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# Sediment trapping by chaetopterid polychaetes on a Hawaiian fringing reef

by Julie H. Bailey-Brock[1]

## ABSTRACT

The role of chaetopterid polychaetes in determining sediment grain-size composition and community structure on a south shore fringing reef flat of Oahu, Hawaii was examined. Quantitative samples taken from within and adjacent to dome-shaped mounds of chaetopterid tubes along a shore to seaward gradient were analyzed for grain size and faunal composition. The two chaetopterid species that form the mounds, *Phyllochaetopterus verrilli* and *Mesochaetopterus sagittarius*, together reached densities of 62,400/m² in mounds and comprised 71% of the polychaete fauna. Polychaete densities varied from 12,320-23,804/m² adjacent to mounds, and within mounds from 67,043-88,260/m². Polychaete species richness was greatest near shore (22 species) and ranged from 15-18 at the other two stations. Biomass estimates of all taxa were much greater within mounds than outside them.

Grain-size distribution varied across the reef with a greater proportion of fines near shore and in the mounds, and more coarser grains nearest the edge of the reef. Estimated water velocity integrated over a twenty-four hour period ranged from 9.8 cm/sec at the seaward station to 6.9 cm/sec nearshore. Transport of sedimentary materials across the reef is attributed to tidal fluctuation and winds.

It is hypothesized that the structure and large area covered by chaetopterid mounds leads to the retention of sediments that would otherwise be transported closer to shore. The formation of the mounds themselves is dependent on the vertical orientation and tube building activities of the chaetopterids and larval recruitment. Processes that may affect the physical stability of mounds include the foraging behavior of larger predators, burrowing crustaceans and the effects of storms. Apart from these disturbances, mounds do appear to be stable areas in an otherwise shifting environment, providing suitable habitats for diverse assemblages of invertebrates that are dominated by these suspension feeding chaetopterids.

## 1. Introduction

The activities of reef organisms as sediment binders are not readily apparent in the field, but are of geological and ecological importance (Aller and Dodge, 1974; Thomassin, 1974). Important sand fixers on central Pacific and eastern Australian reef flats are chaetopterid tube worms which utilize sand for tube construction and where abundant, may have a stabilizing influence on sediments (Bailey-Brock, 1976;

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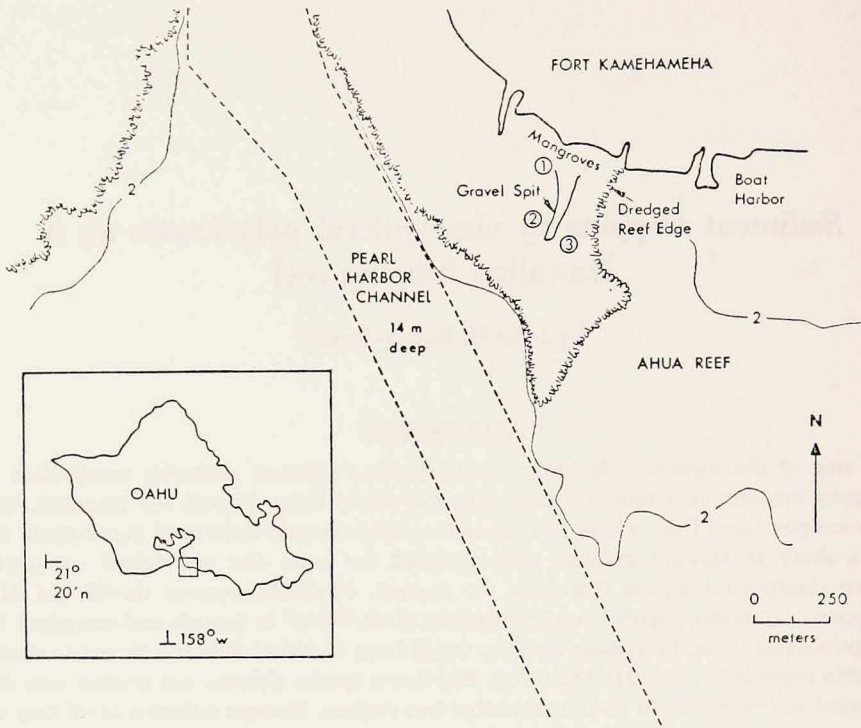
Figure 1. Map showing the location of collecting sites (1,2,3) on the intertidal section of Ahua reef at Fort Kamehameha. Inset shows the location of the study site on the east side of the Pearl Harbor entrance channel on the south shore of Oahu, Hawaii. Depth contours are in meters and increase rapidly on the steep, dredged edge of the channel.

Gibbs, 1978). In temperate intertidal regions the tube worms *Diopatra cuprea* and chaetopterids stabilize sediments (Woodin, 1978) while subtidally oweniids (Yingst and Rhoads, 1978) and maldanid polychaetes (Mangum, 1964), amphipod and tanaid crustaceans, and spionid polychaetes fix sand grains by building tubes (Myers, 1977a & b). Some polychaetes are selective, removing particles of specific size or dimension (Myers, 1970) while others utilize particular minerals (Fager, 1964).

