# Vertical Distribution of Infauna in Sediments of a Subestuary of Central Chesapeake Bay

ANSON H. HINES
KATHRYN L. COMTOIS
*Smithsonian Environmental Research Center*
*Post Office Box 28*
*Edgewater, Maryland 21037*

ABSTRACT: The vertical distribution of infauna was quantified in eight strata from 0–35 cm in sand and mud sediments of a lower mesohaline subestuary of Chesapeake Bay. Large numbers of small polychaetes, amphipods, and clams occurred in the upper 5 cm of both sediment types, whereas large clams (*Macoma balthica* in mud and *Mya arenaria* in sand) extended down to 30 cm and comprised most of the biomass in their respective sediment types. There was extensive overlap of the species inhabiting both sediment types. Vertical stratification within and among species apparently reflected constraints on burrowing depth related to body size rather than resource partitioning among competitors. The maximal sediment penetration of 35 cm, which was exhibited by *Heteromastus filiformis,* was considerably less than the maximal penetration for deep burrowing species in some marine infaunal communities. Several species which burrowed deeper than 5 cm exhibited significant temporal shifts in their vertical distribution.

## Introduction

Patterns of vertical distribution of infaunal invertebrates in sediments are important aspects of the structure, species interactions, and organismal activity in soft-bottom communities. The vertical distribution of infaunal species has been used both as an indicator of ecological function in the benthos (e.g., "subsurface deposit feeders," Brenchley 1979; Fauchald and Jumars 1979; Whitlatch 1980) and as a measure of accessibility to epifaunal predators (e.g., Virnstein 1979; Blundon and Kennedy 1982). For many species, position in the sediment column may change (becoming deeper) as the individual grows (e.g., infaunal bivalves, Blundon and Kennedy 1982). Vertical partitioning of sediments may effectively mitigate competitive interactions between species in soft-bottom communities if food or space at certain strata is limited (Peterson 1977; Peterson and Andre 1980; Whitlatch 1980). Moreover, biological disturbance ("bioturbation") is a function of greater organismal feeding and burrowing activity near the sediment surface (e.g., Rhoads 1974; Myers 1977).

In addition, the vertical distribution of infauna should be considered in the selection of sampling devices used in studies of benthic communities. Because of differences in sediment penetration among sampling devices, and because of differences in penetration among sediment types for any one device, care should be exercised in selecting devices which penetrate the sediment to depths appropriate for the maximal distribution of species under study. It may be difficult to compare data collected with different devices unless the vertical distributions of the species are known.

Despite its importance, the vertical distribution of species is not well quantified for many soft-bottom communities (however, see Mare 1942; Johnson 1967; Vassallo 1971; Rhoads 1974; Peterson 1977; Reinharz and O'Connell 1981). In the present paper, we describe the vertical distribution of macroinfaunal species in sand and mud sediments of the Rhode River, a subestuary

of central Chesapeake Bay. We also show that the vertical distribution of some species changes through time.

## Methods

This study was conducted at the mouth of the Rhode River, Maryland (38°51′N, 76°32′W), which is in the lower mesohaline zone of the western shore of Chesapeake Bay. Continuous, long-term monitoring of water temperature, salinity, and dissolved oxygen has been conducted in the Rhode River since 1970 (Cory and Dresler 1981; Hines and Correll, unpublished data). Monthly mean water temperatures fluctuate seasonally with a peak of 27–28 °C in July and a low of 2–4 °C in January. Salinities fluctuate seasonally with lows of 4–7‰ in spring to highs of 11–15‰ in late summer and fall. Except for heated surface water during calm summer days, a thermocline does not develop, and the water column is well-mixed. Although anaerobic conditions lasting a few hours at night occasionally occurred during summer, all parts of the Rhode River are shallower than the pycnocline which developed at 8–10 m depths in the main-stem of central Chesapeake Bay during the time of the present study (Officer et al. 1984; M. Tyler, pers. commun.).

