Pacific Science (1996), vol. 50, no. 2: 211–229

Macrobenthic Community Structure, Secondary Production, and Rates of Bioturbation and Sedimentation at the Kāne'ohe Bay Lagoon Floor[1]

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ABSTRACT: The Kāne'ohe Bay lagoon floor is one of the largest shallow-water, muddy habitats in Hawai'i and is a major repository for sediments and, possibly, pollutants from the Kāne'ohe watershed. Nonetheless, macrobenthic community structure, secondary production, and particle-mixing rates at the lagoon floor remain largely unstudied. During 1990–1991, we surveyed macrobenthic community structure at four stations 12 m deep at the lagoon floor and evaluated macrobenthic secondary production, as well as particle mixing and sedimentation, at one representative station. Macrobenthic abundance in the lagoon during our survey was high (44,000–100,000 individuals m^{-2}), with very small deposit-feeding polychaetes dominating the community. This low-diversity assemblage was relatively similar throughout the bay and resembled the communities found in highly depositional environments (e.g., river deltas, and zones of active erosion and redeposition). Macrobenthic secondary production at the representative station was low, with a best estimate of 4.9 g m^{-2} yr^{-1} ash-free dry weight (reasonable range 1.2–20 g m^{-2} yr^{-1}); this appeared to be enough production to support <2% of the annual fish yield in Kāne'ohe Bay. Tracer-particle experiments at the representative station, sampled after 7 months and 1 yr, indicated low sediment-mixing rates (diffusive mixing coefficient ~0.9 cm^2 yr^{-1}), little size dependence in particle mixing, and relatively high short-term rates of sedimentation (6–7 cm yr^{-1}). After corrections for sediment compaction, these short-term sedimentation rates (2.7–3.7 cm yr^{-1}) are about three-fold higher than longer-term (decadal) sedimentation rates (~1.0 cm yr^{-1}) estimated using Pb-210 geochronology at a nearby site; the discrepancy may be caused by sediment transport from nearby fringing reefs, resuspension of bottom sediments by alpheid shrimp, or interannual variability of sediment flux into the bay. We conclude that the Kāne'ohe Bay lagoon harbors a low-diversity, low-productivity macrobenthic assemblage largely structured by high gross sedimentation rates. In addition, we conclude that sand-sized particles entering the bay are rapidly (within months) sequestered below the sediment-water interface, where they remain for at least 1-yr time scales.

KĀNE'OHE BAY IS A semienclosed embayment on the northeastern coast of the island of O'ahu, Hawai'i. The bay is used heavily as a site for recreational and commercial fishing, and provides diverse resources for boating, diving, and scientific research (e.g., S. V. Smith et al. 1973, 1981, Everson 1994). In addition, the bay acts as a repository for terrestrial sediments and pollutants running off the Kāne'ohe watershed, as well as carbonate sediments derived from barrier and fringing reefs (Roy 1970, S. V. Smith et al. 1973, Hollett 1977, Mackenzie et al. 1981). Because the bay supports a broad range of human activities, its environmental quality is of prime interest to the human population of

[1] This work was supported by a grant from the Hawai'i Department of Land and Natural Resources to C.R.S. This is contribution no. 3499 from the School of Ocean and Earth Science and Technology, University of Hawai'i. Manuscript accepted 2 August 1995.

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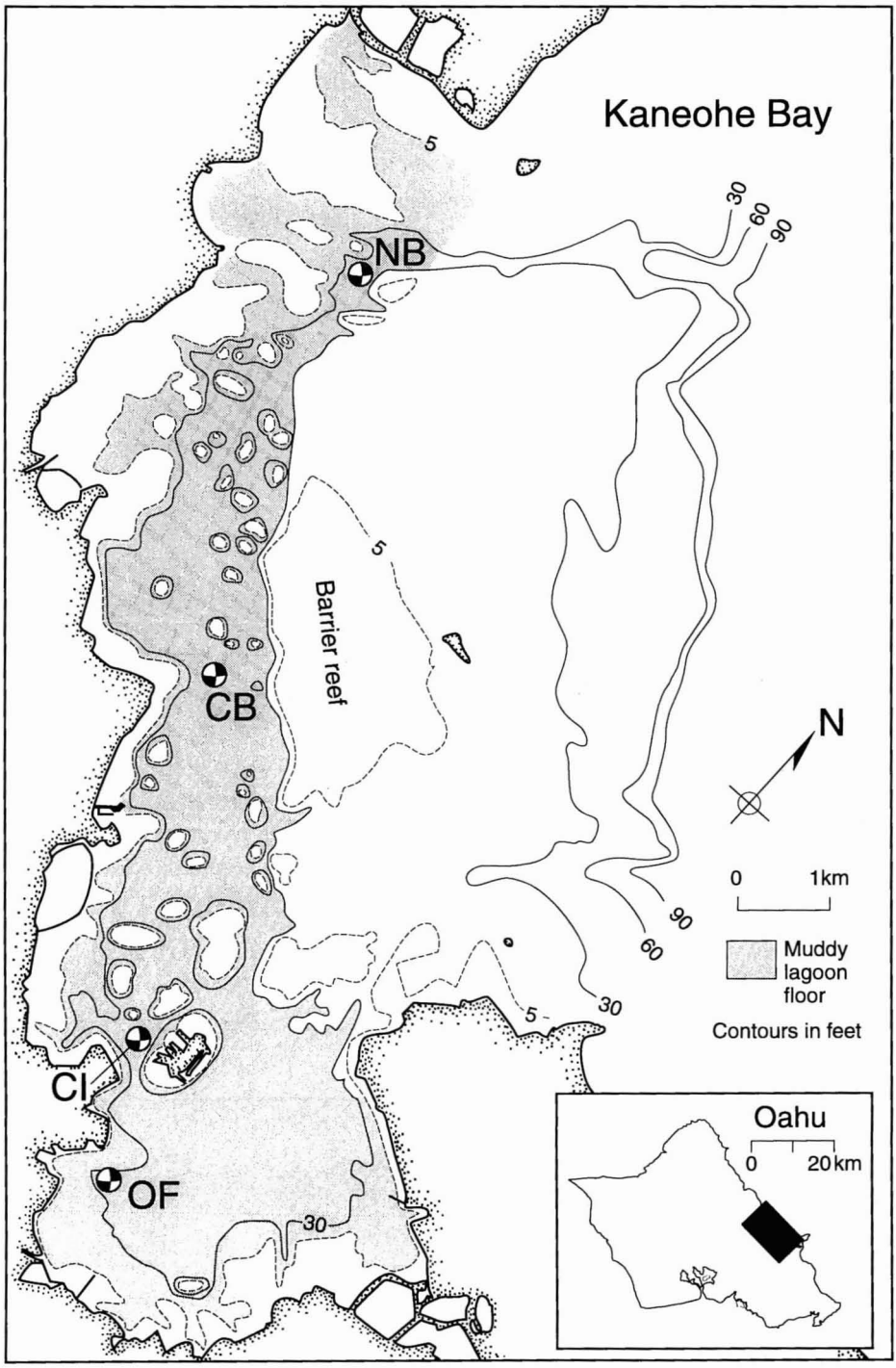

FIGURE 1. Bathymetric map of Kāne'ohe Bay showing the positions of our macrobenthic survey stations. Station CI was the representative site at which secondary-production and particle-dynamic studies were conducted. Shading indicates the area of the muddy lagoon floor. Depth contours are in feet (1 ft = 0.31 m). (Figure modifed from Roy 1970)

Hawai'i. In many respects, Kāne'ohe Bay might be considered a model for embayments on high Pacific islands increasingly influenced by human population growth.

Inner Kāne'ohe Bay (that portion of the bay lying landward of the barrier reef) (Figure 1) covers a plan area of roughly 31 km^2 (S. V. Smith et al. 1981). Because of its relative proximity to shore, the inner bay receives the brunt of terrestrial and anthropogenic impacts. About 48% of the inner bay is underlain by the lagoon floor, a predominantly silt-clay (or "mud") habitat at water depths of ca. 12–16 m (S. V. Smith et al. 1981); this is one of the largest shallow-water, muddy habitats in the state of Hawai'i. Past studies have identified the lagoon floor as a zone of high sedimentation (i.e., 1.4–3.7 cm yr^{-1} over the period 1927–1976 [Hollett 1977]); it thus may be a major repository for particle-bound pollutants entering the bay from urban and agricultural areas in the Kāne'ohe watershed.