Hawaiian fringing reefs are high energy environments, subjected to tidal and wind generated water motion and surf, and are characterized by accumulation of sedimentary materials on the underlying limestone platform. A common component of these shallow reef habitats are extensive, low domed mounds one square meter or more in size formed by aggregations of chaetopterid tube worms (Bailey-Brock, 1976). The most abundant species is *Phyllochaetopterus verrilli* Treadwell, but *Mesochaetopterus sagittarius* (Claparède) is also well represented (Bailey-Brock,

1976). Both worms build vertically oriented, nonrigid tubes encrusted with sand, which comprise the mounds.

A comparative study was undertaken to examine the effect of chaetopterid mounds on grain-size composition of sediments within mounds and in adjacent areas, and to inventory the invertebrate communities in both habitats.

## 2. Study Site

The fringing reef at Fort Kamehameha (also known as Ahua reef) is a typical south shore reef on Oahu, Hawaii (Fig. 1). The study area has been subjected to dredging on both east and west margins. A stand of mangroves (*Rhizophora mangle*) extends approximately 100-150m from shore, and a gravel spit of coral rubble that originates at the mangroves runs perpendicular to the shoreline for 225 meters. Sediment (15-25 cm thick) covers the underlying limestone platform and the surface is littered with small coral boulders (up to 0.5m diameter) and rubble debris. Trade winds blow from the northeast for about 70 percent of the year (Banner, 1974), but seasonal periods of southerly winds generate surf and high energy conditions across the reef. The dredged, eastern edge of the reef receives wind driven water movement most of the year and can be described as a windward reef face. This dredged edge is encrusted with coralline algae, and sabellid worms protrude from cracks in the platform.

## 3. Sampling procedure

Six samples 500 cm$^2$ in surface area were collected with a cylindrical corer (25.25 cm internal diameter) to a depth of 10 cm from three locations on the reef in April, 1978. Samples 1 and 1A (Fig. 1) were from the base of the most seaward mangrove tree approximately 150m from shore, 2 and 2A were from the lee of the gravel spit approximately 185m from samples 1 and 1A, and 3 and 3A were 125m from the dredged eastern edge of the reef flat. One of each pair of samples was from the center of a chaetopterid mound (1,2,3) and the other was taken adjacent to the mound (1A, 2A, 3A). Samples were bagged, labelled and fixed in 10% formalin in the field.

An additional six samples were collected for grain size analyses from the same locations, in the same manner, and were fixed in buffered formalin.

## 4. Water motion

Tidal range in Hawaii is always less than one meter, but south to southwesterly winds affect wave height and the movement of water across south shore reefs of Oahu. Such winds are most frequent during winter months (October to April) although northeasterly trade winds persist for 50% of the time during winter and 90% during summer months. Tropical cyclones originating in the southern hemisphere of the Pacific may affect the southern aspect of the Hawaiian Islands, but these are in-

frequent although more damaging to coastal regions than winter storms from the south (NOAA, Marine Services Chart 13—Hawaiian waters). Such conditions influence sediment distribution, stability of chaetopterid mounds (Bailey-Brock, unpublished), inland location of strand line debris and the transport of fishes across reefs (Brock, 1977; Gosline, 1964).

Estimates of relative water velocity on the reef were made to compare conditions at the six stations. Preweighed "clod cards" consisting of calcium sulphate blocks on a plastic base were attached to bricks and placed at the six stations for a 24 hour period during normal spring tides. This method (Doty, 1971) measures the dissolution of the cubes, which is increased by water motion. At the end of a known period of time (24h) the cards are collected, dried and reweighed. Calibration of cards is necessary and is done by allowing dissolution of a series of cards to occur in still water. A calibration value $(K)$ is arrived at with the equation:

$$K = \frac{Mc \ (te)}{(tc)}$$

where $Mc$ is the mass lost for the calibration period $(tc)$ and $(te)$ is the field exposure period. The calibration value is divided into the weight lost by each clod card during the time of immersion in the field so that a diffusion factor $(DF)$ is obtained. The diffusion factor is a measure of the dissolution enhanced by water movement.

A series of clod cards were immersed for known periods of time in sea water moving at known constant velocities. This calibration resulted in the following equation for the relative velocity $(V)$:

$$V = 3.65 \ (DF\text{-}1)$$

where 3.65 is a constant and $DF$ is the diffusion factor.

## 5. Distribution of mounds on the reef flat

Five, twenty meter transects were laid parallel to shore at each of the three study sites and the coverage by mounds was recorded. A percentage value was calculated for each location.