Samples were collected from two distinct sediment types: mud (5% sand, 95% silt and clay) in the boat channel at a depth of 3.8 m, and sand (73% sand, 27% silt and clay) outside the channel at a depth of 2 m. Because the water column is well mixed, the two sampling sites were not different with respect to temperature, salinity, or dissolved oxygen. Preliminary sampling with 50-cm deep cores in both sediment types during fall 1980 and again in spring 1981 showed that no macro-organisms were found deeper than 35 cm. For detailed quantitative samples in each sediment type, 10 cores of 0.008-m$^2$ surface area and 35 cm depth were taken in June 1981 at haphazard locations within each 900-m$^2$ sampling station using scuba gear. Intact cores were extruded into a trough and cut into eight sections at the following distances from the sediment surface: 2, 5, 10, 15, 20, 25, 30, and 35 cm. Ten cores were also taken from each sediment type in June 1982 and in

September 1982. The 1982 cores were processed in the same method as those in 1981, however they were cut into only two sections: 0–5 and 5–35 cm. Comparison of the three sampling periods provided estimates of variation in vertical distribution on the temporal scale of a season (June 1982 and September 1982) to a year (June 1981 and June 1982) in the distribution of shallow (0–5 cm) and deep (5–35 cm) organisms.

The sections from each core were fixed in 10% Formalin, stained with rose bengal, and sieved on a 0.5-mm mesh. All organisms were sorted under a dissecting microscope, identified to species, heads of organisms counted, and the total biomass of each species in each core section determined after drying at 60 °C for 24 h. For organisms which extended from one core section to another, such as worms or clams, only the section with the head present was counted in density estimates, but biomass determinations were based on those portions and/or whole organisms present in each section.

## Results

Infaunal communities of the two sediment types in June 1981 were composed primarily of 15 common species, as well as several relatively uncommon species (Fig. 1). The total density and standing crop of each sediment type were similar: 34,000 organisms and 119 g per m$^2$ in mud; 22,000 organisms and 177 g per m$^2$ in sand (Fig. 1). There was extensive overlap in the species inhabiting both sediment types, with only four species in mud and five species in sand not occurring in the other sediment type (Fig. 1). In addition, there was a significant rank correlation of overlapping species in the two sediments (Spearman's rank correlation = 0.52, p < 0.05). However, densities and biomass of species were significantly different in the two sediment types (multivariate analysis of variance, Wilks criterion, p = 0.0003 for densities and p = 0.006 for biomass), and the densities of seven species and biomass of five species in the two communities were significantly different (Bonferroni $t$ tests, p < 0.05; Fig. 1). Clams contributed most of the biomass, with *Mya arenaria* accounting for 75.8% of the
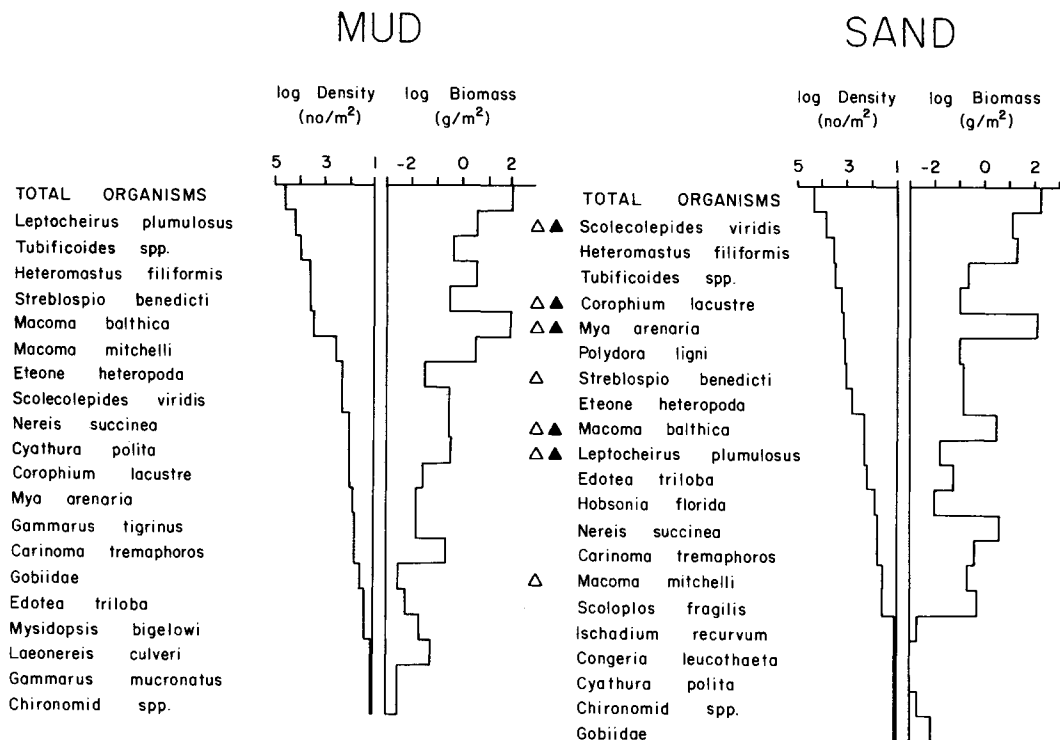
Fig. 1. Community composition of infauna in mud and sand sediments in June 1981. For each species, the mean log density and mean log dry weight per m² are shown, arranged in decreasing density. Species with significantly different densities and biomass between mud and sand sediments are indicated by open and closed triangles, respectively (Bonferroni $t$ tests, $p < 0.05$).