Despite the size of the lagoon-floor habitat, we know little concerning community structure and production of its macrobenthos (animals roughly 0.5–10 mm in smallest body dimension). Published environmental studies from the bay have evaluated macrobenthic biomass (e.g., S. V. Smith et al. 1973, 1981, and studies cited therein), but not taxonomic structure, functional group composition, or secondary production of lagoon-floor benthos. Community structure and production data typically are very useful in evaluations of the environmental quality of marine sedimentary habitats (e.g., Pearson and Rosenberg 1978, Rhoads et al. 1985, Weston 1990) and in assessments of the potential for benthos to support bottom-fish (e.g., weke) production (Collie 1985, Highsmith and Coyle 1990).

In spite of the lagoon floor's potential role as a repository for pollutants, current rates of particle mixing (or "bioturbation") and sedimentation also remain uncharacterized in the bay. Both particle mixing and sedimentation are critical terms in equations used to model the fate of reactive chemicals bound to sedimenting particles (e.g., Berner 1980, Kramer et al. 1991, C. R. Smith et al. 1993); these parameters must be evaluated to determine whether deposited materials ultimately are recycled to the water column or entombed in lagoon sediments.

Our study was designed to begin to fill the gaps in knowledge of lagoon-floor community structure and sediment dynamics. We began this project with three specific goals in mind: (1) To survey macrobenthic community abundance, taxonomic structure, and functional-group composition at four widely separated sites on the lagoon floor; (2) to evaluate, at one representative site, macrobenthic biomass, size structure, and (at least roughly) secondary production; and (3) to assess at the representative site modes and rates of solid-phase sediment mixing, and short-term rates of sedimentation.

Our results suggest that Kāne'ohe Bay lagoon harbors, by tropical standards (sensu Alongi 1990), a macrobenthos of low diversity, small mean body size, low biomass, and relatively low productivity. This assemblage, and sediment dynamics at the lagoon floor in general, appears to be largely controlled by high rates of sedimentation occurring in the bay.

MATERIALS AND METHODS

Our study involved three major phases: (1) macrobenthic community survey, (2) evaluation of macrobenthic biomass and production at a single representative site, and (3) evaluation of particle mixing and sedimentation at the representative site.

Macrobenthic Community Survey

For our survey, four stations in water depths of 12–16 m were selected along the length of the lagoon floor (Figure 1). Stations were chosen to cover the major sectors of the bay and to correspond to sites (stations OF, CB, and NB) where water-column parameters were being evaluated by other investigators (e.g., Laws and Allen 1996). In addition, a site near Coconut Island (CI) was selected because it falls within the marine-preserve waters of the Hawai'i Institute of Marine

Biology and thus was likely to be minimally disturbed by the activities of fishermen and the general public.

Pilot studies indicated that to capture traditional macrobenthic taxa (e.g., polychaetes, molluscs, peracarid crustaceans) efficiently at our stations, a sieve size of ≤ 300 μm was necessary for processing core samples. In addition, these studies indicated that diver-inserted cores of 35-cm^2 plan areas recovered large numbers of infaunal macrobenthos (100–400 individuals per core), with the overwhelming majority occurring in the top 10 cm of cores.

Thus, for our survey, three 35-cm^2 tube cores were collected by scuba divers from each of the four stations during the summer of 1990 (CI sampled on 9 June 1990, OF and NB on 11 July 1990, CB on 5 September 1990). Cored sediments were extruded and sectioned into two 5-cm intervals (i.e., core depths of 0–5 and 5–10 cm), and then fixed for >24 h in a 10% buffered formalin-seawater solution. After fixation, samples were washed on a 300-μm sieve, stained with rose bengal to facilitate recognition of animals, and sorted for metazoans (excluding the meiofaunal taxa Nematoda, Ostracoda, and Harpaticoidea) under a dissecting microscope (cf. Kukert and Smith 1992). The >5000 animals thus collected were then identified to the lowest possible taxon under dissecting and compound microscopes using published taxonomic literature (e.g., Fauchald 1977, Kay 1979, Devaney and Eldredge 1987) and the aid of local taxonomic experts (e.g., J. Bailey-Brock for polychaetes). Assignment of species to functional groups was based on observations on live cores held in aquaria, examination of gut contents, and natural-history descriptions in Fauchald and Jumars (1979) and Devaney and Eldredge (1987).

Differences in mean abundance of total macrofauna and individual species were evaluated with nonparametric Kruskal–Wallis tests (Conover 1980). Species diversity was evaluated using Hurlbert's (1971) modification of Sanders's (1968) rarefaction technique. The 95% confidence intervals for rarefaction diversity were computed from the t distribution using core samples from individual stations as replicates, as in Kukert and Smith (1992).

Macrobenthic Biomass and Production

Station CI exhibited intermediate levels of macrofaunal abundance, species diversity, and abundance of the dominant macrofaunal species (see *Results* section); we thus selected this as our "representative" station for more intensive study. Samples for biomass and production estimates were collected from this station using diver-operated 400-cm^2 Ekman corers (Kukert and Smith 1992) collected in November 1991. Three cores, each processed to a sediment depth of 20 cm, were used for these analyses. Greater corer size and depth were used than in the macrobenthic survey to enhance the likelihood of collecting large, rare individuals that may contribute substantially to biomass and production, but little to faunal abundance; nonetheless, deep-burrowing megafauna (e.g., alpheid shrimp [Harrison 1981]) are likely to have avoided our Ekman samplers. After collection, samples were fixed immediately with 10% buffered formalin-seawater solution and, within 1 week, washed on nested sieves of 1400-, 1000-, 710-, 500-, and 300-μm mesh size. Animals retained on sieves (or "sieve fractions") were then enumerated under a dissecting microscope and identified to major taxa (i.e., polychaetes, crustaceans, molluscs, and miscellaneous). Biomass, in units of ash-free dry weight (AFDW), of each sieve fraction was then determined by drying in a preweighed aluminum boat for 48 hr at 60°C followed by ashing in a muffle furnace for 2 hr at 500°C (Edgar 1990); AFDW was then measured by difference.

Secondary production (in AFDW units) was evaluated using Edgar's (1990) equations for benthos relating production to mean body size and environmental temperature. The mean weights for the polychaete and nonpolychaete components of each sieve fraction from each core were determined by dividing AFDWs by the number of individuals retained on the sieve (Edgar 1990);

the mean weights, and mean annual lagoon-floor temperature of 24°C (Bathen 1968), were then inserted into Edgar's general equation no. 1 to estimate production for sieve fractions. Total production per core sample was then estimated by summing the production estimates from individual sieve fractions.

Particle Mixing and Sedimentation Rates

To evaluate particle mixing and sedimentation at our CI station over annual time scales, we conducted tracer particle experiments similar to those of C. R. Smith et al. (1986) and Wheatcroft (1992). For emplacement of tracer particles, four 1-m^2 treatment plots were selected at random points along a 50-m transect line on the seafloor at station CI. Plots were positioned 1 m from the transect line and separated from each other by a minimum of 5 m to preclude diver disturbance of adjacent plots during sampling; the corners of each plot were marked with 1.3-cm-diameter plastic stakes to facilitate relocation. At the zero time point (7 December 1990), glass beads (Glas-shot manufactured by the Cataphote Division of the Ferro Corporation) were sprinkled on each experimental plot by divers, using the bead dispensers described in Wheatcroft (1992). Dispensers were held ca. 50 cm above plots and gently shaken horizontally to broadcast beads. The sprinkled beads were a mixture of three nominal size ranges: 315 ml of beads 210–420 μm in diameter, 59 ml of 44–74 μm beads, and 9.5 ml of 5–44 μm beads. The volume used for each bead size class was just enough to create a monolayer over a 1-m^2 area. We used a range of bead sizes for two reasons: (1) to determine whether our tracer particles were passively sinking (via Stokesian settling) into a less dense, essentially fluid sediment, and (2) to determine whether particle mixing was size selective (cf. Wheatcroft 1992). It should be noted that, although sediments at station CI are predominantly silt-clay (i.e., <63 μm in diameter), $\sim 17\%$ of particles (by mass) in the top 10 cm fall between 63 and 500 μm in grain size (H.K. and C.R.S., unpubl. data); thus, the tracer particles spanned a natural range of grain sizes.

