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Importance Of Predation By Crabs And Fishes On Benthic Infauna In Chesapeake Bay

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THE IMPORTANCE OF PREDATION BY CRABS AND FISHES
ON BENTHIC INFAUNA IN CHESAPEAKE BAY[1, 2]

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Abstract. The significance of large motile predators in controlling the distribution and abundance of the macrobenthic invertebrates within the sediments (the infauna) in a shallow subtidal sand community was tested using manipulative field experiments. The blue crab (*Callinectes sapidus*) and 2 species of bottom-feeding fishes, spot (*Leiostomus xanthurus*) and hogchoker (*Trinectes maculatus*), were either excluded from or confined to small areas using wire mesh cages. *Callinectes* and *Leiostomus* effectively reduced infaunal densities; *Trinectes* did not.

The infauna responded to decreased predation with a large increase in density and diversity within 2 mo. The largest population increases were exhibited by opportunistic species, which are considered to be most subject to predation. Species whose populations were least affected by predation were those species which either live deep in or quickly retract into the sediment. These species thus avoid predation and were generally the dominant species in the natural community. For species whose density increased greatly in exclosures, recruitment was by planktonic larvae and growth was very rapid, individuals growing to maturity in only a few months.

Densities of all infaunal species increased in exclosures, suggesting that their population densities under natural conditions are not controlled by competitive interactions. In this community, infaunal population sizes are limited by predation and not by food or space. Severe predation pressure and physical disturbances, particularly sediment instability, keep population levels far below the carrying capacity of the environment. Severe predation, and the rapid growth, short generation times, and rapid turnover rates of constituent populations suggest that such infaunal communities, despite a low standing crop, are an important food source for predator species important to man.

Key words: Benthic, caging experiments; Crustacea; Chesapeake Bay; community; competition; diversity; estuarine; fishes; infauna; Mulinia lateralis; *predation.*

INTRODUCTION

Theories of the origin and maintenance of soft-bottom community structure and organization have grown from studies dependent primarily on sampling approaches stressing static, descriptive aspects of the community (e.g., Thorson 1957, Sanders 1960, Boesch 1971, 1973, Lie 1974). Although this descriptive work is a necessary first step, the important parameters controlling the community structure and observed distributional patterns and abundances of species in the community can be tested by experimental manipulations in the field. This latter approach has proved particularly rewarding on marine rocky intertidal surfaces, where the importance of both physical and biological factors in determining vertical distribution and abundance of organisms has been demonstrated by Connell (1961a, b, 1970), Dayton (1971), Paine (1974), and Menge (1976).

In contrast to the advantages of manipulative experiments in rocky intertidal areas (Connell 1972, 1975), subtidal soft-bottom areas are less accessible; species cannot be removed easily or selectively; and, most importantly, the infauna of most soft bottoms cannot

be enumerated without permanently removing the animals and substrate, thus disturbing and partly destroying that which was to be measured. Due to these inherent difficulties, ecologists working on soft-bottom infauna have only recently progressed past the stage of community descriptions to assess the role of physical and biotic interactions in community structure. One such potentially important biotic interaction is predation by epibenthic crabs and fishes.

Although the assumption is often made that a large proportion of infaunal mortality is due to predation (e.g., Muus 1973, Arntz and Brunswig 1975), few studies have examined the effect of predation on infaunal communities, particularly subtidally. Blegvad (1928) was the first to use wire-mesh exclosures to protect infauna from predators and found that infaunal densities of some species increased up to 60× that of uncaged areas in the Baltic Sea. Woodin (1974) inadvertently found that crabs could reduce the abundance of tube-building polychaetes in a North Pacific intertidal soft-sediment environment. Naqvi (1968) used 6-mm mesh cages to protect intertidal infauna from predation at Alligator Harbor, Florida, and found 4× as many animals inside as outside the cages. No predators, however, were noted, and it was not demonstrated that these results were due to lack of predation.

In the Chesapeake Bay, shallow-water subtidal communities have low infaunal densities in unvegetated areas compared to similar but vegetated sediments only a metre away (Orth 1977), where crabs
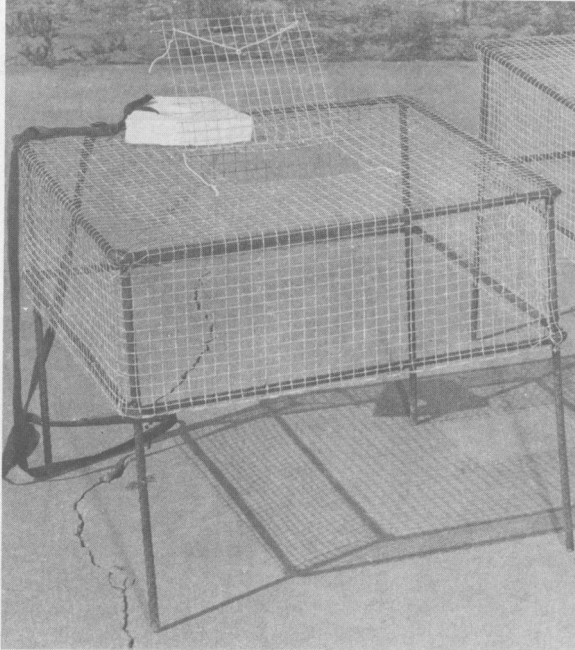
FIG. 1. Photograph of cage. When set out, the lower horizontal rod was pushed below the sediment-water interface.

would have difficulty digging through the rhizome mat of submerged grasses in search of food. Also, these densities are lowest in summer and fall (when crabs and fish have been feeding on the infauna) and highest in winter and spring (when these predators are absent or inactive), suggesting that crab and fish predation plays a significant role in determining infaunal abundances in this system. Because of their bottom-feeding habits and their abundance, attention was focused on the hogchoker (*Trinectes maculatus*), spot (*Leiostomus xanthurus*), and the blue crab (*Callinectes sapidus*), an especially voracious feeder on the infauna. I report here the results of manipulative field experiments to test the significance of large motile predators in controlling the abundance of infauna in a shallow subtidal community.

METHODS AND MATERIALS

The area investigated was a shallow (1.4 m at mean low water [MLW]) sandy bottom 70 m from the MLW line in the lower York River near the Virginia Institute of Marine Science (37°15′N lat., 76°30′W long.). Wire-mesh cages were used either to exclude predators from, or to confine certain predators to, a small area.

The experimental design consisted of randomly assigning various treatments to plots consisting of 50 × 50-cm areas of the bottom. These 0.25-m² plots were spaced 3 m apart in a grid pattern within an area ≈12 × 20 m (long axis parallel to shore). Treatments included various caging combinations and no cage,

i.e., caged plots and uncaged plots. In each separate experiment (1973 and 1974), there were sufficient numbers of each treatment for sampling after various predetermined periods of time (see below). There were two replicates of most treatments. A replicate was the same treatment applied to two separate plots. Each plot (whatever the treatment applied) was sampled only once. A sample from each plot consisted of five cores 8.1 cm in diameter.