standing crop in sand and *Macoma balthica* accounting for 85.2% in mud.

For both sediment types, most organisms (74.1% in mud and 72.8% in sand) occurred in the upper 5 cm of sediment, with few organisms (4.6% in mud and 4.0% in sand) occurring deeper than 20 cm (Fig. 2). However, the greatest fraction of biomass of infauna was composed of a few relatively large organisms occurring from 10 to 30 cm in mud and from 10 to 25 cm in sand (78.5% and 83.5%, respectively). Almost no organisms or biomass were found deeper than 30 cm in either sediment. Detailed analysis of vertical distributions of only the 15 most abundant species which were present in both the 1982 and 1981 samples is presented below.

Annelid and nemertean worms occurred primarily in the upper 15 cm of both sand and mud (Fig. 3). Spionid polychaetes were abundant in the upper 5 cm of sediment. *Scolecolepides viridis* occurred primarily in

sand and was most abundant in the 2–5 cm level, but the greatest standing crop was composed of large worms in the 5–15 cm layers. *Streblospio benedicti* was most abundant and had the greatest biomass in the upper 2 cm. Similarly, *Polydora ligni* was most abundant in the upper 2 cm of sand. However, the capitellid *Heteromastus filiformis* was most abundant in the 5–15 cm layers in both mud and sand, with some individuals extending to 35 cm. As indicated by comparisons of the biomass and density in each layer, *H. filiformis* in mud were mostly small individuals found at all sediment depths, whereas larger individuals occurred in the 10–15 cm layer of the sandy sediment. The oligochaete *Tubificoides* spp. was most common in the 2–5 cm level, particularly in mud. *Eteone heteropoda* occurred in low densities in the upper 5 cm of sediment, whereas *Nereis succinea* occurred primarily deeper than 5 cm, with peak abundance in the 10–15 cm layer. The ne-
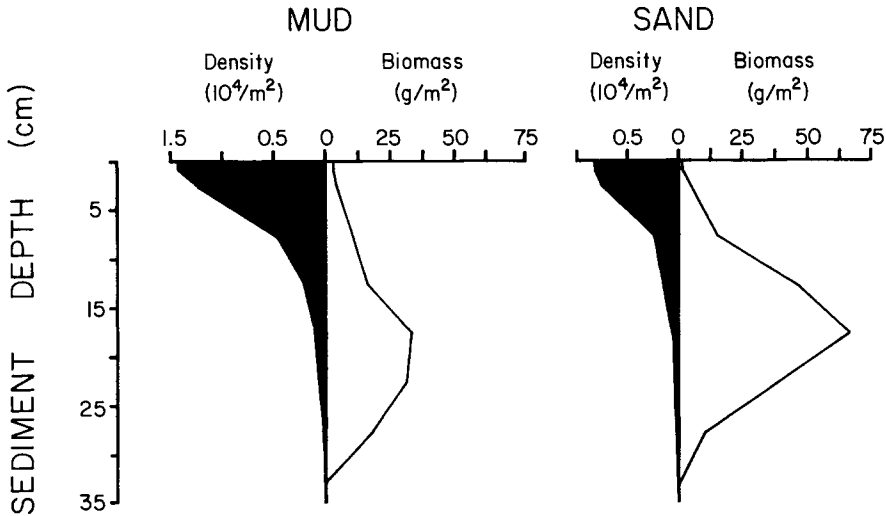
Fig. 2.   Vertical distribution of all macro-infauna in sand and mud in June 1981. Mean density (dark) and mean standing crop (open) per m² are shown in the following strata from the sediment surface: 0–2, 2–5, 5–10, 10–15, 15–20, 20–25, 25–30, and 30–35 cm.

mertean *Carinoma tremaphoros* also was most abundant below 5 cm, with a peak in the 5–10 cm layer of the mud.