## 6. Sample processing

*a. Grain size analyses.* Samples collected for grain size analyses of the pure carbonate sediments were wet sieved in a graded series of $1\phi$ intervals from 0.063 mm − 7.9 mm (2 mm sieve was not available) and each fraction was oven dried at $100°C$ until constant weight was attained. Comparative statistical analyses of the grain-size distribution within and adjacent to mounds were made using chi-square tests.

*b. Faunal composition.* Samples for faunal analyses were processed by dissolving the calcareous sand matrix in an acid bath (Brock & Brock, 1977) and the inverte-
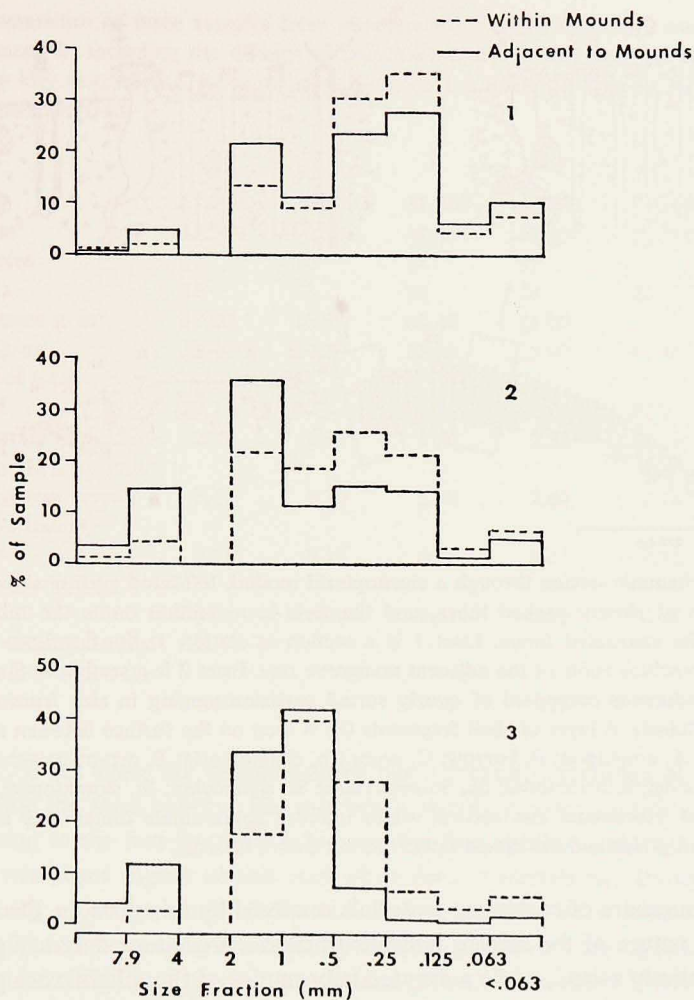
Figure 2. Histograms showing the distribution of grain sizes in sand samples from the three
locations at Fort Kamehameha. Grain sizes from within mounds and adjacent to mounds are
indicated for each of the three sampling sites (1,2,3). Station 1 is nearest to shore in the man-
groves, and 3 is most seaward. The 7.9 fractions at Station 1 overlap. Chi-square analysis
yield significant differences in grain-size distributions between "within" and "adjacent to"
mounds, i.e., Station 1, 1A: $x^2 = 24$, $P \gg 0.01$; Station 2, 2A: $x^2 = 48$, $P \gg 0.001$; Station
3, 3A: $x^2 = 403$, $\gg P$ 0.001.

brates sorted to taxa and identified with the aid of a dissecting microscope. Poly-
chaetes were identified using the keys of Hartman (1966), Day (1967) and Fauchald
(1977). No attempt was made to distinguish between species of nematodes. Dimen-
sions of the chaetopterid parchment tube, which remains after decalcification, were
estimated with an ocular micrometer. Settled volumes made before and after dissolu-
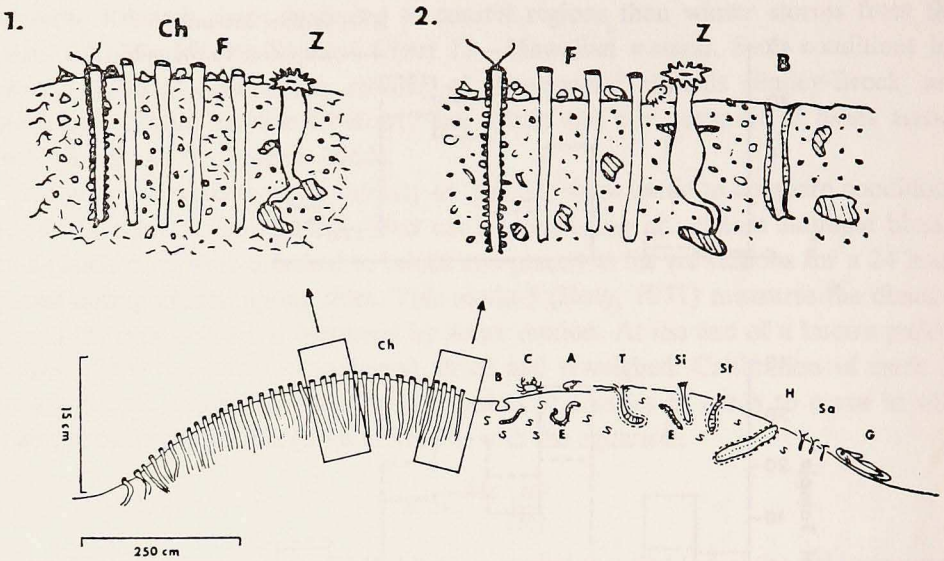
Figure 3. Schematic section through a chaetopterid mound, left-hand portion shows the vertical orientation of closely packed tubes, and the right-hand section omits the tubes to display some of the associated fauna. Inset 1 is a section at station 1; the fine lines represent the fibrous, branching roots of the adjacent mangrove tree. Inset 2 is a section at Stations 2 and 3 showing sediments composed of poorly sorted particles ranging in size from fines to coral rubble (hatched). A layer of shell fragments (F) is seen on the surface between tube openings. Symbols—A, amphipod; B, burrow; C, crab; Ch, chaetopterid; E, errant polychaete; G, goby; H, holothurian; S, nematodes; Sa, Saccocirridae; Si, sipunculan; St, stomatopod; T, terebellid; Z, zoanthid. Horizontal and vertical scales indicate approximate dimensions of the mound. Tubes, sand grains and associated fauna are not drawn to scale.