To sample the infauna in a cage, the cage was carefully pulled out of the sediment and set aside. A grid was visually placed over the caged plot and the 5 cores taken at positions determined by randomly selected two-digit numbers. No cores were taken within 5 cm of the edge of the cage. Cores were taken with an 8.1-cm inside diameter (0.005 m²) hand-held polyvinyl-chloride (PVC) pipe corer to a depth of 10 cm. In 1973, samples were sieved through a 0.5-mm mesh screen and then fixed in Formalin with the vital stain, phloxine *B* added. In 1974, samples were fixed in Formalin first and then sieved. This latter procedure most likely increased the number of animals retained, because many thread-like worms (especially oligochaetes) would crawl through the screen if sieved alive. Therefore, absolute densities are not necessarily comparable between 1973 and 1974, except for larger animals. The retained animals were sorted from the sediment under a dissecting microscope, identified and counted. Many were measured, and all preserved in ethanol. Excluded from counts and analyses were those animals which are strictly epifaunal (e.g., barnacles and caprellid amphipods) or are generally classed as meiofauna and inadequately sampled (e.g., nematodes and copepods). Samples were taken in the same manner from randomly assigned uncaged plots whenever cages were set out or sampled, as well as during most other months.

Cages measuring 50 × 50 × 15 cm high were constructed of 12-mm mesh wire hardware cloth over a frame of 9-mm-diameter steel rods (Fig. 1). All cages were this size unless otherwise noted. A trapdoor in the top of each cage provided access inside the cages. The 30-cm legs and 5 cm of the bottom edge of the sides were pushed into the sediment to keep the cage in place and to prevent predators from digging under the cage. Fouling organisms were removed by scrubbing the cages frequently (weekly after the first 3 wk) with a wire brush.

Predators tested for effects on infauna were blue crabs *Callinectes sapidus* Rathbun, a portunid; hogchokers *Trinectes maculatus* (Bloch and Schneider), a soleid flatfish; and spot *Leiostomus xanthurus* Lacepede, a sciaenid. The crabs were 9- to 11-cm carapace width; the hogchokers and spot were 12- to 13-cm total length. The fish were measured before being put in the cages and then again at the end of the experiment (if they could be recaptured). All fish survived, but no crab survived the full 2 mo of an experi-

ment, having an average life expectancy of 1 mo in the cages. When a crab died, it was replaced by another within a few days.

Samples for analysis of sediments were taken with a 5-cm-diameter corer 5 cm deep, and analyzed for particle size according to methods given by Folk (1968). The sand fraction was separated from the silts and clays by wet sieving through a 62-μm mesh sieve and analyzed by dry sieving through a Wentworth sieve series. The silt-clay fraction was measured by pipette analysis. Orange-painted sand was placed on the sediment surface both inside and outside cages so that any differences in sediment stability and transport by currents and waves could be observed. All servicing of cages, sampling and observations were carried out using self-contained underwater breathing apparatus (SCUBA) gear.

I examined stomach contents of fishes from the lower York River. These fishes were collected in survey trawl samples in summer 1973.

Because faunal abundances in replicate treatments were generally quite similar ($P > .05$), quantitative analyses of faunal samples were done using the pooled data from both replicates. In the few cases where replicates were quite different, each replicate was treated separately. Comparisons of total density, number of species and number of individuals of common species (defined as a mean density >1/core) were made for each major sampling between the treatments using a one-way analysis of variance (Sokal and Rohlf 1969). Homogeneity of variance was tested using the F_{max} test. If a significant departure from homogeneity was found, a logarithmic transformation (log[x + 1]) was applied, and the transformed data then retested with the F_{max} test. If the analysis of variance indicated significant differences between means, all means were compared using the a posteriori Student-Newman-Keuls multiple comparison test. A t-test was used to test whether a sample mean was significantly greater than zero. Significance was chosen to be the $\alpha = .05$ level. Any departures from this standard procedure are noted.

To determine which treatments resulted in similar infaunal assemblages, a similarity analysis was performed on the collections using log-transformed abundance as an importance value and the Czekanowski (Bray-Curtis) similarity index, followed by agglomerative clustering of treatments using flexible ($\beta = -0.25$) sorting strategy (Clifford and Stephenson 1975).

1973 experimental treatments

Treatments tested in 1973 were (summarized in Table 1): cages excluding all larger predators ("empty" cages); cages each containing 1 hogchoker ("hogchoker" treatment); and cages each containing 1 blue crab ("crab" treatment). Some cages were divided into quadrants of 25 × 25 cm each by wire mesh and a crab put in each quadrant (called "4-crabs"

TABLE 1. The 1973 experiments. The number of samples of each replicate treatment at each sampling date. The same plot was never resampled. The entry "5 + 5" indicates 5 cores sampled from each of 2 replicate treatments or plots

Treatment	At start experiment (31 Jul)	After 2½ weeks (17 Aug)	After 2 months (29 Sep)
Uncaged area	5 + 5	5	5 + 5
Empty cage		5	5 + 5
Empty quadrant of cage			5
Cage with hogchoker			5 + 5
Cage with crab		5	5 + 5
Cage with crab in each quadrant		3	5 + 5
Cage with 2 sides			5

treatment, because there were 4 crabs in the same area as a cage) to test the effect of increased crab density or increased crab predation. Other cages divided into quadrants were left empty ("empty ¼" treatment) to test the effect of cage size. A cage control was used because it was suspected that cages might affect water currents and sedimentation. For this purpose, a cage with a top but only 2 sides was used ("2-sided" treatment) with the 2 sides perpendicular to the direction of flow of tidal currents, so as to have maximum effect on currents, while the 2 open sides would allow crabs and fish access to the infauna under the cage. In the course of the experiment, crabs were observed digging within this partially open cage. In addition to these treatments, natural sediments from uncaged plots were sampled ("outside cages" or "out").

All cages were set out at the end of July; some treatments were sampled after 2.5 wk and others after 2 mo to determine the time course of the response of the infauna (Table 1).