Crustaceans also occurred primarily in the upper layers of sediment (Fig. 3). Amphipods occurred almost exclusively in the upper 5 cm of sediment, with *Leptocheirus plumulosus* and *Corophium lacustre* predominating in mud and sand, respectively. Similarly, isopods were restricted to the upper layers of sediment, with *Cyathura polita* predominating in mud to a depth of 15 cm and *Edotea triloba* occurring primarily in the top 2 cm of sand sediments.

Although clams were most abundant in the upper 10 cm of sediment, large individuals occurred only in deeper layers, where they comprised the bulk of the biomass of both sand and mud communities (Fig. 3). *Macoma balthica* occurred primarily in mud sediments, with a large number of new spring spat in the upper 5 cm, and larger clams from previous year classes in the 15–30 cm layers (Figs. 3 and 4). *Macoma mitchelli* does not attain as large a size as *M. balthica* and primarily occurred in the upper 10 cm of mud, with larger individuals residing in the 5–10 cm layers (Figs. 3 and 4). The soft clam, *Mya arenaria,* was abundant only in sand, with newly settled spat occurring in the upper 2 cm and larger clams from a

previous recruitment living from 10 to 20 cm deep in the sediment (Figs. 3 and 4).

Temporal shifts in the vertical distribution of each major species of the mud and sand communities were tested by ANCOVA with total density or total biomass of each species for the entire core used separately as covariates to adjust for overall changes in abundance (Table 1). In mud, four species (*Heteromastus filiformis, Tubificoides* spp., *Nereis succinea,* and *Carinoma tremaphoros*) exhibited significant temporal changes in the vertical distribution of their density and biomass. In addition, *Macoma balthica* showed significant temporal changes in density, but not biomass. In sand, three species (*H. filiformis, Tubificoides* spp., and *Scolecolepides viridis*) had significant temporal changes in the vertical distribution of their density and biomass. The vertical distribution of the density but not biomass of *N. succinea* changed significantly, whereas there was a significant change in the vertical distribution of the biomass but not the density of *Mya arenaria.* The temporal changes in vertical distribution mainly reflected significant differences between June 1982 and September 1982 for these species (Bonferroni $t$ tests on means adjusted by ANCOVA, $p < 0.05$). Heavy spring recruitment in 1981 resulted
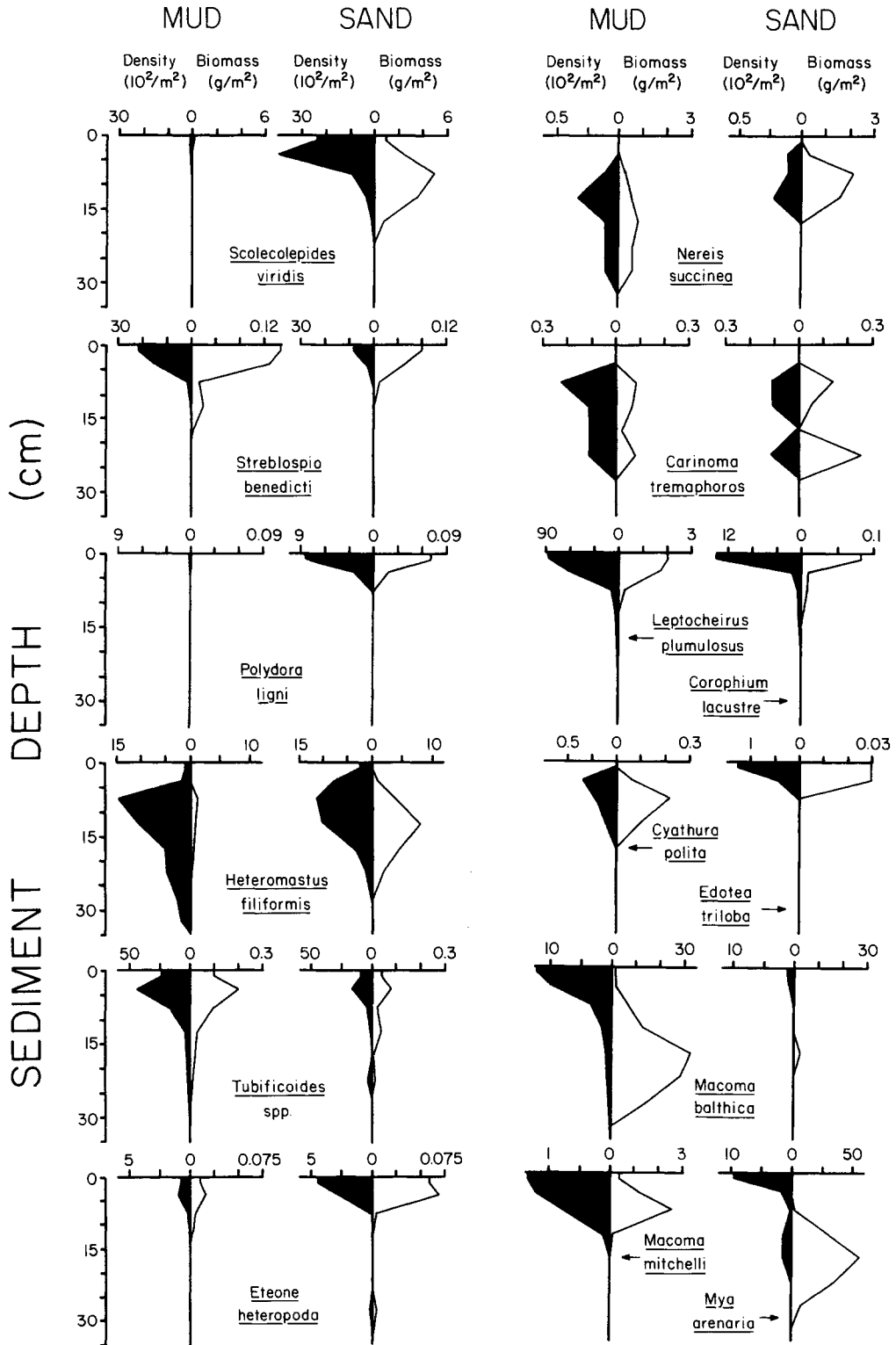
Fig. 3. Vertical distribution of 15 common infaunal species in sand and mud in June 1981. Key to axes labels and symbols as in Fig. 2.
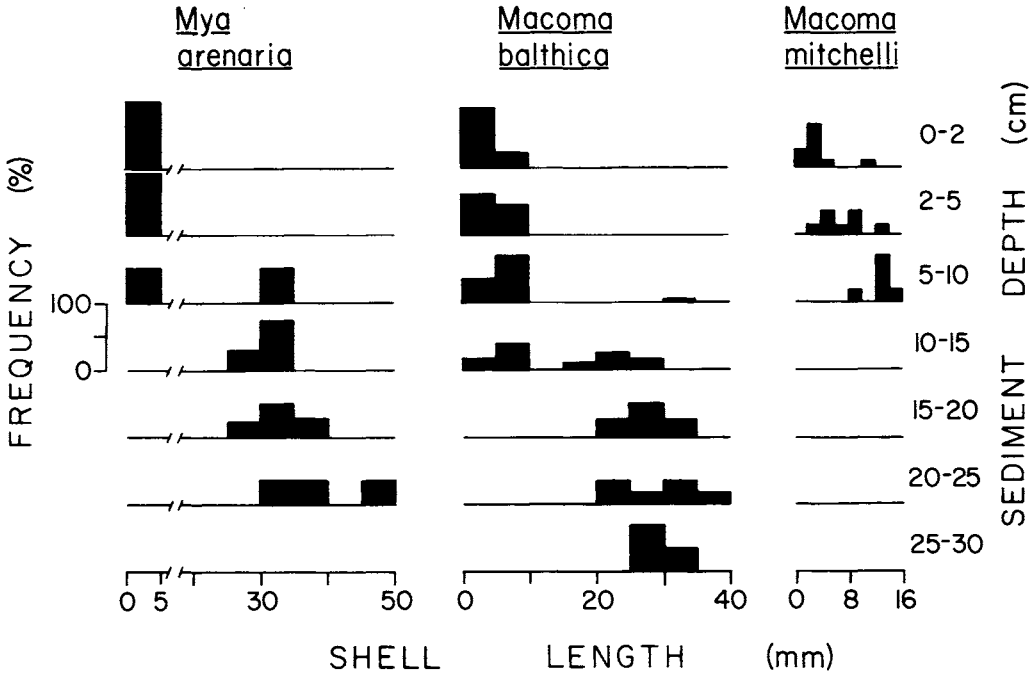
Fig. 4. Vertical distribution of clam size-frequencies for *Mya arenaria, Macoma balthica,* and *Macoma mitchelli* in June 1981.