tion give a measure of carbonate materials removed by this process. Due to the time consuming nature of the sorting and identification procedure only samples 1A and 3A were entirely sorted, while measured subsamples of the others were processed.

Species diversities were calculated using the Shannon-Weaver diversity index (H′), and evenness measured by the method outlined by Heip (1974).

## 7. Results

*a. Grain size.* A greater percentage of fine sand (0.25-0.063 mm) is present within the mounds as compared to the adjacent areas (Fig. 2) where coarser materials predominate (0.5-7.9 mm). Sample 1 from a mound near the mangroves was composed of (Fig. 2, 1) 76% fines (0.25-0.063 mm), whereas the adjacent area has 64% of these fine particles but almost double the amount of coarse grain sizes (>1.0 mm). Samples 2 and 2A (Fig. 2,2) show similar distributions with a greater proportion of fines in the mound and more of the >1.00 mm fraction in the adjacent area. Samples 3 and 3A were comprised of coarser particles than both stations 1

Table 1. Characteristics of three samples from chaetopterid mounds and three samples taken
adjacent to mounds, including the density of polychaetes/m², species diversity at each site,
standing crop (dry weight) and water velocity. Samples 1 and 1A are nearest shore while 3
and 3A are most seaward.

|  | 1 | 1A | 2 | 2A | 3 | 3A |
|---|---|---|---|---|---|---|
| Polychaetes/m² | 67,043 | 20,280 | 88,260 | 23,804 | 87,360 | 12,320 |
| Chaetopterids/m² | 34,904 | 9,520 | 62,400 | 11,220 | 23,580 | 60 |
| Polychaete species | 22 | 22 | 18 | 15 | 17 | 18 |
| Number of taxa | 35 | 33 | 25 | 28 | 25 | 25 |
| Polychaete biomass g/m² | 38.60 | 16.40 | 63.40 | 21.90 | 53.03 | 1.04 |
| Total biomass g/m² | 52.40 | 24.30 | 65.00 | 23.60 | 60.90 | 1.37 |
| % Polychaetes of total biomass | 73.7 | 67.5 | 97.5 | 92.8 | 87.0 | 76.0 |
| Species diversity (H′), all taxa | 2.08 | 2.49 | 1.58 | 2.52 | 2.20 | 1.44 |
| Species diversity (H′), without *Phyllochaetopterus verrilli* | 2.49 | 2.70 | 2.58 | 2.67 | 2.14 | 1.43 |
| Evenness (Heip's Index), all taxa | 0.21 | 0.35 | 0.16 | 0.42 | 0.32 | 0.13 |
| Evenness (Heip's) without *P. verrilli* | 0.34 | 0.43 | 0.51 | 0.50 | 0.30 | 0.13 |
| Relative water velocity cm/sec (measured at 5cm above the sediment surface) | 6.60 | 7.07 | 7.99 | 8.68 | 9.95 | 9.63 |

and 2 (Fig. 2,3), but again the mound sample has a greater percentage of finer sedi-
ment sizes while the sand between the mounds is mostly coarser particles with only
9% contributing to the fine fraction. It is expected that coarser materials would re-
main on the windward aspect of this reef while finer materials are transported to-
ward the lee. In all cases small shells and shell fragments were present (Fig. 3,
Insets 1 and 2) on the surface of mounds, among the projecting openings of the
chaetopterid tubes (Fig. 3). Sample 1 was held together by the finely branching roots
of the mangrove tree (Fig. 3, Inset 1). Mangrove prop roots act as baffles above the
sediment surface and the network of subterranean tree roots anchor sedimentary
materials as they accumulate (Scoffin, 1970).