For sampling, 1-m^2 quadrates were divided into 16 squares; one 35-cm^2 tube core was collected by a diver from a random, previously unsampled square in each quadrat at time zero and after ca. 7 months (3 July 1991) and 1 yr (8 December 1991). In the field, recovered cores were extruded, sliced at 1-cm intervals, and the outside, ca. 1-cm thick, "rind" from each interval was discarded. The remaining volume of each interval was measured in a graduated cylinder.

To facilitate counting of glass beads, we reduced the volume of material in samples by treatments to remove diatom tests, organic material, and calcium carbonate. Control experiments indicated that our glass tracer beads were unaffected by the treatments. Samples were first soaked in 0.2 M NaOH for 12–16 hr to remove diatom tests. Subsequently, they were washed into glass beakers, dried at 60°C, and combusted in a muffle furnace at 550°C to remove organic material. Combusted material was redissolved and calcium carbonate removed by adding 30 ml of concentrated HCl to each sample, followed by stirring until the reaction was completed. Samples were then diluted with water and sonicated for 15–20 min to disaggregate any remaining particles. Samples were then allowed to settle in beakers for ≥ 12 hr, the supernatant was decanted and replaced with tap water, and the sample was washed through nested nitex screens of 425-, 300-, 202-, 130-, and 63-μm mesh.

Beads retained on sieves were enumerated in one of three ways. Samples with less than ca. 1000 beads were counted directly under a dissecting microscope. For sieve fractions with >1000 beads, bead numbers were estimated by weighing or by counting of random subsamples. Before weighing, bead samples were examined microscopically to be certain only tracer beads remained and then dried. After weighing, weights for particular sieve fractions were converted to bead numbers based on control experiments in which appropriate bead mixtures were run through our sample-processing protocol, washed onto

nested sieves, counted, and then weighed. Replicate control experiments indicated that bead numbers estimated by weight were in error by no more than 5%.

Tracer beads retained on 63-μm sieves were typically very numerous and, after $t = 0$, fouled with large amounts of sponge spicules. For these samples containing >1000 beads, bead numbers were estimated by counts of random subsamples. Subsampling was achieved by spreading samples on counting dishes marked with concentric rings; beads in randomly selected rings totaling 13% of the dish area were then counted under a dissecting microscope. Total beads in the sample were then estimated by multiplying the number counted by a factor of $(0.13)^{-1}$.

To evaluate particle mixing rates, bead profiles from 7-month cores were fitted to normal distributions and eddy diffusion coefficients (D_b) calculated from the relationship

$$D_b = s^2/4t$$

where s is the standard deviation of the normal distribution and t is time (Guinasso and Schink 1975). This approach assumes both a constant eddy-diffusive mixing rate over the depth of mixing and that sedimentation rates are relatively high (Guinasso and Schink 1975). The fact that most of the 7-month bead profiles were essentially symmetrically Gaussian indicated that these two assumptions are reasonable over the time and depth scales of our 7-month tracer profiles (cf. Guinasso and Schink 1975). Sedimentation rates for 7-month bead profiles were estimated by calculating the mean depth of beads associated with the primary peak in bead concentrations (Guinasso and Schink 1975). Given sediment mixing, this approach may yield overestimates of sedimentation rates (cf. Guinasso and Schink 1975). However, because bead profiles after 7 months were essentially vertically symmetrical, overestimation errors for sedimentation rates must be small (i.e., $<25\%$).

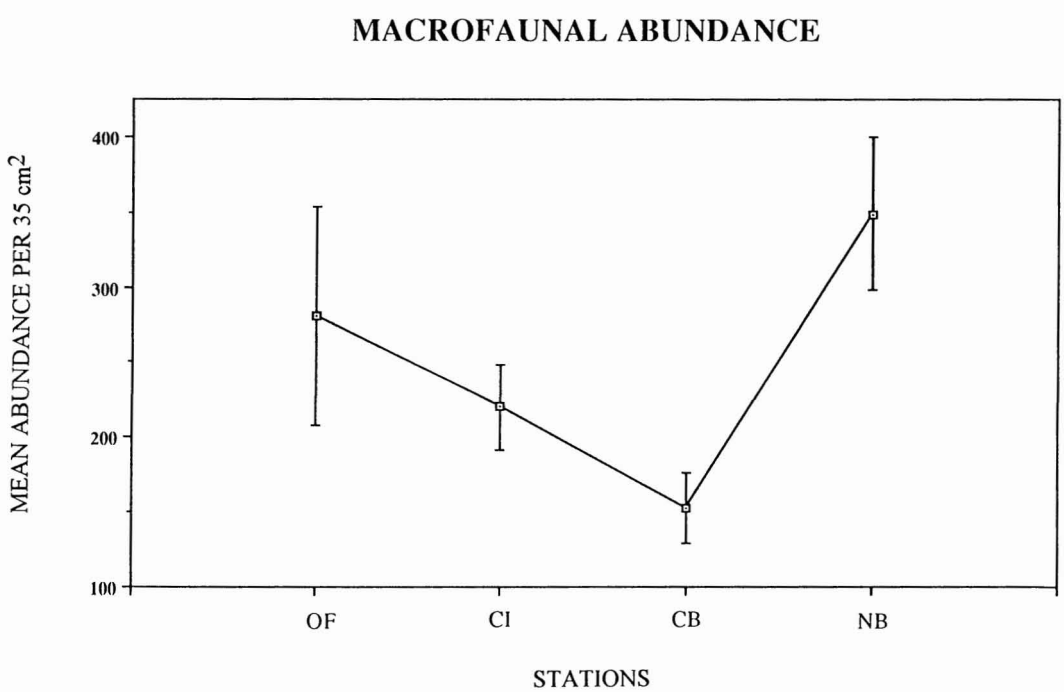

FIGURE 2. Mean macrofaunal abundance per 35-cm^2 core sample ($\pm$SE) at our survey stations.

RESULTS

Macrobenthic Community Survey

Macrofaunal densities were high at all four stations surveyed (Figure 2), with mean abundances ranging between ca. 150 and 350 individuals per 35 cm^2 (i.e., 44,000–100,000 per square meter). Between-station differences in abundances were not significant (Kruskal–Wallis test, df = 3, $P = 0.133$), suggesting that macrobenthic densities were relatively similar along the length of the bay. At all stations, at least 70% of the total macrofauna occurred in the upper 5 cm of core samples. The CI station harbored intermediate levels of total macrobenthic abundance and thus could be considered "representative."

Mean diversity, as measured by rarefaction curves (Figure 3), also was relatively invariant between stations, with all curves falling within the 95% confidence envelope for station CI. Again, station CI exhibited intermediate levels of this variable.

Species composition at all stations was heavily dominated by a few species. Although a total of 46 species was collected in the survey, at least 80% of the community abundance at all stations was composed of only five species (Table 1). Three of the species (the polychaetes *Sternaspis* sp. [family Sternaspidae], *Cossura coasta* Kitamari [Cossuridae], and *Laonome* sp. [Sabellidae]) exhibited relatively high abundance at all four stations (Figure 4). The polychaete *Armandia intermedia* Fauvel (Opheliidae) and an unidentified priapulid species were each abundant at only one station: the former in the central bay (CB) and the latter in the north bay (NB).

