-2. SEM (scanning electron microscopy) images of internal sediments (from reef cores) and suspended sediments (collected with Niskin samplers). Components are fine calcareous sand and silt.

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