Chi-square analyses of grain-size distribution indicates that the size distribution
is in all cases significantly different $(P \gg 0.01)$ within chaetopterid mounds than
adjacent to mounds. The presence of these vertically oriented tubes must trap and
retain reef sediments that would otherwise be transported elsewhere.

*b. Water motion.* Estimates made with the calcium sulphate cubes show that water
motion progressively decreases across the reef to the mangrove area near shore. The
most seaward stations (3 and 3A) have the greatest water motion with a mean of
9.8 cm/sec, while those in the lee of the spit (2 and 2A) averaged 8.3 cm/sec and
those nearest shore (1 and 1A) had a mean value of 6.8 cm/sec (Table 1). The de-

crease of water motion in a shoreward direction may be responsible for the greater amount of finer carbonate materials toward shore. The gravel spit may also affect water velocity and the proportions of coarse and fine particles deposited on either side of it.

*c. Distribution of mounds.* The percentage of reef flat covered by mounds was 14% at the mangrove stations, 54% at stations 2 and 2A and 42% at stations 3 and 3A. The area within and around the mangrove tree at Station 1 was almost entirely composed of tubes and was 7-10 cm higher than the surrounding sandy area, and Station 1A.

*d. Faunal assemblages.* The density chaetopterids per square meter was greater in the mounds with values ranging from 23,580/m² at Station 3 to 62,400/m² at Station 2 (Table 1). Station 2A had the most chaetopterids of the three sites adjacent to mounds (11,200/m²) and 3A the fewest (60/m²). These chaetopterid tubes are composed of a parchment-like lining secreted by the worm, covered with sand grains that are selected and attached by the extensible cephalic palps (Barnes, 1965). Tubes are flexible and vertically oriented. The parchment tubes of *Phyllochaetopterus verrilli* are approximately 45 mm long and 0.06 mm in diameter. Preserved worms in the tubes measured 11-14 mm in length. *Mesochaetopterus sagittarius* tubes vary in length from 25-30 mm with diameters of 1.3-1.9 mm (excluding sand grains). Body lengths of worms without palps, which readily became detached, are 9-10 mm. The thicker organic lining of *M. sagittarius* is less flexible and transparent than those of *P. verrilli*.

Greater species richness is evident at the mangrove locations (Stations 1 and 1A) with more species of polychaetes and other invertebrates present than at the two other sites (Table 1, Appendix).

Species diversity was higher in areas adjacent to mounds except at 3A where values were considerably lower (Table 1). Calculated evenness values follow the same trend (Table 1), emphasizing the effect of the dominant chaetopterid species on species diversity (Table 1).

Faunal biomass (dry weight) at all stations was greater in the mounds than adjacent to them, with polychaetes contributing 68-98% of the total standing crop (Table 1). Amphipods, isopods and tanaids were well represented at Stations 1, 1A and 2A, and nematodes were numerous at all stations except for 2A (Appendix). The zoanthid *Palythoa vestitus* and three micromollusk species (mollusks 10 mm or less at greatest dimension), consisting of two gastropods and the bivalve *Brachidontes crebristriatus* were also collected in the samples. *Phoronis ovalis*, a boring phoronid, reached densities estimated at 500/m² at 3A, but was not found at any of the other stations (Appendix). This phoronid also occurs in Kaneohe Bay, Oahu (Emig, 1977) but its distribution in Hawaii is not well known. Other invertebrates seen at these stations or in the near vicinity, but not collected in the quantitative samples include

the holothurians *Chirodota hawaiiensis* and *Holothuria parvula*, crustaceans *Gonodactylus falcata, Alpheus lobidens, Calappa hepatica*, several xanthid and portunid crabs, and the enteropneust, *Ptychodera flava*. Fishes seen on the reef include *Psilogobius mainlandii, Mulloidichthys flavolineatus* (which probably feeds on chaetopterids), a crustacean-eating moray eel *Echidna nebulosa*, and *Diodon holocanthus* (a crustacean and mollusk feeder).

The polychaete fauna includes burrowers, tube dwellers and errant worms with the Syllidae, eunicid complex and Questidae being the most diverse and numerous. The archiannelid *Saccocirrus* sp. comprised 9,660 of the total 12,340 polychaetes/m² at 3A (Appendix), but was not collected in the other samples.

These chaetopterids are known to be suspension feeders that sieve food materials from the water as it is drawn through bags within the tube, but may also trap food particles in mucus strands or select suitable particles with the grooved palps (Barnes, 1965). Sabellids are suspension feeders using the branchial crown to sieve food particles; but the remaining polychaetes are predaceous, herbivorous (some syllids, Woodin, 1974) or deposit feeders. Four species are known borers of carbonate materials, the spionid *Polydora armata*, the eunicids *Nematonereis unicornis* and *Lysidice collaris*, and the cirratulid *Dodecaceria laddi*. It is most likely that these boring species were inhabiting small pieces of coral rubble comprising the larger particle fractions of the sand.