1974 experimental treatments

Based on results of 1973 experiments, similar but revised experiments were set up in 1974. Experiments were started in the spring (May) when more species were spawning, and before blue crabs became abundant. Because the hogchoker apparently had not preyed on the infauna, it was replaced by the spot, known to prey on infauna (L. N. Chao, personal communication, Hildebrand and Schroeder 1928, Stickney et al. 1975), to be dominant in this area (Pacheco 1962a, b, Illowsky and Colvocoresses 1975), and observed to feed in the experimental area ("spot" treatment). To further test the effect of different crab densities, crabs in 3 different sizes of cages were used: a 1-m² cage with a crab, a standard size cage (0.5-m square = 0.25 m²) with a crab ("crab" treatment = 4 crabs/m²), and a standard size cage divided by wire mesh into quadrants with a crab in each quadrant ("4-crabs" treatment = 16 crabs/m²). To test the effect of confining a crab to a small area without the presence of a cage, a crab was

TABLE 2. The 1974 experiments. The number of samples of each replicate treatment at each sampling date. The entry "5 + 5" indicates 5 cores sampled from each of two replicate treatments or plots. See p. 000 for explanation of treatment designations

Date sampled (and number of months cages were in place)	Uncaged	Empty	Empty, then crab	Crab	Crab/m²	4-crabs	Tethered crab	Spot	Hand
17 May (6)	5 + 5	5 + 5							
18 Jul (2)	5 + 5	5 + 5		5 + 5	5 + 5	5	5 + 5	5 + 5	5 + 5
18 Sep (4)	5 + 5	5	5						
16 Nov (1)	5 + 5	5							
16 Nov (6)	5 + 5	5 + 5							
16 Nov (12)	5 + 5	5							

tethered to a buried stake by a cord attached to a wire looped around the lateral spines of the crab's carapace ("tethered crab" treatment). The 28-cm tether allowed the crab to roam over the same area as a cage (0.25 m²). These crabs fought to escape the tether, appeared to be more active than the crabs in cages, and averaged either 1 escape or death per month. Tethered crabs and crabs in cages were replaced as soon as they were found to be dead or missing (a maximum of 1 wk).

An attempt was made to differentiate the effects of crabs caused by: (1) the actual eating of infaunal animals; and (2) physical burying, crushing and tube or burrow disruption caused by digging activities associated with feeding and protective burrowing. To make this distinction, I tried to duplicate the physical disturbances caused by a crab. Every 4–5 days, the top 2–3 cm of sediment was disturbed and fairly well mixed by reaching through the trap door opening of a cage and walking my fingers heavily through the sediment (as in mixing biscuit dough) and by pushing my fist into the sediment (to simulate the activities of crabs digging for food and burrowing), referred to as the "hand" treatment. Enough exclosures were set out in May to sample after 2, 4, 6 and 9 mo. A summary of 1974 treatments, replicates and sampling dates is given in Table 2. Other exclosure cages were set out at other times to assess recruitment at other seasons of the year.

Basic Assumptions of the Experimental Design

One assumption is that the infauna throughout the area where the cages were placed was homogeneous, i.e., that significant differences did not exist from one cage-sized plot to another a few metres away, so that when cages were placed over different plots on the same date, they all originally enclosed the same infaunal community. This assumption was tested by comparing uncaged replicate plots using a one-way analysis of variance. Total density and number of species showed no significant differences ($P > .05$) between replicate plots from any one month. The assumption of no preexisting differences was therefore valid.

The second assumption is that if 2 cages were put in

at the same date (t_o), and 1 cage sampled at time t_1 and another at time t_2, then both cages contained the same infauna at time t_1. Because cages could not be nondestructively sampled, this assumption was unfortunately untestable.

RESULTS AND INTERPRETATION
The natural community

The area investigated, a shallow, sandy, unvegetated bottom in the normally polyhaline region of the lower York River (salinity 16–23‰ during the study period), is probably representative of many of the extensive shoal areas of the Chesapeake Bay and its subestuaries. Sediments were poorly sorted ($\sigma I = 1.10 \phi$) fine sands ($Md_\phi = 2.52$ $\phi = 0.178$ mm) (Folk 1968) with a 15% silt-clay content.

Rank analysis (Fager 1957) was used to determine dominant species based on samples from uncaged areas in the 10 sample periods of 1974 (Table 3). For each month's sample, the top-ranked species was given 10 points, second-ranked 9 points, etc., for the top 10 species. Maximum possible score (for a species top-ranked in every sample) is 100. Of the 13 top-ranked species, 11 are annelids (1 oligochaete and 10 polychaetes). The top 5 species build vertical tubes or burrows in the sediment but exhibit diverse feeding types: 2 feed on the sediment surface (Spiochaetopterus oculatus and Streblospio benedicti), 2 feed anterior end down at the bottom of their tubes or burrows (Peloscolex gabriellae and Heteromastus filiformis), and 1 species is a tentaculate suspension feeder (Phoronis psammophila = P. architecta). Phoronis psammophila is the only suspension-feeding species of the top 13 species; the other 12 species ingest sediments or surface deposits. Of significant note is the complete absence of bivalves and crustaceans from this list of dominant species.

The ranking of the dominant species was rather constant throughout the year. For example, in the 10 samples, Peloscolex ranged in rank only from 1–3, Spiochaetopterus ranked 2–5, Heteromastus 1–5, and Glycinde solitaria 4–9. A relative index of constancy, calculated as the ratio of the variance of the monthly means to the yearly mean (Table 3), indicates that
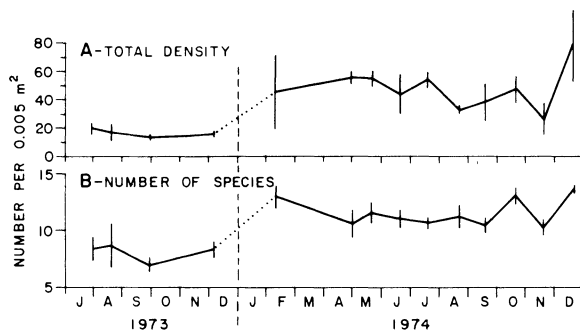
FIG. 2. Monthly abundance patterns, 1973–1974, of total density and number of species. Means ($\pm s_x$) are plotted.

Spiochaetopterus was the species most constant in abundance throughout the year, and *Streblospio* and *Polydora* were the least persistent.

Although many species spawn most heavily in early spring, there is generally a poor success of recruitment at this time. Total density did not increase in summer, in spite of this spawning effort. Blue crabs and many fishes move into the shallow areas of the estuary in spring and continue feeding throughout the summer. Thus, in spite of favorable temperatures and abundant productivity during spring and summer after this major recruitment effort, the infauna may have been prevented from increasing in abundance by the continual predation throughout the summer. Total density in December 1974 was significantly greater than in November, possibly indicating a rapid repopulation of infauna when predators leave, or a spawning—death—recruitment cycle (Fig. 2).