in a greater proportion of individuals in the upper 5 cm in June 1981 than in June 1982. Some species (*M. balthica, N. succinea,* and *C. tremaphoros* in mud; *H. filiformis* and *Tubificoides* spp. in sand) also showed significant differences in their vertical distribution between June 1982 and September 1982 (Bonferroni *t* tests on means adjusted by ANCOVA, p < 0.05). The proportion of these species in the shallow strata declined from June 1982 to September 1982.

### Discussion

The infaunal community composition of the mud and sand sediments of the Rhode River subestuary is similar to that of other areas of central Chesapeake Bay (Mountford et al. 1977; Loi and Wilson 1979). Infaunal species composition in June 1981 was typical of the period from 1979 to 1985, although densities of most species were at the annual high following spring recruitment (Hines and Comtois, unpublished data). Although sand supported a predominantly suspension-feeding biomass (*Mya arenaria*), and mud had a predominantly deposit-feeding biomass (*Macoma balthi-*

ca), there was extensive overlap of the species inhabiting both sediment types in the Rhode River. The vertical distribution of infauna in both sediment types exhibited a pattern of large numbers of small organisms in the upper 5 cm of sediment, while a few large bivalves living at sediment depths to 30 cm comprised most of the biomass of the Rhode River communities.

Although the vertical distributions in the present study probably do not reflect the normal feeding positions of some species, core sampling produces minimal disturbances of vertical distribution (Whitlatch 1980). Disturbance during sampling would cause organisms to withdraw to the bottom of tubes and burrows. For example, *Scolecolepides viridis* and *Nereis succinea* feed at the surface (Fauchald and Jumars 1979; Dauer et al. 1981), but they were found below the surface in the present study (Fig. 3). However, disturbance does not affect the vertical distribution of many species which have horizontal tubes or which withdraw appendages without altering body position (e.g., amphipods and clams) (Reading and McGrorty 1978; personal observations).

TABLE 1. Temporal changes in vertical distribution of density and biomass of 15 common species in mud and sand sediments sampled in June 1981, June 1982, and September 1982. Significant changes in the distribution from 0–5 cm and 5–35 cm strata were tested by ANCOVA with total density or total biomass of each species per core as the covariates. Levels of significance for F values were adjusted by the Bonferroni method: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; ns = not significant; blanks = not present.

| Species | Mud | | Sand | |
| --- | --- | --- | --- | --- |
| | Density | Biomass | Density | Biomass |
| **Bivalvia** | | | | |
| *Macoma balthica* | ** | ns | | |
| *Macoma mitchelli* | ns | ns | ns | ns |
| *Mya arenaria* | | | ns | *** |
| **Annelida** | | | | |
| *Heteromastus filiformis* | *** | * | *** | *** |
| *Tubificoides* spp. | *** | *** | *** | ** |
| *Nereis succinea* | ** | * | * | ns |
| *Eteone heteropoda* | ns | ns | ns | ns |
| *Scolecolepides viridis* | ns | ns | ** | *** |
| *Polydora ligni* | | | ns | ns |
| *Streblospio benedicti* | ns | ns | ns | ns |
| **Nemertinea** | | | | |
| *Carinoma tremaphoros* | * | * | ns | ns |
| **Crustacea** | | | | |
| *Leptocheirus plumulosus* | ns | ns | ns | ns |
| *Corophium lacustre* | ns | ns | ns | ns |
| *Cyathura polita* | ns | ns | ns | ns |
| *Edotea triloba* | ns | ns | ns | ns |

Vertical distributions in the present paper can be viewed conservatively as representing the maximum sediment depths to which infauna might escape from benthic sampling devices or large epibenthic predators such as blue crabs (*Callinectes sapidus*) (Blundon and Kennedy 1982).