The high-level taxonomic and functional-group composition of the lagoon-floor ben-

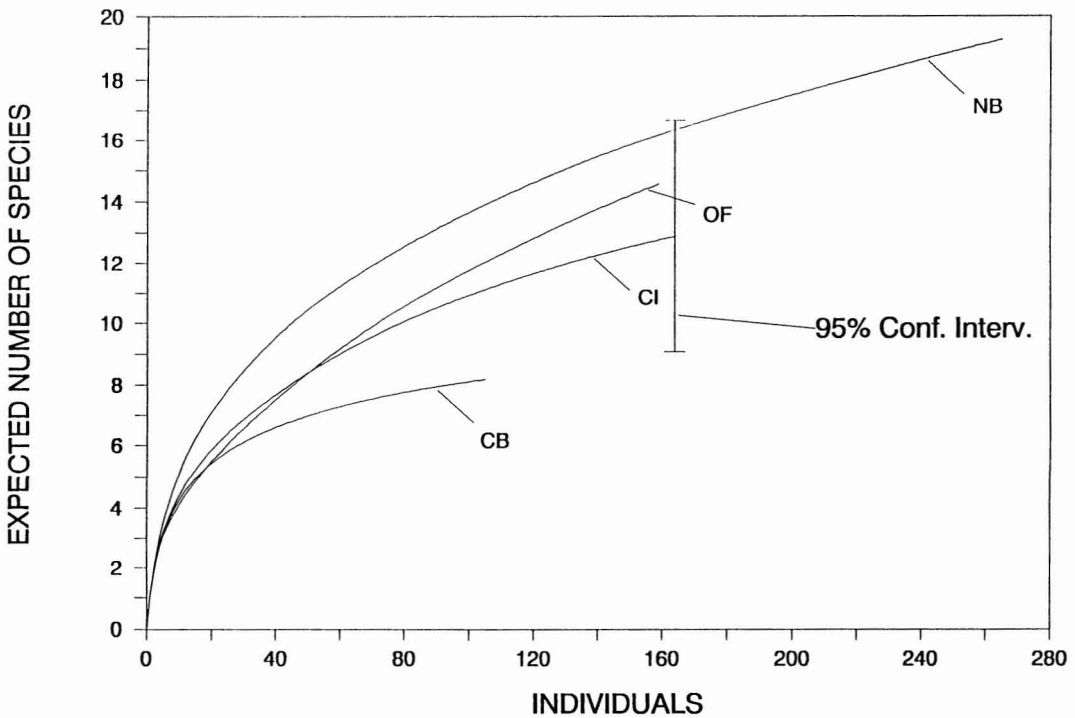

FIGURE 3. Mean rarefaction diversity curves for macrobenthos at our four survey stations. Note that the 95% confidence interval for station CI overlaps the curves, or their projections, for all the other stations, indicating that the curves are not significantly different at the $P = 0.05$ level.

TABLE 1

MEAN ABUNDANCE OF THE FIVE DOMINANT MACROFAUNAL SPECIES PER 35-CM^2 CORE (OUT OF A TOTAL OF 46 SPECIES COLLECTED)

	STATION			
SPECIES	OF	CI	CB	NB
Sternaspis sp.	122	87	19	54
Cossura coasta	76	57	30	47
Laonome sp.	46	33	28	46
Armandia intermedia[a]	2	3	57	2
Priapulid sp.[a]	2	0	0	128
% of total fauna	88%	82%	88%	80%

[a] Species abundant at only one station.

thos was remarkably uniform. Polychaetes constituted more than 50% of the macrobenthos at all stations (Table 2), and the summed abundance of vermiform (wormlike) taxa made up at least 95% of the total. Greater than 80% of the macrobenthos at each station were judged to be deposit feeders, while at least 72% were capable of burrowing within the sediment (Table 2). In addition, the sampled macrofauna was extremely diminutive; all collected individuals were less (usually much less) than 1 cm in length.

Macrobenthic Biomass and Production

Macrobenthic biomass at the intensively studied CI station in November 1991 was estimated as 0.44 g m^{-2} (Table 3); this is not signficantly different from macrobenthic biomass measured in the south and central bay lagoon by S. V. Smith et al. (1981) in 1979. Annual macrobenthic secondary production estimated for that site is 4.9 g m^{-2} yr^{-1}

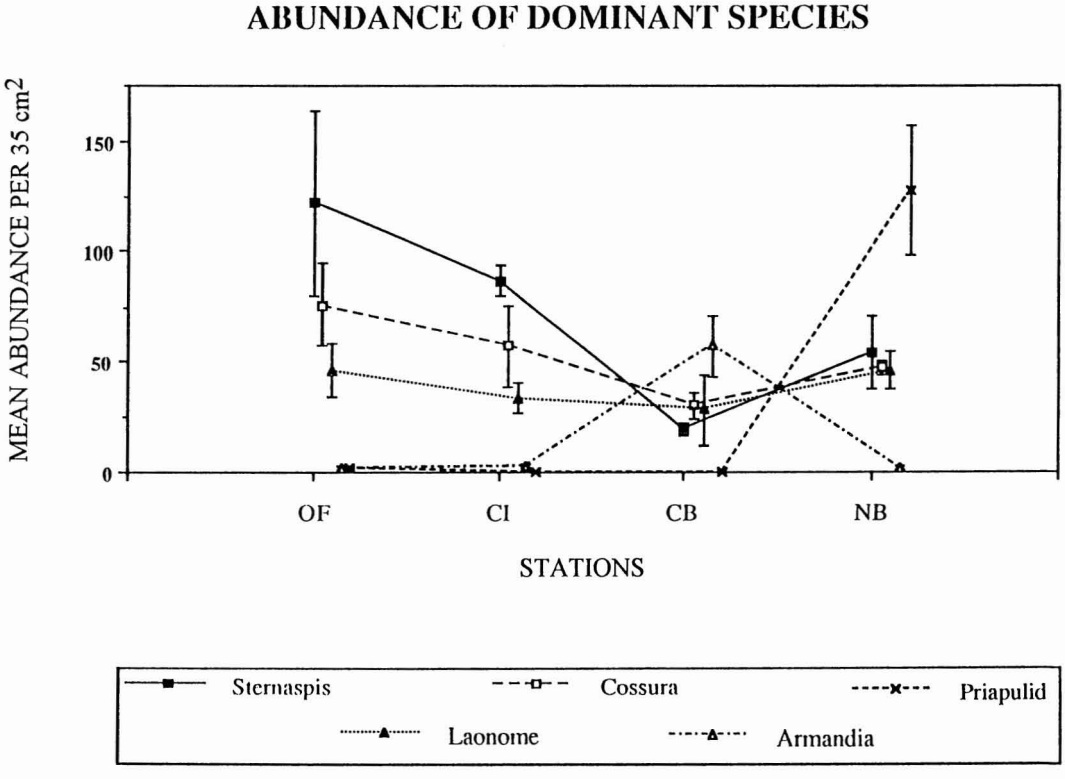

FIGURE 4. Mean abundance per 35-cm^2 core sample (±SE) at our survey stations of the five dominant macrofaunal species in the survey.

TABLE 2

TAXONOMIC AND FUNCTIONAL-GROUP COMPOSITION OF MACROFAUNA AT EACH SURVEY STATION

GROUP	STATION			
	OF	CI	CB	NB
Polychaetes	92%	89%	93%	55%
Vermes	95%	99%	97%	96%
Deposit feeders	>90%	>90%	>90%	>89%
Burrowers	>74%	>75%	>72%	>87%

TABLE 3

MEAN MACROBENTHIC ABUNDANCE, BIOMASS, AND SECONDARY PRODUCTION (±SE) ESTIMATED FOR STATION CI IN WINTER 1991

TOTAL ABUNDANCE (m^{-2})	MEAN AFDW BIOMASS ($g\ m^{-2}$)	MEAN AFDW PRODUCTION ($g\ m^{-2}\ yr^{-1}$)	ANNUAL P/B RATIO
17,510 (±1,510)	0.44 (±0.106)	4.9 (±0.7)	~11

(Table 3), yielding a mean production-to-biomass ratio of ca. 11.