Sediments

The cages did affect sediment size and movement. Empty cages, the least disturbed treatment, tended to have a higher percentage (up to 35%) of fine sediments (silts and clays) than physically disturbed sediments (18–19%), or cages with crabs or spot (14–16%), or

TABLE 4. July to August 1973 experiment, after cages had been in place 2.5 wk. Means per 0.005 m² and standard error of total individuals and number of species

Treatment	Total individuals ($\bar{x} \pm SE$)	Number of species ($\bar{x} \pm SE$)
Empty cage (exclosure)	22.4 ± 5.0	10.0 ± 1.4
Uncaged at start (31 Jul)	22.3 ± 3.8	8.3 ± 1.0
Uncaged at end (17 Aug)	20.8 ± 5.8	8.6 ± 2.0
Cage with 1 crab	17.6 ± 4.9	7.8 ± 1.1
Cage with 4 crabs	7.7 ± 2.2	5.3 ± 1.2

areas outside cages (11–16%). This increase in fine sediments in the empty cage could be due either to reduction of currents or to increased biodeposition and binding of fine particles by animals such as *Streblospio benedicti* or *Polydora ligni*.

Orange-painted sand placed outside the cages was noticeably dispersed in the direction of tidal currents within a few hours, whereas inside the cages this sediment did not move for at least 7 days. Part of this effect may have been due to increased binding of sediments by the greater density of animals in the cages. However, on one occasion in November when painted sand was put out, within a few hours it was covered over and stabilized by diatoms, mainly by *Nitzschia closterium*, both inside and outside cages (Holland et al. 1974).

1973 caging experiments

Results after 2.5 wk.—On 17 August 1973, after the cages had been in place 2.5 wk, there were few significant differences between any of the treatments sampled. Although there was less than half the total density in the 4-crabs treatment (Tables 4, 5), none of the differences was significant ($P > .05$). The number of species per core in the empty cage was significantly greater than all other treatments, and was significantly less ($P < .01$) in the 4-crabs treatment than any other treatment. Of all the abundant species, only the

TABLE 3. Rank analysis of dominant species in the natural community based on samples from natural sediments in 1974. Maximum possible score is 100. O = oligochaete, P = polychaete, Ph = phoronid, G = gastropod

| Species	Rank	Score	Average density (N/m^2)	Variability of density (variance of monthly means about the yearly mean)
Peloscolex gabriellae (O)	1	96	3971	7.03
Spiochaetopterus oculatus (P)	2	80.5	890	0.36
Heteromastus filiformis (P)	3	79	1424	1.00
Streblospio benedicti (P)	4	63	1162	10.06
Phoronis psammophila (Ph)	5	50.8	436	0.68
Glycinde solitaria (P)	6	45.3	349	0.89
Polydora ligni (P)	7	27	450	11.90
Paraprionospio pinnata (P)	8	22.3	167	0.46
Scolelepis squamata (P)	9	15.5	153	0.51
Scoloplos robustus (P)	10	15.3	107	0.54
Eteone heteropoda (P)	11	13	105	1.34
Nereis succinea (P)	12	9.5	110	0.37
Acteon punctostriatus (G)	13	9	89	0.64
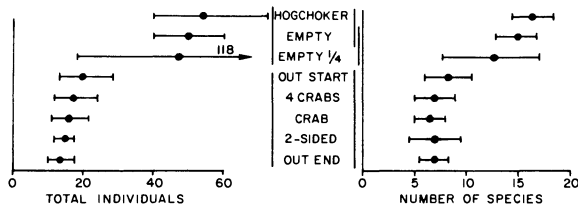
FIG. 3. July to September 1973 experiment, after cages had been in place 2 mo. Means and 95% confidence limits of total density and number of species. A vertical line extending between 2 treatments indicates a nonsignificant difference (*P* > .05) between the means. See p. 1201 for explanation of treatment designations.

chaetopterid polychaete *Spiochaetopterus oculatus* showed any significant differences between treatments, the 4-crabs treatment having significantly fewer individuals per core than any other treatment.

Results after 2 mo.—On 29 September 1973, after the cages had been in place 2 mo, there were many more significant differences between treatments than after only 2.5 wk (Table 5).

Densities in the two-sided cage were generally not significantly different from uncaged areas or cages with crabs, but were significantly less than empty cages (Figs. 3, 4), implying that the main effect of the cage was exclusion or inclusion of crabs, and that results were not due in some way to the physical presence of the cage.

Total density, number of species per core (Fig. 3), and number of individuals per core of six species were significantly greater (*P* < .05) in the empty cage than in either of the cages with crabs. These 6 species were *Paraprionospio pinnata*, *Spiochaetopterus oculatus*, *Streblospio benedicti*, *Scoloplos robustus*, *Mulinia lateralis* and *Edwardsia elegans*.

Showing few significant differences between treatments were *Peloscolex gabriellae*, *Heteromastus filiformis*, *Phoronis psammophila* and *Mya arenaria*, all of which live or can retract rather deeply into the sediment, and could thus avoid predation and surface disturbances. *Spiochaetopterus oculatus* (also with a tube extending deep into the sediment) did not follow this pattern because it was recruiting heavily at the time these cages were set out; 45% of the individuals from uncaged areas were juveniles (<4 mm) in June. There were no juveniles collected in April or May.

Both total density and number of species per core were significantly greater (*P* < .001) in 3 treatments— empty cages, empty ¼ cages and cages with a hogchoker—than in any other treatment, with an average of >3× the total density and 2× as many species per core (Fig. 3). These 3 treatments resulted in similar increases (although all were not significant) in the densities of 7 of the 12 species tested: *Paraprionospio pinnata*, *Streblospio benedicti*, *Spiochaetopterus oculatus*, *Nereis succinea*, *Mulinia lateralis*, *Mya arenaria* and *Edwardsia elegans*.

TABLE 5. Densities of infauna (mean number per 0.005 m² core) in exclosures set out in July 1973 and sampled after 2.5 wk or 2 mo. Each cage was sampled only once. An asterisk (*) indicates significantly greater density (*P* < .05) than uncaged area at same sampling date

Taxa	At start of experiment (31 Jul)	After 2.5 wk (17 Aug)	After 2 months (21 Sep)
OLIGOCHAETE			
Peloscolex gabriellae	4.1	3.2	10.1
POLYCHAETES			
Paraprionospio pinnata	0.1	0.2	8.6*
Streblospio benedicti	0	0	7.2*
Spiochaetopterus oculatus	2.8	3.0	5.1*
Heteromastus filiformis	2.1	4.4	2.2
Glycinde solitaria	4.6	2.2	4.0*
Nereis succinea	0.9	0.8	1.3
Scoloplos robustus	0.2	0	1.1*
BIVALVE			
Mulinia lateralis	0.3	0.6	1.5*
ANEMONE			
Edwardsia elegans	0	0	1.7*
PHORONID			
Phoronis psammophila	1.0	0.8	1.8
TOTAL INDIVIDUALS	22.2	22.4	51.6*
NUMBER OF SPECIES	8.1	10.0*	14.8*

There was a general pattern of greater density of most species in empty cages, with the hogchoker treatment producing the same results as an empty cage (Fig. 4). Thus hogchokers had little controlling influence on the infauna. Both hogchokers survived the 2 mo in the cages, but lost an average of 15% of their body weight over this period. They are abundant (Dovel et al. 1969) nocturnal feeders (Castagna 1955), and may feed also on animals such as mysids and cumaceans, which are more epifaunal than infaunal, although mainly annelids were found in hogchoker stomachs by Castagna (1955) and by Hildebrand and Schroeder (1928). Captivity may have inhibited feeding behavior and caused this discrepancy. Hogchokers are more abundant on mud than sand bottoms, although they were often observed in the study area.