Patterns of vertical stratification of infauna may reflect both differences in burrowing abilities, often related to body size (Vassallo 1971; Blundon and Kennedy 1982; Fig. 4), and resource partitioning among species competing for food or space (Levinton 1977; Peterson and Andre 1980; Whitlatch 1980). Despite the possible artifacts for some species in the present study, vertical stratification by size occurred both within and among similar species. In most cases the stratification probably reflected simple physical constraints by size on burrowing depth rather than resource partitioning induced by competition. Thus, *Ma-*

*coma balthica* and *Mya arenaria* occurred at greater sediment depths as they increased in size and developed long siphons to reach the sediment surface (Fig. 4; see also Vassallo 1971; Reading and McGrorty 1978; Blundon and Kennedy 1982). *Macoma mitchelli* (a small species) occurred only in the upper layers, whereas larger *M. balthica* occurred much deeper. The vertical stratification of these surface deposit-feeding clams or of other species which feed at the surface and have similar diets (e.g., the predatory species *Nereis succinea* and *Eteone heteropoda*) does not affect their potential competition for food (Levinton 1977; Fauchald and Jumars 1979; Haddon and Hines, unpublished observations). However, stratification of the subsurface deposit-feeders *Heteromastus filiformis* and *Tubificoides* spp. (Fig. 3) would mitigate possible competition for similar food resources (e.g., Whitlatch 1980). Even so, burrowing depth of *Tubificoides* spp. is limited by body size, because the tail remains above the surface during feeding (Diaz 1980).

The relative abundance of shallow (<5 cm) and deep (>5 cm) burrowing individuals exhibited temporal shifts for several species of deep burrowing clams and worms. Some shifts in vertical distribution may have resulted from annual fluctuations in the intensity of spring recruitment, when small individuals restricted to the surface strata became very abundant. Other shifts probably reflected differentially greater reduction of individuals in the upper 5 cm as they were consumed by predators or grew and burrowed deeper. Seasonal shifts in the vertical distribution of *Macoma balthica* in an intertidal mudflat have been measured as an adaptive response to predation by short-billed shore birds (Reading and McGrorty 1978). Predation by blue crabs (*Callinectes sapidus*) and fish (*Leiostomus xanthurus* and *Trinectes maculatus*) in the benthic communities of central Chesapeake Bay is also markedly seasonal (Holland et al. 1980; Hines, unpublished data). However, the measurements of vertical distribution in the present study were not frequent enough to test for the presence of an annual cycle. Temporal changes in the vertical distribution of surface-dwelling polychaetes and crustaceans could not be detected in this

study, because they did not occur below 5 cm.

This vertical pattern of community organization is similar to other soft-bottom marine and estuarine communities (Mare 1942; Johnson 1967; Vassallo 1971; Rhoads 1974; Peterson 1977; Reinharz and O'Connell 1981). However, in California marine mudflats, lagoons, and subtidal areas, components of the macroinfauna (e.g., some bivalves, thalissinid shrimp, echiuroid worms, polychaetes) frequently burrow to sediment depths over twice that of the deepest clam in estuarine waters of central Chesapeake Bay and San Francisco Bay (Vassallo 1971; Peterson 1977; Hines and Loughlin 1980; Hines, unpublished observations). In addition, some species appear to have markedly different vertical distributions in different areas. For example, large *Macoma balthica* in Chesapeake Bay and San Francisco Bay were found in the 15–30 cm strata, whereas the same sized clams in sandier substrate in England only burrowed to about 7.5 cm (Vassallo 1971; Reading and McGrorty 1978; Fig. 4). Because vertical stratification of so few infaunal communities has been documented adequately, the difference between systems remains unclear. More extensive and intensive analyses of the temporal and spatial variation in vertical distributions are needed to understand the regulation of infaunal community structure.

## ACKNOWLEDGMENTS

## LITERATURE CITED

BLUNDON, J. A., AND V. S. KENNEDY. 1982. Refuges for infaunal bivalves from blue crab, *Callinectes sapidus* Rathbun, predation in Chesapeake Bay. *J. Exp. Mar. Biol. Ecol.* 65:67–81.

BRENCHLEY, G. A. 1979. On the regulation of marine infaunal assemblages at the morphological level: A study of the interactions between sediment stabilizers, destabilizers, and their sedimentary environment. Ph.D. Dissertation, The Johns Hopkins University, 248 p. Baltimore.