## 8. Discussion

The chaetopterids, *Phyllochaetopterus verrilli* and *Mesochaetopterus sagittarius*, are dependent on a vertical orientation of the tube for feeding and tube building (Barnes, 1965; Day, 1967). The worms avoid tube blockage with shifting reef sediments by building tubes with openings that project slightly above the surface of the mound (Fig. 3). Another factor that would reduce the potential negative effects of sedimentation to these benthic forms is the elevation of the tops of the mounds 10-14 cm above the level of the reef flat. Sand may accumulate between the tubes, solidifying the mounds, while adding to their overall height.

Reef dwelling chaetopterids may be dependent on mound formation and tube orientation (Fig. 3) for success in this otherwise shifting environment. The mounds provide stable habitats for the associated invertebrates as evidenced by the larger standing crops, species richness and abundance of invertebrates within mounds as compared to adjacent areas. The relatively large numbers of chaetopterids present in the sand adjacent to mounds (9,520/m² at 1A and 11,220/m² at 2A, Table 1) may represent an initial stage in mound formation, when worms are less abundant, less closely packed, and hence less able to trap and hold sediments; or the situation following the demise of a mound. The critical density for mound formation is unknown, but is probably greater than 11,000 worms/m².

Factors that lead to the formation of chaetopterid mounds are also unknown, but larval behavior prior to settlement may result in these dense aggregations of worms. Similar groupings of tube dwelling polychaetes are attributed to the gregariousness of larvae (Knight-Jones, 1951). *Phyllochaetopterus* spp. and *M. sagittarius* have planktonic larvae (Bhaud, 1966, 1972) which could be carried across the reef flat where they settle out in the general vicinity of the mounds. The projecting tops of the tubes may also serve to attract or trap larvae as they are carried over the mounds by currents.

Communities associated with mounds are apparently diverse and closely packed when compared to communities outside the mounds (Fig. 3, Table 1). Other invertebrates may reside in mounds because of the possible refuge effect created by the mounds where the substratum is more stable, or because potential food sources for predators are more available than in areas surrounding mounds. Many polychaetes (e.g. lumbrinerids, amphinomids) are carnivores (Day, 1967) and may be predators on chaetopterids and associated fauna. Predation by nemerteans, small crabs and stomatopods that also form burrows in the mounds is probably common. Nonresidents of mounds, such as fish and calappid crabs, also feed on polychaetes and associated fauna, although adult calappids are also known molluscivores (Shoup, 1968).

The relative stability of sediments within mounds provides a more amenable habitat for many benthic species. Perhaps the importance of sediment stability and community structure is best exemplified by the demise of *Owenia fusiformis* beds off Southern California after four species of rays had torn up the compacted sediments (Fager, 1964). Sediment stability in this case was due in part to the vertically oriented *O. fusiformis* tubes, but also credited to a solitary anemone that attached to the worm tubes below the sand. When densities of anemones and worms were great there were extensive sand deposits without ripple marks. After the rays dug tracks through the sediments the beds broke up and gradually deteriorated until worms and anemones were only sparsely present. In Hawaii, the zoanthid *Palythoa vestitus* may have a similar stabilizing effect on reef flats as the anemone. Although zoanthids were not found attached to the worm tubes, they do attach to pieces of rubble (Fig. 3, Insets 1 and 2) within the sediment and were most abundant in the mounds where they may help to trap sediments.

Factors that disturb mounds have not been addressed in the present study, but calappid crabs burrow in the sand (Thomassin, 1974) and have been observed burrowing in mounds within the study area. Stomatopods excavate shallow burrows within mounds as do alpheid shrimps (*Alpheus lobidens*). The puffer fish, *Diodon hystrix*, may disturb mounds while feeding, but this was not observed in the field. The most likely disturbance leading to erosion of mounds is stormy weather, which loosens sediments and tears up rubble which may in turn abrade the dome-shaped mounds. The predators may create a level of disturbance in the mound community

that enhances diversity (Woodin, 1978). In summary, species richness and density of polychaetes are greater in mounds than adjacent to them, and the faunal composition of the two habitat types differ.

Extensive areas of chaetopterid mounds seem to be instrumental in holding sediments on reefs and retaining different proportions of grain sizes than are found in areas without mounds. Both tube building activities and the presence of aggregations of tubes, trap and hold sand grains. In this way chaetopterids are important in defining the composition of sediments on near-shore fringing reefs where they occur.