The cages with crabs had essentially the same infauna as the two-sided cage and uncaged areas, implying that natural areas are as disturbed or as preyed-upon as an area in which there was a caged crab.

The dendrogram (Fig. 4) resulting from similarity analysis indicated 2 main groups. Those treatments that excluded crabs and most fish (empty, empty ¼, and hogchoker treatments) formed 1 highly similar group distinct from those other treatments where crabs had access to the sediments and infauna. These 2 groups had a low similarity to each other.

1974 caging experiments

Results after 2 mo.—On 18 July 1974, after cages had been in place 2 mo, composite community parame-
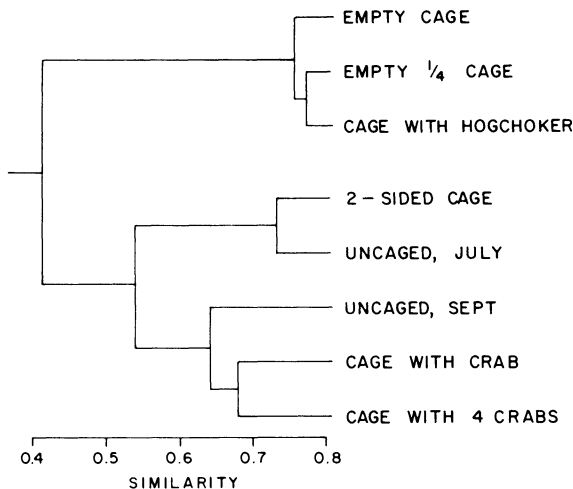
FIG. 4. Dendrogram resulting from similarity analysis of treatments sampled in September 1973, after cages had been in place for 2 mo. The Czekanowski index based on log-transformed abundance was used with a flexible sorting strategy.
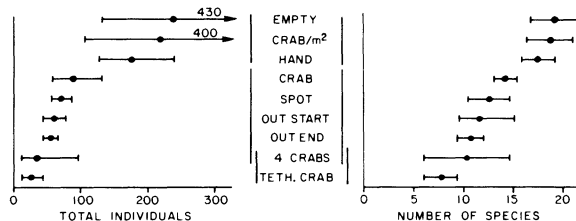

FIG. 5. May to July 1974 experiment, after cages had been in place 2 mo. Means and 95% confidence limits of total density and number of species. A vertical line extending between two treatments indicates a nonsignificant difference ($P > .05$) between the means. See p. 1201 for explanation of treatment designations.

ters and most common species showed significant differences between treatments (Table 6). Both total density and number of species per core followed the same pattern; the empty cage, crab/per square metre and hand treatments were not significantly different from each other, but were significantly greater than all other treatments (Fig. 5). Total density and number of species per core were significantly less in the tethered crab treatment than in all other treatments except the cage with four crabs.

Abundances of individual species also followed a pattern similar to 1973. For 12 of the 14 common species, two of the three treatments with greatest densities were from among the empty, hand, or crab/m^2 treatments. For 12 of the 14 species, the lowest abundance of all treatments sampled in July was either the 4-crabs treatment or the tethered crab treatment.

For all species except the bivalves and the polychaete *Heteromastus filiformis*, the hand treatment was not significantly different than the empty cage. Thus, most decreases in abundances due to crabs must be due either to physical disturbances more severe than the hand treatment, or to actual eating of the infaunal animals, or to a combination of both.

The 3 species of bivalves, *Mya arenaria*, *Mulinia lateralis* and *Lyonsia hyalina*, were effectively eliminated by the hand treatment and by any treatments where a crab or fish (spot) was present. *Mya* was sig-

TABLE 6. Densities of infauna (mean number per 0.005 m^2 core) in exclosures set out in May 1974 and sampled after 2, 4 or 6 mo. Each cage was sampled only once. An asterisk (*) indicates significantly greater density ($P < .05$) than uncaged area at same sampling date

| Taxa	At start of experiment (17 May)	After 2 mo (18 Jul)	After 4 mo (18 Sep)	After 6 mo (16 Nov)
OLIGOCHAETE				
Peloscolex gabriellae	11.9	28.8	48.0*	53.3*
POLYCHAETES				
Heteromastus filiformis	2.8	173.4*	15.4*	35.7*
Streblospio benedicti	24.2	52.4*	0.2	3.5
Glycinde solitaria	1.3	7.7	1.4	1.9
Spiochaetopterus oculatus	3.6	3.5	1.0	2.8
Polydora ligni	0.4	4.1*	12.6*	3.8*
Nereis succinea	0.2	4.5*	3.8*	5.8*
Pectinaria gouldii	0	1.7*	5.2*	3.5*
Pseudeurythoe sp.	0.1	0.1	5.0*	1.2*
Eteone heteropoda	2.5	0.5	0	1.7*
BIVALVES				
Mulinia lateralis	0.1	44.1*	41.0*	20.3*
Mya arenaria	3.3	2.0*	1.2	4.2*
Lyonsia hyalina	0	1.6*	2.6*	0.1
PHORONID				
Phoronis psammophila	0.8	4.4	1.6	1.4
TOTAL INDIVIDUALS	57.4	344.2*	145.8*	150.1*
NUMBER OF SPECIES	11.6	19.8*	15.4*	18.3*
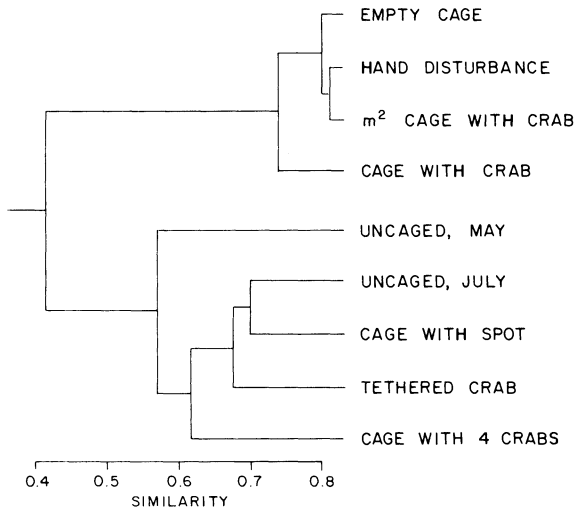
FIG. 6. Dendrogram resulting from similarity analysis of treatments sampled in July 1974, after cages had been in place for 2 mo. The Czekanowski index based on log-transformed abundance was used with a flexible sorting strategy.
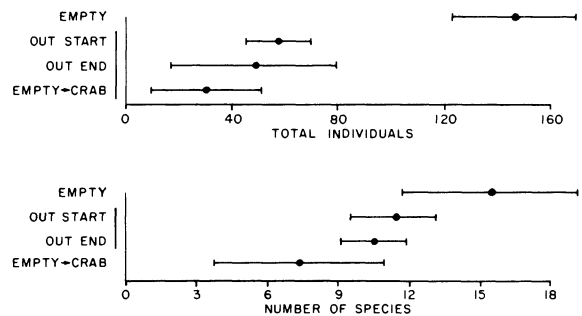