Data collected for the biomass and production estimates also provide insight into the size distribution of abundance, biomass, and production at station CI (Table 4). Most of the macrobenthic abundance was concentrated in very small individuals that pass through a 500-μm sieve; in contrast, 50% of the biomass fell in the largest sieve size class (>1400 μm). Because smaller animals tend to have higher production-to-biomass ratios (Edgar 1990), estimated secondary production was fairly evenly distributed among the five sieve-size classes measured (Table 4).

It is important to note that this production estimate should be used with caution for several reasons. First, Edgar's size-class method for estimating production can have substantial error; Edgar suggested that for a community dominated by five species, 95% confidence limits for the production should be ca. 60–170%. Second, our estimate of annual production is based on sampling at a single time point (in November 1991); given the high production-to-biomass ratio of ca. 11 (which implies that the macrobenthic community turns over every ~5 wks), substantial temporal variability in macrobenthic structure and production is quite possible. In fact, our benthic-survey data from summer 1990 indicate a four-fold higher macrofaunal abundance than measured during sampling for our production estimates in fall 1992. A four-fold difference in abundance could translate to a several-fold difference in estimated production (cf. Edgar 1990), especially if higher abundances were concentrated in smaller size classes. Given these potential errors, the actual annual production at the CI station could reasonably fall somewhere between 25 and 400% of our estimate (i.e., between 1.2 and 20 $g\ m^{-2}\ yr^{-1}$); we suspect that it falls near the lower end of that range.

TABLE 4

SIZE DISTRIBUTION OF MACROBENTHOS AT STATION CI IN WINTER 1991 (BASED ON THREE 400-cm^2 CORE SAMPLES COLLECTING ~1,850 INDIVIDUALS

SIZE CLASS (mm)	% OF ABUNDANCE	% OF BIOMASS	% OF PRODUCTION
>1.4	1	50	28
1.0–1.4	2	11	11
0.71–1.0	9	17	22
0.50–0.71	18	12	18
0.30–0.50	70	10	21

Particle Mixing and Sedimentation Rates

Particle mixing and sedimentation were addressed through tracer-bead experiments at the CI station. At $t = 0$, all sizes of tracer beads were very heavily concentrated in the top (0–1 cm) layer of the cores (Figure 5). This indicates that deployment and sampling of our tracer experiments yielded essentially no detectable penetration of tracer beads into the cores (i.e., sampling artifacts were at most very minor).

After 7 months, tracer particles of all sizes had penetrated substantially into the sediments (Figure 6). In most cases, the bead profiles appeared to be essentially Gaussian

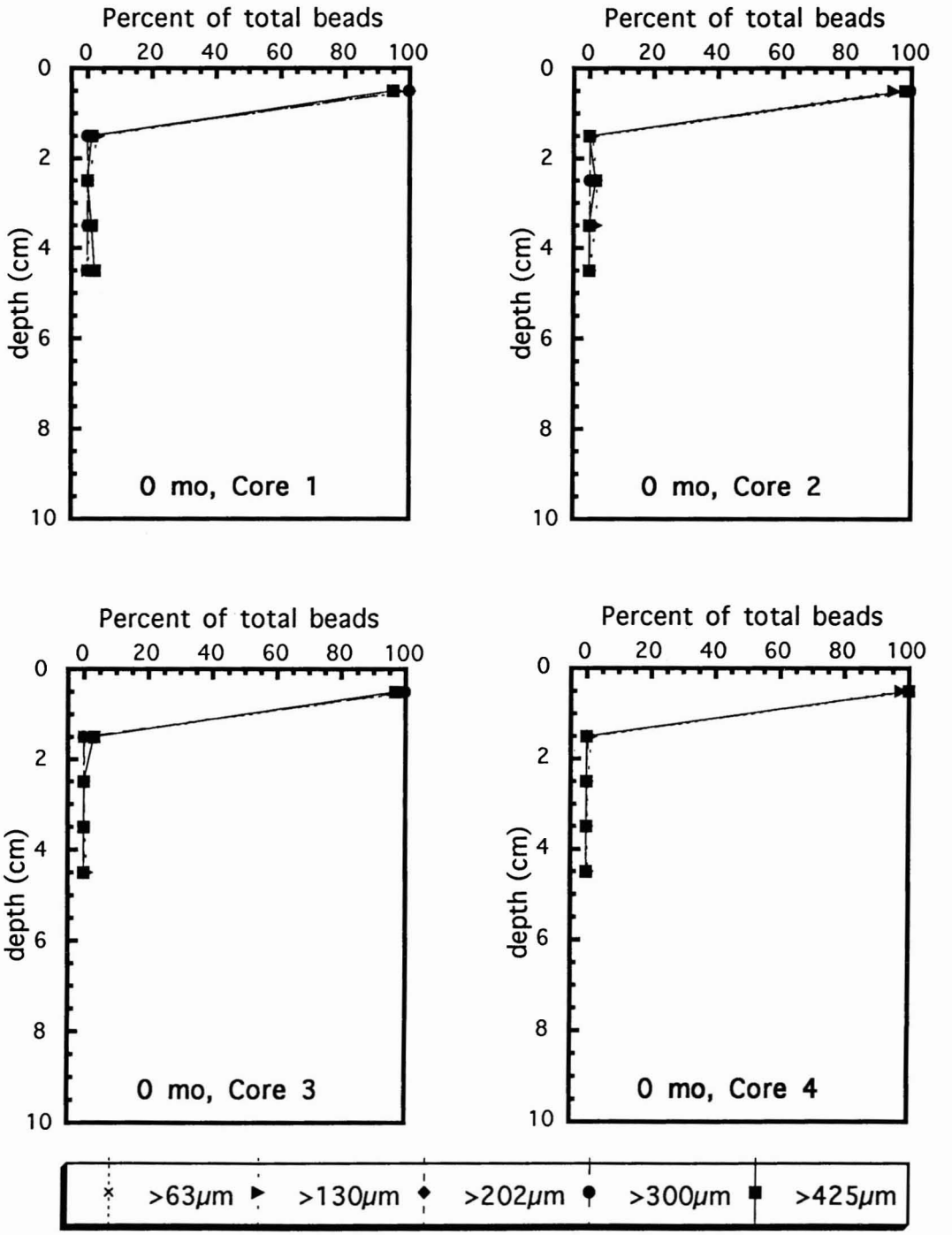

FIGURE 5. Depth profiles of concentrations for the various size fractions of tracer beads in cores taken 0 month after tracer emplacement. Core numbers correspond to treatment sites at the CI station.