## APPENDIX

Taxonomic inventory of organisms collected in the quantitative samples at Fort Kamehameha reef flat. Samples 1, 2, 3 are from within chaetopterid mounds, samples 1A, 2A, 3A were adjacent to mounds, and densities are estimated /m².

| | Mound | | Mound | | Mound | |
|---|---|---|---|---|---|---|
| Polychaeta | 1 | 1A | 2 | 2A | 3 | 3A |
| Amphinomidae | 317 | 360 | 1020 | 2156 | 3660 | 360 |
| Syllidae | | | | | | |
| Syllid sp. 1 | 997 | | | | | |
| Syllid sp. 2 | 725 | 420 | 2160 | | 480 | 160 |
| Syllid sp. 3 | 45 | 40 | | 660 | 900 | |
| *Ehlersia cornuta* | 11,831 | 2800 | 4740 | 1892 | 8820 | 660 |
| Syllid sp. 4 | | | | 1100 | | |
| Syllid sp. 5 | | | 60 | | | |
| *Exogone verugera* | | 440 | 960 | 572 | 960 | |
| Nereidae | | | | | | |
| *Neanthes caudata* | 136 | 80 | 60 | | 60 | |
| Eunicidae | | | | | | |
| *Marphysa* sp. | | | 60 | 132 | | |
| *Nematonereis unicornis* | 363 | 180 | 420 | 1408 | 540 | |
| *Lysidice collaris* | 45 | 20 | | | | |
| Lumbrineridae | | | | | | |
| *Lumbrineris tetraura* | 1541 | 400 | 2220 | 748 | 900 | 100 |
| *Lumbrineris* sp. | 2947 | 1040 | 4740 | 2772 | 6540 | 20 |
| Dorvilleidae | 227 | 140 | | 44 | | |
| Orbiniidae | 272 | | | | | |
| Spionidae | | | | | | |
| *Polydora armata* | 91 | 60 | | | | 40 |
| *Pygospio* sp. | | 240 | | | | |
| Paraonidae | 227 | 40 | 180 | | 120 | 20 |

| Appendix. (continued) | Mound 1 | 1A | Mound 2 | 2A | Mound 3 | 3A |
|---|---|---|---|---|---|---|
| Cirratulidae | | | | | | |
| *Cirriformia punctata* | 91 | 120 | 300 | 264 | 480 | 80 |
| *C. crassicolis* | | | | | | 200 |
| *Dodecaceria laddi* | | | | | | 60 |
| Chaetopteridae | | | | | | |
| *Mesochaetopterus sagittarius* | 1179 | 580 | 420 | 2860 | 1380 | 60 |
| *Phyllochaetopterus verrilli* | 33,726 | 8940 | 61,980 | 8360 | 22,200 | 20 |
| Opheliidae | | | | | | |
| *Armandia intermedia* | 589 | 560 | | | | |
| Capitellidae | 8250 | 5220 | 2280 | | 5700 | 100 |
| Maldanidae | | | 840 | 792 | 60 | |
| Questidae | | | | | | |
| *Questa* sp. | 91 | 40 | 600 | | 7320 | 120 |
| *Novaquesta* sp. | 3264 | 1200 | 5220 | | 27,240 | 300 |
| Terebellidae | | | | | | |
| *Trichobranchus ?glacialis* | 91 | | | 44 | | 20 |
| Sabellidae | | 20 | | | | 360 |
| Saccocirridae | | | | | | |
| *Saccocirrus* sp. | | | | | | 9660 |
| other taxa | | | | | | |
| Porifera | | 20 | | | | |
| Zoanthidae | | | | | | |
| *Palythoa vestitus* | 1224 | 500 | 600 | 440 | 2460 | 40 |
| Polycladida | | | | 44 | | |
| Nemertea | 136 | 20 | | | | 200 |
| Nematoda | 1677 | 1880 | 3000 | | 9060 | 1040 |
| Sipuncula | | | | | | |
| Aspidosiphonidae | 952 | 600 | 300 | 616 | 60 | 40 |
| Sipunculan | 45 | | 300 | 1804 | 60 | |
| Phoronida | | | | | | |
| *Phoronis ovalis* | | | | | | 500 |
| Bryozoa | | | | | | |
| encrusting sp. | | | | | | 20 |
| Crustacea | | | | | | |
| Copepoda | 136 | 20 | 60 | | 120 | |
| Isopoda sp. a | | | | 220 | | |
| sp. b | | | | 88 | | |
| Tanaidacea sp. a | 3536 | 2220 | | 44 | | |
| *Apseudes* sp. | 91 | 240 | | 88 | | |
| *Leptochelia* sp. | | 200 | 180 | 44 | 300 | |
| Amphipoda sp. a | 1088 | 3420 | 3960 | 2772 | | |
| sp. b | 272 | | | | | 20 |
| Caprellidae | | | | | | |
| *Metapograpsis* sp. | | | | 44 | | |
| Bivalvia | | | | | | |
| *Brachidontes crebristriatus* | 91 | 20 | | | 60 | |
| Gastropoda sp. a | 181 | 120 | | 88 | 60 | |
| sp. b | 181 | | | 44 | | |

REFERENCES

Aller, R. C. and R. E. Dodge. 1974. Animal-sediment relations in a lagoon, Discovery Bay, Jamaica. J. Mar. Res., *32*, 209–232.