FIG. 7. May to September 1974 experiment. Means and 95% confidence limits of total density and number of species. A vertical line extending between 2 treatments indicates a nonsignificant difference ($P > .05$) between the means. See below for explanation of treatment designations.

nificantly more abundant in uncaged areas at the start of the experiment (May) than in empty cages in July; otherwise, the densities of all three bivalves were significantly greater in the empty cages than in any other treatment. *Mulinia* and *Lyonsia* both live very close to the sediment surface and thus are available to predators and would be disturbed, buried or crushed by the hand treatment.

Infaunal densities in the crab per square metre treatment were greater than the crab treatment (a density of 4 crabs/m²) for 9 of the 14 common species (2 of these differences were significant). Densities in the crab treatment were greater than in the 4-crabs treatment (16 crabs/m²) for all species except *Scoloplos robustus* (5 of these differences were significant). Thus, as blue crab density increases, infaunal densities decrease.

Densities in the tethered crab treatment were less than or equal to those in the 4-crabs treatment for 9 of the top 14 species, but were never significantly less. Apparently the increased activity of the tethered crab (noted above) was sufficient to disturb the infauna as much as 16 crabs/m².

The spot (*Leiostomus xanthurus*) also effectively reduced infaunal densities. Densities of 12 of the 14 common species were less in the cages with the spot than in empty cages (seven of these differences were significant). Densities in the spot treatment were intermediate between those in the crab per square metre and 4-crabs treatments for 10 of the top 14 species, and intermediate between those in the crab and 4-crabs treatments for 7 species. Thus, the spot was at least as effective as a crab in reducing infaunal densities of most species.

Densities in natural (uncaged) sediments at the time of sampling the cages (July) were intermediate be-

tween those of the crab per square metre and 4-crabs treatments for 7 of the top 14 species, were less than in the crab treatment for 11 of the species (significantly less for 4 species), and were greater than in the 4-crabs treatment for 7 of the species. Thus, the infauna of the natural uncaged sediments is at least as disturbed as a caged area with a crab (a density of 4 crabs/m²).

The dendrogram (Fig. 6) resulting from the similarity analysis indicates 2 main groups. The low-predation treatments (empty cage, m² cage with crab and hand disturbance treatments) were all highly similar. Inexplicably, the crab treatment was similar to this group of treatments. At the time of sampling, the crabs in both replicates were dead, but for a maximum of only 8 days—perhaps this allowed recruitment by other species. Those treatments with supposedly greater predation intensity formed another similar group.

The ranks of treatments averaged over all species and composite parameters tested in Table 6 were arranged from highest rank (highest density) to lowest rank in the following order: empty cage, cage with sediment disturbed by hand, m² cage with crab, cage with crab, cage with spot, uncaged area at end of experiment (July), uncaged at start of experiment (May), cage with 4 crabs, and the area with a tethered crab. This ordering might be considered as ranking the treatments from low to high predator disturbance.

Results after 4 mo.—On 18 September 1974, after cages had been in place 4 mo, the following treatments were sampled (Table 2, above): an uncaged area, an empty cage, and a cage empty for 2 mo, but then with a crab in it for the next 2 mo ("empty→crab" treatment).

Results were very similar to those of July 1974. The empty cage had significantly greater total density, more species and more individuals per core of most species than any other treatment (Table 6, above; Fig. 7). Species not significantly more abundant in the empty treatment were deeper-living *Spiochaetopterus oculatus*, *Mya arenaria* (mean size = 32.7 mm), and *Phoronis psammophila*. Total density, number of

species per core, and densities of half of the species tested were lowest in the empty→crab treatment.

The densities of most species in the uncaged area were more nearly equal to and usually not significantly different from densities in the empty→crab treatment, again indicating that the uncaged natural areas are highly preyed upon.

Results after 6 mo.—When sampled on 16 November 1974, the empty cages in place since May (6 mo) had greater total density and species per core ($P < .01$), and greater density ($P < .05$) of 9 of the 14 species tested than the uncaged areas (Table 6). Species with especially high densities in the empty cages were: the oligochaete *Peloscolex gabriellae*; the polychaetes *Heteromastus filiformis*, *Pectinaria gouldii*, *Polydora ligni* and *Nereis succinea*; and the bivalves *Mulinia lateralis* and *Mya arenaria*. All of the above species had also been abundant in empty cages in July (after 2 mo) and September (after 4 mo), with the exception of *Mya* in September (Table 6).

The empty cage: General results

The general pattern of results from the empty cage treatments (exclosures) is given here; individual species patterns will be presented in a forthcoming paper. The empty cage resulted in increased densities of most species, but the specific results depended on a number of factors.

The length of time a cage had been in place determined whether there were any significant differences in density between the infauna in an empty cage and in an uncaged area. After 2.5 wk in 1973, there were no significant differences for any of the species. After 2 mo, densities of 7 species were significantly greater in empty cages than in uncaged areas (Table 5). In 1974, after 1 mo there were only 2 species with significantly greater densities in the empty cages; after 2, 4, 6 and 12 mo, there were 8, 8, 9 and 9 species, respectively, that had significantly greater densities in the empty cage than in an uncaged area. Thus, few significant differences occur in 1 mo or less, but many significant differences occur after 2 mo. Leaving the cage in longer than 2 mo did not, however, appreciably change the results. Essentially the same species were more abundant in exclosures set out at the same time and then sampled after 2, 4, or 6 mo.

It is possible that density-dependent regulation of these populations prevented further increases after 2 mo. Number of species per core, total density, diversity and species composition did not change much from 2 to 6 mo, indicating that succession was not taking place after 2 mo (Fig. 8). I do not know how long, if ever, it would take for this caged community to approach the "natural" community. I suspect that a higher-density community could be maintained indefinitely in exclosures. Species composition would probably change with time but opportunistic species would probably continue to play a large role in such ex-

closure-maintained communities. Such communities (*sensu latu*) may correspond to Sutherland's (1974) "multiple stable points."