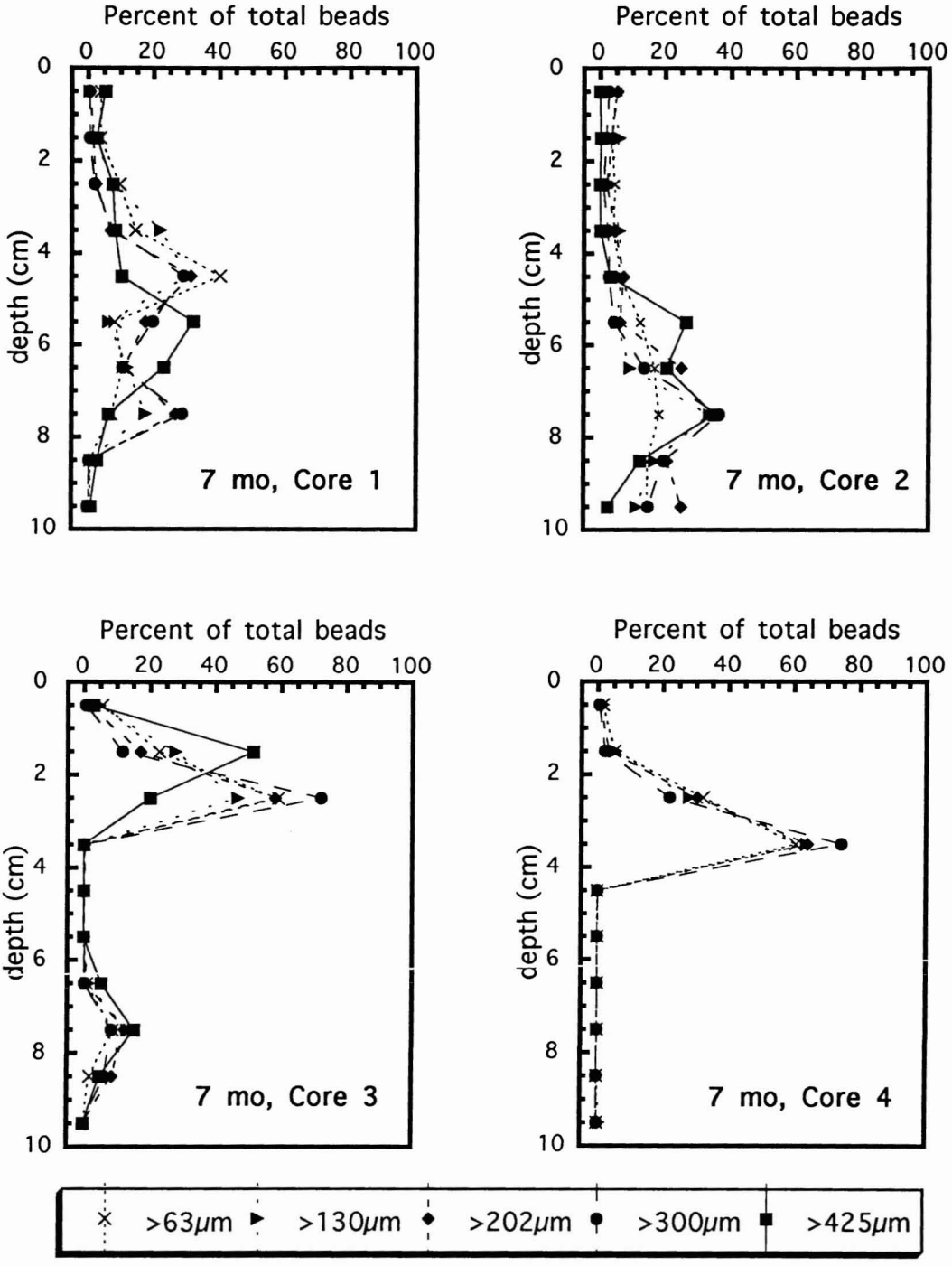

FIGURE 6. Depth profiles of concentrations for the various size fractions of tracer beads in cores taken 7 months after tracer emplacement. Core numbers correspond to treatment sites at the CI station.

in their vertical distribution, at least within the resolution of our sampling. In two cores (1 and 3), there was a substantial secondary peak in the profiles of most or all bead size classes at roughly 8-cm depth, suggesting nonlocal mixing. It is likely that these secondary peaks represent passive or active entrainment of tracer particles into large burrows in the sediment, such as those produced by the common alpheid shrimp *Alpheus mackayi* (Harrison 1981). Despite the presence of these secondary peaks, most of the particles in each profile were contained within relatively symmetrical, Gaussian-like distributions consistent with "diffusive" mixing processes. Diffusive mixing coefficients estimated from the Gaussian portions of profiles ranged from 0.4 to 4.4 $cm^2\ yr^{-1}$, with an overall mean (averaging across cores and bead size classes) of 0.9 $cm^2\ yr^{-1}$ (Tables 5 and 6). Although the finest tracer particles (63–130 μm) in treatment 2 exhibited a substantially higher mixing coefficient than any other sized particles in any treatment, overall there were no significant size-dependent patterns in mixing coefficients (Kruskal–Wallis test, $df = 4$, $P > 0.230$).

Short-term sedimentation rates estimated from bead profiles in the 7-month cores ranged between 3.0 and 10.2 cm yr^{-1}, with an overall mean of 5.9 cm yr^{-1} (Tables 5 and 6). There was no evidence of tracer size dependence in estimated sedimentation rates (Kruskal–Wallis test, $df = 4$, $P > 0.800$). This indicates that tracer-particle penetration into sediments was not caused primarily by Stokesian settling (i.e., passive sinking through a less dense, essentially fluid sediment), because such settling scales as the square of bead diameter (Reineck and Singh 1980) (i.e., it is heavily size dependent [e.g., the >425-μm particles would be expected to settle ca. 20 times faster than particles in the 63–130 μm size class]). After correcting for possible biases in sedimentation-rate estimates introduced by sediment mixing, we estimate that a minimum of 4.5 cm of sediment accumulated at the CI station during the period 7 December 1990–3 July 1991.

After 12 months, virtually all tracer-bead profiles exhibited a similar pattern: very few

TABLE 5

ESTIMATED SEDIMENTATION RATES AND MIXING COEFFICIENTS (D_b) FOR TRACER BEADS OF DIFFERENT SIZES COLLECTED IN THE 7-MONTH CORE SAMPLES

TREATMENT NO.	TRACER BEAD SIZE (μm)	SEDIMENTATION RATE (cm yr^{-1})[a]	MIXING COEFFICIENT ($cm^2\ yr^{-1}$)
1	>425	10.2	1.1
	300–425	8.8	0.4
	202–300	8.8	0.4
	130–202	7.1	0.9
	63–130	7.7	0.9
2	>425	—[b]	—[c]
	300–425	—[b]	0.9
	202–300	—[b]	—[c]
	130–202	—[b]	1.3
	63–130	—[b]	4.4
3	>425	3.0	0.7
	300–425	4.2	0.6
	202–300	3.9	0.7
	130–202	3.5	0.7
	63–130	3.7	0.8
4	>425	—[c]	—[c]
	300–425	5.6	0.4
	202–300	5.4	0.4
	130–202	5.4	0.5
	63–130	5.4	0.4

[a] The sedimentation rate (in cm yr^{-1}) equals the mean depth of beads in the primary peak times 0.57.

[b] The entire depth of the primary peak was not contained within the core sample (i.e., within the top 10 cm), so the sedimentation rate could not be estimated.

[c] These profiles could not be reasonably fitted with a normal curve because of multiple modes, missing data points, or too few beads in the profile (<50).

TABLE 6

MEAN SEDIMENTATION RATES AND MIXING COEFFICIENTS (± SD), AVERAGED ACROSS THE FOUR TREATMENTS, FOR TRACER-BEAD SIZE CLASSES FROM THE 7-MONTH CORE SAMPLES

TRACER BEAD SIZE (μm)	MEAN SEDIMENTATION RATE (cm yr^{-1})	MEAN MIXING COEFFICIENT ($cm^2\ yr^{-1}$)
>425	6.6 ± 5.1	0.9 ± 0.3
300–425	6.2 ± 2.4	0.6 ± 0.2
202–300	6.0 ± 2.5	0.5 ± 0.2
130–202	5.3 ± 1.8	0.8 ± 0.2
63–130	5.6 ± 2.0	1.6 ± 1.9
Overall mean	5.9 ± 0.5	0.9 ± 0.4