Bailey-Brock, J. H. 1976. Habitats of tubicolous polychaetes in the Hawaiian Islands. Pacif. Sci., *30*, 69–81.

Banner, A. H. 1974. Kaneohe Bay, Hawaii: urban pollution and a coral reef ecosystem. In Proc. Second Int. Coral Reef Symp., *2*, Great Barrier Reef Committee, Brisbane, 685–702.

Barnes, R. D. 1965. Tube-building and feeding in chaetopterid polychaetes. Biol. Bull., *129*, 217–233.

Bhaud, M. 1966. Étude du développement et de l'écologie de quelques larves de Chaetopteridae (Annelids Polychètes). Vie et Milieu, *17*, 1087–1117.

—— 1972. Quelques données sur le déterminisme ecologique de la reproduction des annelides polychètes. Mar. Biol., *17*, 115–136.

Brock, R. E. 1977. Occurrence and variety of fishes in mixohaline ponds of the Kona, Hawaii, coast. Copeia, *1*, 134–139.

Brock, R. E. and J. H. Brock. 1977. A method for quantitatively assessing the infaunal community in coral rock. Limnol. Oceanogr., *22*, 948–951.

Day, J. H. 1967. A monograph of the Polychaeta of Southern Africa. Part 1. Errantia, Part 2. Sedentaria. British Museum (National History), London, 878.

Doty, M. S. 1971. Measurement of water movement in reference to benthic algal growth. Botanica Mar., *14*, 32–35.

Emig, C. C. 1977. Notes sur la localisation, écologie et la taxonomie des Phoronidiens. Tethys, *4*, 357–364.

Fager, E. W. 1964. Marine sediments: Effects of a tube building polychaete. Science, *143*, 356–359.

Fauchald, K. 1977. The polychaete worms: Definitions and keys to the orders, families and genera. Nat. Hist. Mus., Los Angeles County, Science Series, *28*, 1–190.

Gibbs, P. E. 1978. Macrofauna of the intertidal sand flats on low wooded islands, northern Great Barrier Reef. Phil. Trans. R. Soc. Lond. *B, 284*, 81–97.

Gosline, W. A. 1965. Vertical zonation of inshore fishes in the upper water layers of the Hawaiian Islands. Ecology, *46*, 823–831.

Hartman, O. 1966. Polychaetous Annelids of the Hawaiian Islands. Occ. Pap. Bernice P. Bishop Mus., *23*, 163–252.

Heip, C. 1974. A new index measuring evenness. J. mar. biol. Ass. U. K., *54*, 555–557.

Knight-Jones, E. W. 1951. Gregariousness and some other aspects of the setting behavior of *Spirorbis*. J. mar. biol. Ass. U. K., *30*, 201–222.

Mangum, C. P. 1964. Studies on speciation in maldanid polychaetes of the North American Atlantic coast. II. Distribution and competitive interactions of five sympatric species. Limnol. Oceanogr., *9*, 12–26.

Myers, A. C. 1970. Some palaeoichnological observations on the tube of *Diopatra cuprea* (Bosc): Polychaeta, Onuphidae. *In*, Trace fossils, edit. T. P. Crimes and J. C. Harper, 331–334.

—— 1977a. Sediment processing in a marine subtidal sandy bottom community: I. Physical aspects. J. Mar. Res., *35*, 609–632.

—— 1977b. Sediment processing in a marine subtidal sandy bottom community: II. Biological consequences. J. Mar. Res., *35*, 633–647.

Scoffin, T. P. 1970. The trapping and binding of subtidal carbonate sediments by marine vegetation in Bimini lagoon, Bahamas. J. Sedim. Petrol., *40*, 249–273.

Shoup, J. B. 1968. Shell opening by crabs of the genus *Calappa*. Science, *160*, 887–888.

Thomassin, B. A. 1974. Soft bottom carcinological fauna *sensu lato* on Tulear coral reef complexes (S. W. Madagascar): distribution importance, roles played in trophic food-chains and in bottom deposits. Proc. 2nd Int. Coral reef Sym., *1*, Great Barrier Reef Comm. Brisbane, 297–320.

Woodin, S. A. 1974. Polychaete abundance patterns in a marine soft-sediment environment: the importance of biological interactions. Ecol. Monogr., *44*, 171–187.

—— 1978. Refuges, disturbance, and community structure: a marine soft-bottom example. Ecology, *59*, 274–284.

Yingst, J. Y. and D. C. Rhoads. 1978. Sea floor stability in Long Island Sound. Part II. Biological interactions and their potential importance for seafloor erodibility. Fourth Biennial Estuarine Research Conference, Mt. Pocono, Pa. Oct. 2-5, 1977.