CORY, R. L., AND P. V. DRESLER. 1981. Diel oxygen variations in the Rhode River estuary, Maryland, 1970–1978. U.S. Geological Survey, Water Resources Investigations 81-10, 14 p. Reston.

DAUER, D. M., C. A. MAYBURY, AND R. M. EWING. 1981. Feeding behavior and general ecology of several spionid polychaetes from the Chesapeake Bay. *J. Exp. Mar. Biol. Ecol.* 54:21–38.

DIAZ, R. J. 1980. Ecology of tidal freshwater and estuarine Tubificidae (Oligochaeta), p. 319–330. *In* R. O. Brinkhurst and D. G. Cook (eds.), Aquatic Oligochaeta Biology. Plenum Press, New York.

FAUCHALD, K., AND P. A. JUMARS. 1979. The diet of worms: A study of polychaete feeding guilds. *Oceanog. Mar. Biol. Ann. Rev.* 17:193–284.

HINES, A. H., AND T. R. LOUGHLIN. 1980. Observations of sea otters digging for clams at Monterey Harbor, California. *Fish. Bull.* 78:159–163.

HOLLAND, A. F., N. K. MOUNTFORD, M. H. HIEGEL, K. R. KAUMEYER, AND J. A. MIHURSKY. 1980. Influence of predation on infaunal abundance in upper Chesapeake Bay, U.S.A. *Mar. Biol.* 57:221–235.

JOHNSON, R. G. 1967. The vertical distribution of the infauna of a sand flat. *Ecology* 48:571–578.

LEVINTON, J. S. 1977. Ecology of shallow water deposit-feeding communities Quisset Harbor, Massachusetts, p. 191–227. *In* B. C. Coull (ed.), Ecology of Marine Benthos, Vol. 6. Belle W. Baruch Library in Marine Science, Univ. South Carolina Press, Columbia.

LOI, T-N., AND B. J. WILSON. 1979. Macroinfaunal structure and effects of thermal discharges in a mesohaline habitat of Chesapeake Bay, near a nuclear power plant. *Mar. Biol.* 55:3–16.

MARE, M. F. 1942. A study of a marine benthic community with special reference to the micro-organisms. *J. Mar. Biol. Assoc. U.K.* 25:517–554.

MOUNTFORD, N. K., A. F. HOLLAND, AND J. A. MIHURSKY. 1977. Identification and description of macrobenthic communities in the Calvert Cliffs region of the Chesapeake Bay. *Chesapeake Sci.* 18: 360–369.

MYERS, A. C. 1977. Sediment processing in a marine subtidal sandy bottom community: I. Physical aspects. *J. Mar. Res.* 35:609–647.

OFFICER, C. B., R. B. BIGGS, J. L. TAFT, L. E. CRONIN, M. A. TYLER, AND W. R. BOYNTON. 1984. Chesapeake Bay anoxia: Origin, development, and significance. *Science* 223:22–27.

PETERSON, C. H. 1977. Competitive organization of the soft-bottom macrobenthic communities of southern California lagoons. *Mar. Biol.* 43:343–359.

PETERSON, C. H., AND S. V. ANDRE. 1980. An experimental analysis of interspecific competition among marine filter feeders in a soft-sediment environment. *Ecology* 61:129–139.

READING, C. F., AND S. MCGRORTY. 1978. Seasonal variations in the burying depth of *Macoma balthica* (L.) and its accessibility to wading birds. *Estuarine Coastal Mar. Sci.* 6:135–144.

REINHARZ, E., AND A. O'CONNELL. 1981. Animal-sediment relationships of the upper and central Chesapeake Bay. Final Report, United States Environmental Protection Agency Grant No. R80594. Washington.

RHOADS, D. C. 1974. Organism-sediment relations on the muddy sea floor. *Oceanog. Mar. Biol. Ann. Rev.* 12:263–300.

VASSALLO, M. T. 1971. The ecology of *Macoma inconspicua* (Broderip & Sowerby, 1819) in central San Francisco Bay. Part II. Stratification of the *Macoma* community within the substrate. *Veliger* 13:279–284.

VIRNSTEIN, R. W. 1979. Predation on estuarine infauna: Response patterns of component species. *Estuaries* 2:69–86.

WHITLATCH, R. B. 1980. Patterns of resource utilization and coexistence in marine intertidal deposit-feeding communities. *J. Mar. Res.* 38:743–765.