The season when a cage was set out determined which species increased in abundance in the empty cage. Recruitment into empty cages was predominantly by larvae rather than by adults, as indicated by the small size of new recruits. Thus, if, during the time the cage was in place, the larvae of species A were in the plankton and ready to set, but those of species B were not, species A would increase in abundance in the empty cage and species B would not. In general, any empty cage left for 2 mo or longer had significantly greater total density, more species per core, and more individuals per core of most species than there were outside the cage in natural uncaged sediment. Those species that increased most in abundance were the ones that were recruiting at the time the cages were first set out.

Individual species patterns

In general, the species least affected by increased predation were those which live deep in the sediment or can retract quickly into the sediment, thus avoiding predators: the annelids *Peloscolex gabriellae*, *Heteromastus filiformis*, *Spiochaetopterus oculatus*, *Paraprionospio pinnata*, the phoronid *Phoronis psammophila* and large individuals of the bivalve *Mya arenaria*. This list includes four of the top 5 ranked species in the natural community (Table 3), suggesting that avoidance of predators allows their success.

Those species which live very close to the sediment surface and are thus available to predators showed large responses to decreased intensity of predation: the polychaetes *Streblospio benedicti*, *Polydora ligni*, *Pectinaria gouldii*, and the bivalves *Lyonsia hyalina*, *Mulinia lateralis* and small *Mya arenaria*. The combination of fish predation on juveniles, crab predation on small individuals and cow-nosed ray predation on the largest individuals (Orth 1975) may be responsible for the relative lack of bivalve dominance in Chesapeake Bay.

Opportunistic eurytopic species play a large role in response to disturbances, and are abundant in most Chesapeake Bay habitats (Copeland 1970, Boesch 1973, 1977), indicating stressed or unpredictable environments, characteristic of most estuaries. These *r*-strategists are able to react rapidly to changing environments, stresses, temporarily open space and relaxed predation pressures (Levinton 1970, Grassle and Grassle 1974, Boesch et al. 1976a, Boesch 1977). Pollution may also exclude predators in a manner similar to experimental exclosures, allowing densities of these eurytolerant opportunistic species to increase (Young and Young 1977).

Opportunistic species played a large role in the community studied. Two of the most abundant species, *Heteromastus filiformis* and *Streblospio benedicti*,
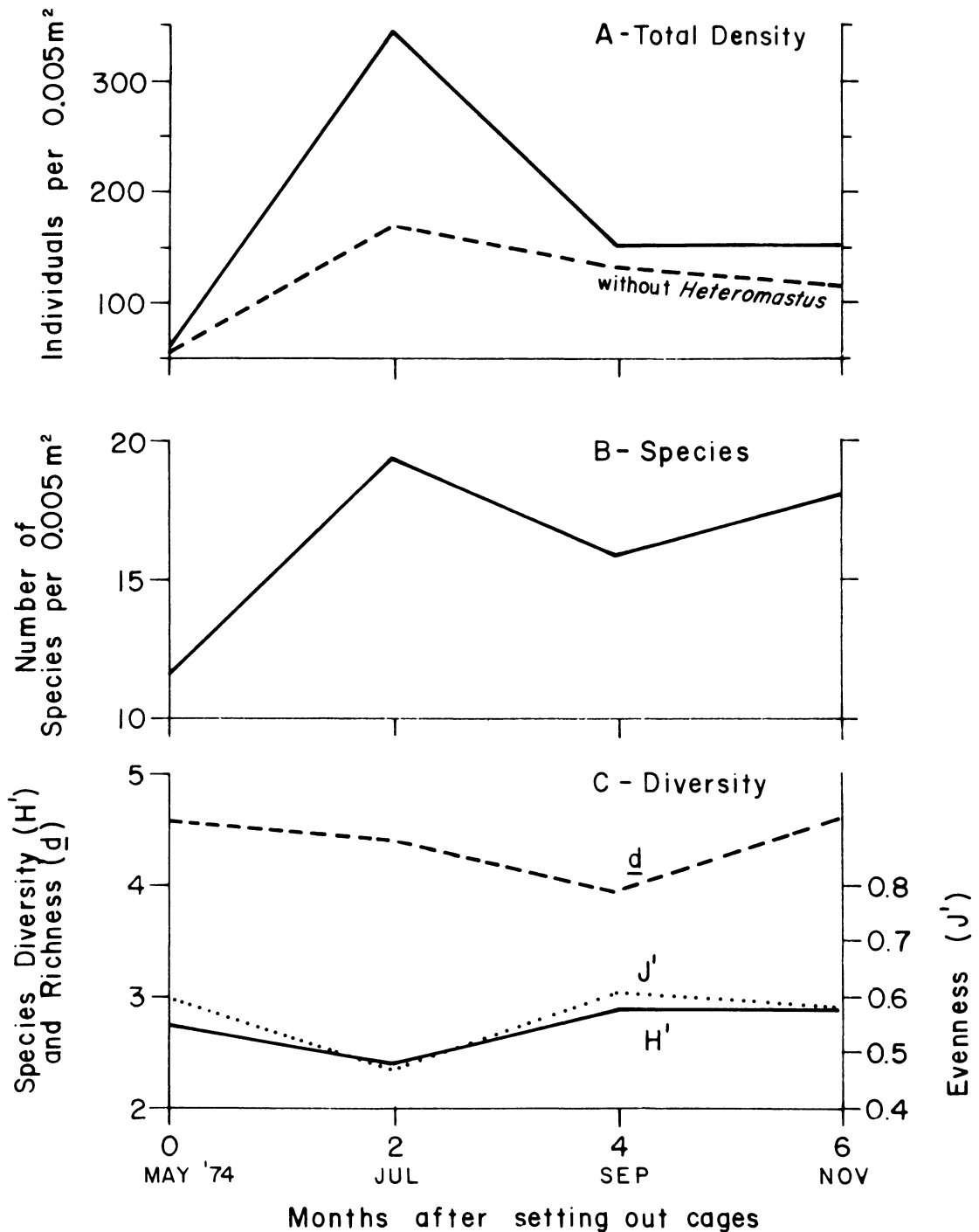
FIG. 8. Community parameters of infauna *versus* time in exclosures: (A) total density, (B) number of species, and (C) diversity (H'), including richness $(d = S - 1/\ln N)$, and evenness $(J' = H'/\log_2 S)$ components, where S = number of species.

both reputed opportunists, were among the most abundant species in natural sediments and in cages with predators. Together with the opportunistic *Mulinia lateralis*, these species dominated most exclosures, with densities 1 to 2 orders of magnitude greater than outside exclosures.