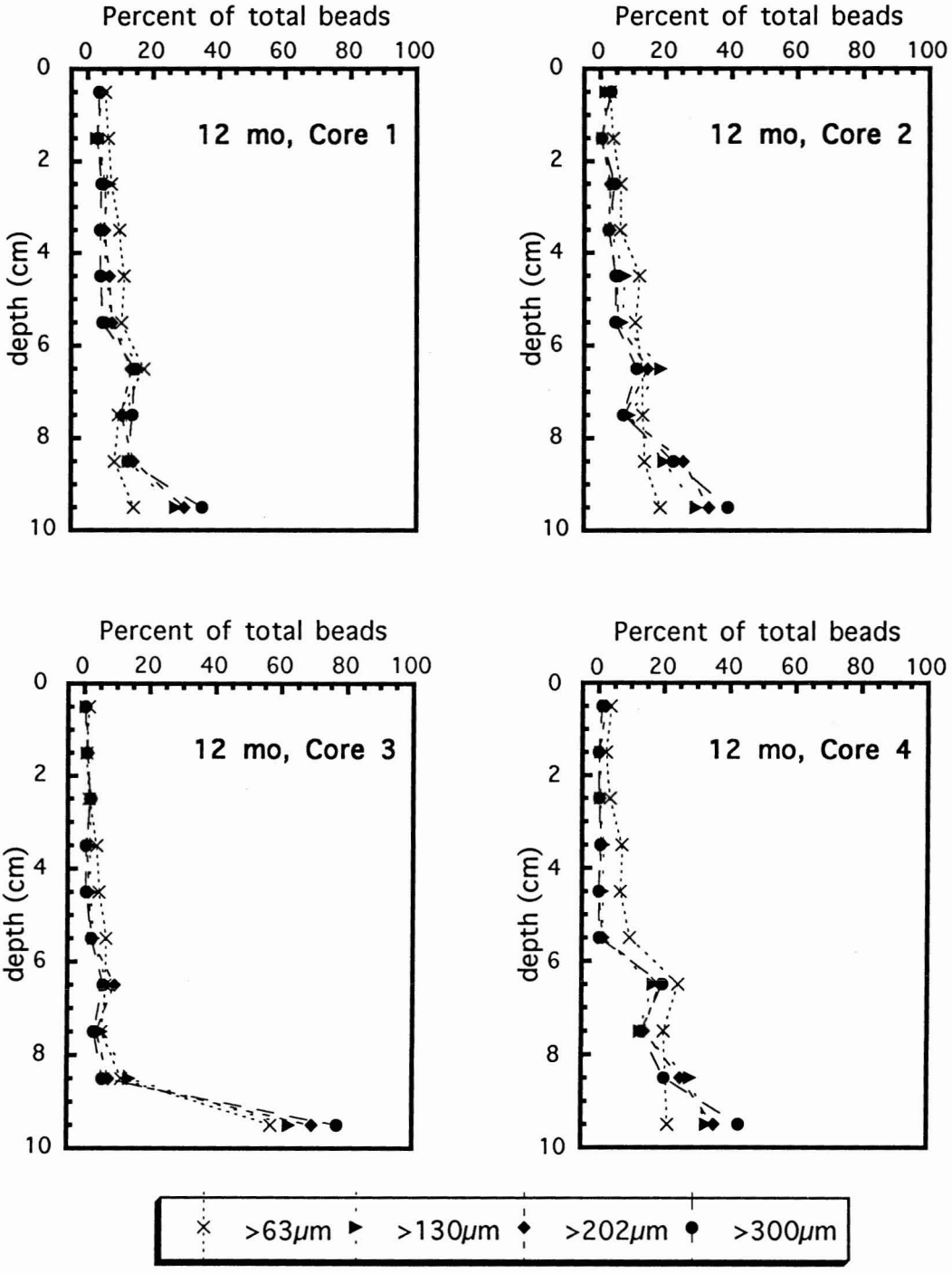

FIGURE 7. Depth profiles of concentrations for the various size fractions of tracer beads in cores taken 12 months after tracer emplacement. Core numbers correspond to treatment sites at the CI station.

beads above the 6-cm level, with a maximum concentration in the bottom level (9–10 cm) of the core (Figure 7). There was little evidence of size dependency in this pattern. These profiles suggest that, after 12 months, the peaks in bead concentration for all bead sizes in all treatments had penetrated to a sediment depth of ≥ 8 cm. Given the low mixing rates indicated in the 7-month cores, this suggests that at least 7 cm of sediment accumulated over the 12-month period from 7 December 1990 to 8 December 1991 at each of the treatment sites. Again, the lack of size dependency in these patterns, as well as the presence of at least a few tracer particles at most levels in the cores, indicates that tracer penetration was not caused by Stokesian settling, but most likely by sediment deposition.

In summary, our tracer-particle experiments suggest relatively low sediment mixing rates (on the order of 1 cm^2 yr^{-1}) and high short-term rates of sedimentation (6–7 cm yr^{-1}) at station CI during the year of our study. The physically quiescent nature of the lagoon floor around station CI (Bathen 1968, Harrison 1981, S. V. Smith et al. 1981; pers. obs. during >30 dives to the lagoon floor during this study) indicates that these sedimentation rates do not result from local physical resuspension and redeposition of lagoon-floor sediments. Thus, these high sedimentation rates represent either net sedimentation onto the lagoon floor (e.g., caused by stream runoff and reef erosion) or net sedimentation plus redeposition of buried sediments from the "mining" activities of infaunal animals (e.g., *Alpheus mackayi*). In either case, the net result was that our tracer particles rapidly were buried beneath the sediment-water interface and were not substantially recycled to surficial sediments during the year of our study.

DISCUSSION

At the time of our benthic survey and production studies, Kāne'ohe lagoon sediments harbored a high-density macrobenthic assemblage; macrofaunal abundances were substantially higher than those measured in other subtidal, mud-bottom sites in the Tropics (Table 7). Despite this high abundance, biomass at the CI station was low compared with other tropical sites because of the small average body size of macrobenthos (Table 7). Macrofaunal body sizes were similarly diminutive at the other survey stations in Kāne'ohe lagoon (OF, CB, and NB), so we suspect that macrofaunal biomass throughout the Kāne'ohe lagoon floor was low.

TABLE 7

MACROBENTHIC ABUNDANCE AND BIOMASS AT VARIOUS SUBTIDAL MUD-BOTTOM SITES IN THE TROPICS (FOR ALL STATIONS, SALINITY >28‰)

LOCATION	MEAN ABUNDANCE (no. m^{-2})	MEAN BIOMASS (g dry wt m^{-2})
Kāne'ohe Bay lagoon, USA	17,500–99,800	0.4
Chilka Lake, India	3,318	~1.4
Huizache Caimnero lagoon, Mexico	11,023	13.7
Florida Keys lagoon, USA	3,840	6.4
Coastal zone, Goa, India	1,257	67
Krishna, Godavari, Mahandi, and Hooghly Rivers, India	1,529	8.1

NOTE: Kāne'ohe Bay data from this study; the remainder from Alongi (1990).

In addition to high abundances and low biomass, the Kāne'ohe lagoon macrobenthos appeared to be low in species diversity. In a study of four tropical shallow-water habitats using an early version of the rarefaction diversity index, Sanders (1968) found 15–45 macrobenthic species per 100 individuals at all his sites. After correcting for potential errors in his calculations (Hurlbert 1971), virtually all of Sanders's sites had higher diversity than our Kāne'ohe Bay stations, which harbored only 8–13 species per 100 individuals (Figure 3).

In several respects, the Kāne'ohe lagoon macrobenthos strongly resembled communities found in silt-clay habitats characterized by high net rates of sedimentation or by high

gross rates of sedimentation caused by periodic benthic storms. For example, in muddy regions of the Changjiang and Mississippi River deltas sustaining high sedimentation rates (2–5 cm yr^{-1}), the macrobenthos were dominated by low-diversity assemblages of small, burrowing, deposit-feeding polychaetes (Rhoads et al. 1985, S. Sun and Dong 1985). Similarly, the HEBBLE site, a muddy abyssal habitat characterized by frequent resuspension and deposition events, harbors a dense, but low-diversity, community of diminutive macrobenthos, dominated by burrowing polychaetes (Thistle et al. 1985, 1991). As noted above, the Kāne'ohe lagoon benthos were also dominated by a low diversity of very small, deposit-feeding, burrowing polychaetes. Thus, the structure of the Kāne'ohe lagoon community appears to have been heavily molded by high rates of sedimentation (gross and/or net) during the period of our study. The fact that community structure was qualitatively similar throughout our stations during summer of 1990, and at station CI during summer 1990 and winter 1991, suggests that high sedimentation rates are widespread in Kāne'ohe lagoon in both space and time.

Our tracer-particle studies at station CI indicate high short-term rates of sedimentation (i.e., ca. 6–7 cm per year). How do these rates compare with estimates of long-term, net sedimentation in Kāne'ohe lagoon? Based on Pb-210 geochronology, C.R.S. and G. M. McMurtry (unpubl. data) estimate net sedimentation rate near the CI site to have been ~ 1.0 cm yr^{-1} between 1987 and 1994. To compare our short-term rates with this longer term rate, we must correct for changes in porosity with depth into the sediment; such corrections can be made using the following formula from Berner (1980):

$$w = (1 - \Phi_f)w_f/(1 - \Phi)$$

Here, w and Φ equal burial velocity (i.e., sedimentation rate) and porosity, respectively, in near-surface sediments, and w_f and Φ_f equal the final burial velocity and porosity after compaction deeper in the sediment.

Porosity in two cores collected near station CI in November 1993 (C.R.S. and G. M. McMurtry, unpubl. data) averaged 85% in the top 5 cm, 83% in the top 10 cm, and ca. 68% for depths of 80–140 cm within the cores. Accordingly, a sedimentation rate of 3.4 cm in 7 months converts to a long-term (i.e., postcompaction) rate of 2.7 cm yr^{-1}, and a rate of 7 cm in 12 months converts to 3.7 cm yr^{-1} after compaction. Thus, our estimated rates of sedimentation at station CI, based on tracer-particle experiments, exceed recent estimates of long-term, net sedimentation near this site by a factor of ~ 3. The higher deposition rates recorded by our experiments could result from at least three causes: (1) Our bead experiments were < 50 m from the fringing reef of Coconut Island (Figure 1), whereas the C.R.S. and McMurtry site was ~ 400 m from the nearest reef; our bead site thus may have received substantially more loading of sediments transported off the fringing reef; (2) Harrison (1981) argued that alpheid shrimp resuspend substantial amounts of sediment at the lagoon floor during deep burrowing; some of the discrepancy between the tracer experiment and Pb-210 sedimentation rates may represent local, biological resuspension; (3) the relatively high deposition rates recorded at the bead site in 1991 may simply reflect short-term (i.e., interannual) variability in sediment inputs to the bay; short-term variability in sedimentation rates is evident in the Pb-210 profiles of C.R.S. and G. M. McMurtry (unpubl. data). Without geochronological studies at our tracer-particle site, however, it is very difficult to differentiate the contribution of these three factors to deposition during our bead experiments.

The particle mixing coefficients estimated from our tracer studies at station CI are relatively low by shallow-water standards. Mixing coefficients (D_b) from quiescent, oxygenated estuarine and shelf habitats typically fall between 0.3 and 100 cm^2 yr^{-1} (Aller 1982, M. Sun et al. 1991); our mean value of 0.9 cm^2 yr^{-1} (Table 6) lies near the bottom of this range. The sediment mixing at our site is almost certainly caused by the particle displacement activities of benthos (i.e., resulting from bioturbation); based on the results of our macrofaunal survey, such low rates of

mixing are not surprising. The magnitude of D_b produced by deposit feeders is directly related to body length squared, as well as to total abundance (Wheatcroft et al. 1990, C. R. Smith 1992). Thus, even though the Kāne'ohe lagoon macrobenthos are relatively abundant, the extremely small mean body size of lagoon benthos apparently yields low rates of sediment mixing. The nonnutritive nature of our glass tracer beads may also have contributed to relatively low sediment mixing rates because deposit feeders may have selectively avoided, and thus less frequently mixed, our experimental particles.

It should be noted that our low mixing rates are at odds with Harrison's (1981) conjecture that megabenthic alpheid shrimp (*Alpheus mackayi*) rapidly mix the top 30 cm of Kāne'ohe lagoon sediments. The intense burrowing activity of *A. mackayi* observed in 15-cm-deep aquarium sediments by Harrison (1981) certainly would have mixed our tracer particles at much higher rates than recorded in our experiments. However, although shrimp burrows were common at our CI site, radiographs of core samples indicated that sediments between burrows frequently were laminated (i.e., essentially unmixed) to depths of 10–12 cm (H.K. and C.R.S., unpubl. data); given a gross sedimentation rate of $\sim$3 cm yr^{-1} from our tracer-bead studies, this implies little alpheid mixing of the top 10 cm of sediment over time scales of (10 cm)/(3 cm yr^{-1}) ~3 yr. Thus, our tracer-particle studies and radiographs force us to conclude that in the field, *A. mackayi* may cause substantially less solid-phase mixing than postulated by Harrison (1981).

The apparent lack of particle-size dependence in our mixing-rate experiments contrasts with results from a recent study of size-dependent bioturbation in a bathyal, silt-clay habitat. In the 1240-m-deep Santa Catalina Basin, Wheatcroft (1992) found that 63–125 μm tracer particles were mixed about five-fold faster than particles 125–420 μm in diameter. The absence of strong size-dependent mixing in our study is somewhat surprising because deposit feeding is thought to typically control bioturbation rates (Wheatcroft et al. 1990, C. R. Smith 1992) and because small deposit feeders (such as those in Kāne'ohe lagoon) often are especially particle-size selective (e.g., Self and Jumars 1988). The nature and sizes of tracer particles used in our study seem unlikely to have obscured size dependency in mixing because identical particles have been used to document both deposit-feeder selectivity and size-dependent bioturbation in other silt-clay habitats (Self and Jumars 1988, Wheatcroft 1992). We conclude that pronounced size-dependent mixing for particles ranging from 63 to 420 μm does not occur in Kāne'ohe Bay lagoon and that size-selective bioturbation is not a uniform attribute of deposit-feeder assemblages.

As a final exercise, it may be informative to estimate (very crudely) the amount of annual fish production sustainable by lagoon-floor macrobenthos. We estimated macrobenthic secondary production at station CI to be ca. 5 g m^{-2} yr^{-1} AFDW. Extrapolation of this rate to the entire lagoon floor, which has an area of 3.5×10^6 m^2, yields $\sim 17 \times 10^3$ kg yr^{-1} AFDW of total lagoon macrobenthic secondary production. Most of this estimated production occurred in populations of very small, burrowing polychaetes (Table 3); thus very little of this production, perhaps 5%, would be directly available to benthic feeding fish (e.g., goatfish or weke). Assuming that 5% of the macrobenthic production was consumed by fish and converted to fish biomass with 10% efficiency (cf. Parsons et al. 1984), this would yield on the order of 85 kg AFDW, or about 850 kg wet weight, of fish production per year. For comparison, the net catch of fish in Kāne'ohe Bay for 1992 totaled ~50,000 kg (Everson 1994). Thus, our best (albeit crude) estimate suggests that Kāne'ohe lagoon-floor macrobenthic production could sustain only a small percentage (<2%) of the annually exploited fish yield in Kāne'ohe Bay. Even if our macrobenthic production estimates are low by a factor of five, the lagoon-floor benthos is likely to sustain only a small fraction of the bay's fish production. We conclude that, from a fisheries perspective, the Kāne'ohe Bay lagoon floor is likely to be a low-productivity habitat.

CONCLUSIONS

The macrobenthic community in Kāne'ohe lagoon during our period of study was characterized by high abundance, low diversity, very small body size, and a preponderance of burrowing deposit feeders. This assemblage resembles those structured by high net or gross sedimentation rates in river deltas and in areas of deep-sea benthic "storms."

Rapid short-term sedimentation rates (e.g., 6–7 cm yr^{-1} at our CI station) combined with low sediment mixing rates cause burial to dominate the vertical distribution of sediment particles in central Kāne'ohe lagoon on annual time scales. Sedimenting particles apparently are rapidly (within months) trapped below the sediment-water interface (some recycling to the sediment surface could occur on longer time scales, however, because of the activities of deep megafaunal burrowers such as alpheid shrimp).

Because of low biomass apparently resulting from very high rates of sedimentation (either gross or net), the lagoon macrobenthos have a low secondary-production potential. The burrowing habits of this diminutive infauna, combined with low production rates, probably limits the importance of lagoon macrobenthos as a food source for benthic feeding fish in Kāne'ohe Bay.

ACKNOWLEDGMENTS

We are grateful to a number of people who helped with the field portions of this study, including Shawn Doan and Ed Parnell. Dan Hoover aided substantially in calculating mixing coefficients and sedimentation rates from tracer profiles. Kimberly Smith, many of the participants in the MHIMRI symposium, and two anonymous reviewers made useful comments on the various versions of this paper.

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