The high degree of dominance by these opportunists was as effective as a predator in keeping informational diversity (Shannon-Weaver H') in exclosures at about the same level as in the natural community (Fig. 8C). Although the number of species was much higher in all exclosures, the low level of species evenness produced
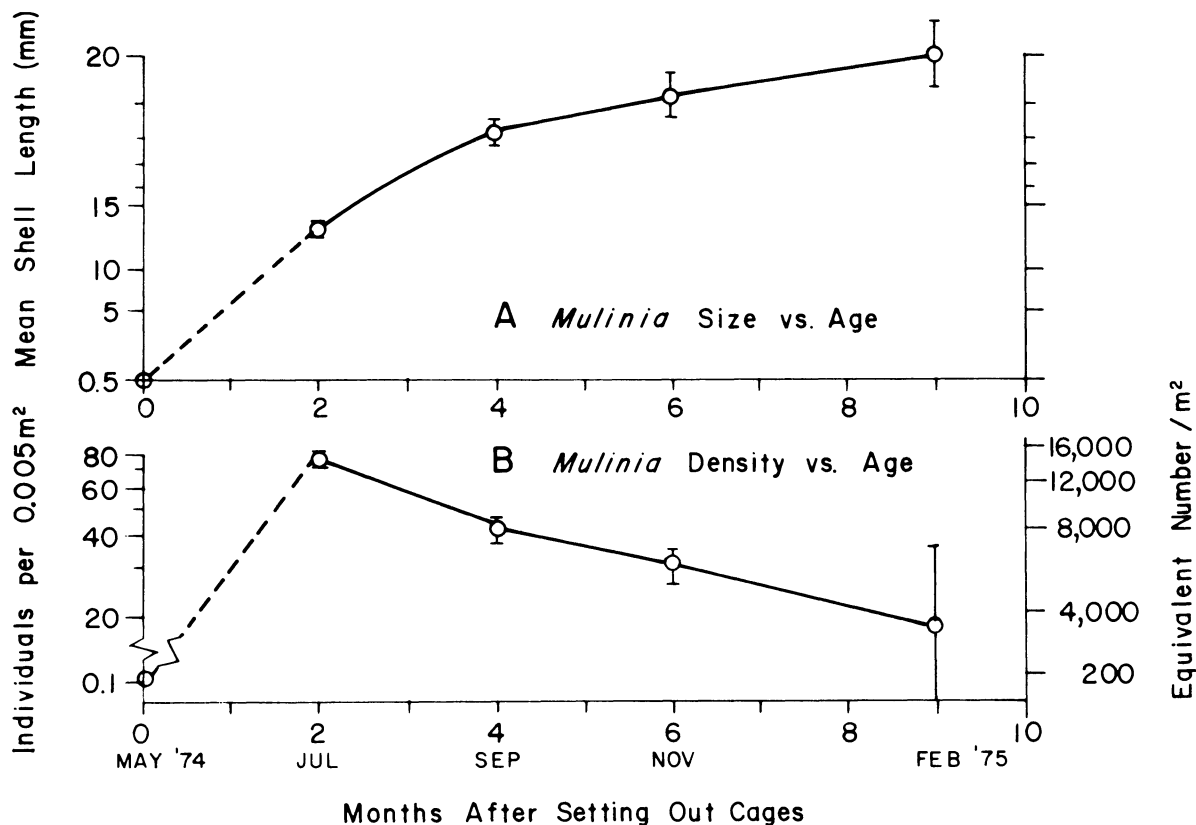
FIG. 9. *Mulinia lateralis* size *versus* age and density *versus* age in exclosures set out in May 1974. Means (log scale) and 95% confidence limits.

by the dominance of these opportunists caused the lowered diversity. The diversity of the natural community is apparently not limited entirely by physical environmental factors, but also by biological factors: predation at low infaunal densities in the natural community, and competition only at high infaunal population densities in exclosures.

Mulinia lateralis (*Say*).—Of all species collected, the mactrid bivalve *Mulinia lateralis* best exemplified the characteristics of an opportunistic species and a desirable prey. This account is presented as an example of such.

Periodic eruptions of very dense populations of *Mulinia* occur in Chesapeake Bay, particularly in deeper muddy sediments in winter or early spring (Boesch 1973, 1974, Huggett et al. 1975, Boesch et al. 1976*b*). These dense populations then experience very high mortalities in early summer, probably due to both predation and high turbidity. *Mulinia* maintains low-density reservoir populations in shallow sandy areas (Wass et al. 1972). Summer densities averaged $20/m^2$ during this study and $37/m^2$ at three 3-m-deep stations in the lower York River from 1972 to 1974 (Virnstein 1975).

Juveniles were found in February, May, June, July, August, September and November. Additional sam-

pling would be likely to show that *Mulinia* juveniles are present year-round; Chanley and Andrews (1971) found *Mulinia* larvae in the plankton from May to November.

Young *Mulinia* grow very rapidly. At temperatures >20°C, they grew to sexual maturity in 6 wk in Long Island Sound (Calabrese 1970). In my cages, they grew to an average length of 18.2 mm in only 4 mo (Fig. 9A). In those exclosures which remained densely populated with *Mulinia*, it was probably the increase in size of individual *Mulinia* which caused overcrowding and a subsequent decline in density (Fig. 9B). The density of the clams was so great that to bury itself, a clam would have to dig through a layer of clams (Figs. 10, 11). By lying on their sides and thrusting their feet out rapidly, clams were observed to "hop" along the sediment surface and thus move laterally. Presumably in response to overcrowding, some clams moved out of the cage in this way. If they moved out during the seasons when crabs were present, these clams were eaten within a few days, as evidenced by the broken *Mulinia* shells outside the cages.

Every exclosure, no matter when set out or sampled, had a greater density of *Mulinia* than outside cages; most of these differences were significant. *Mulinia* densities were significantly greater ($P < .01$) in empty
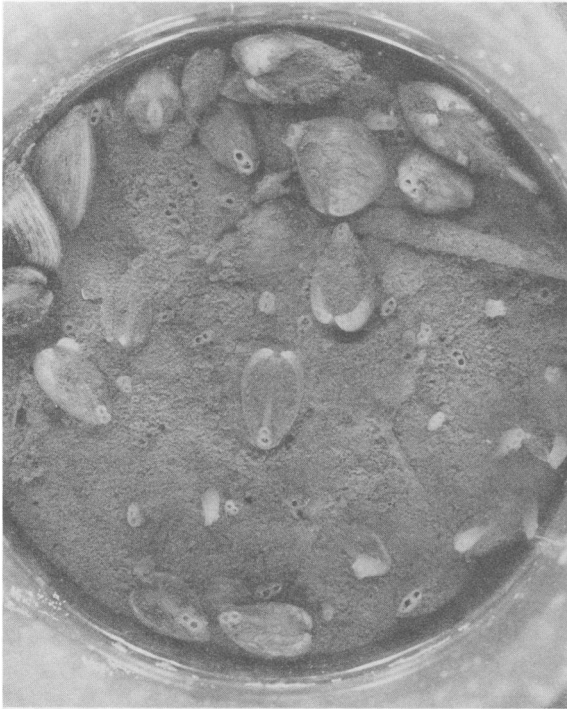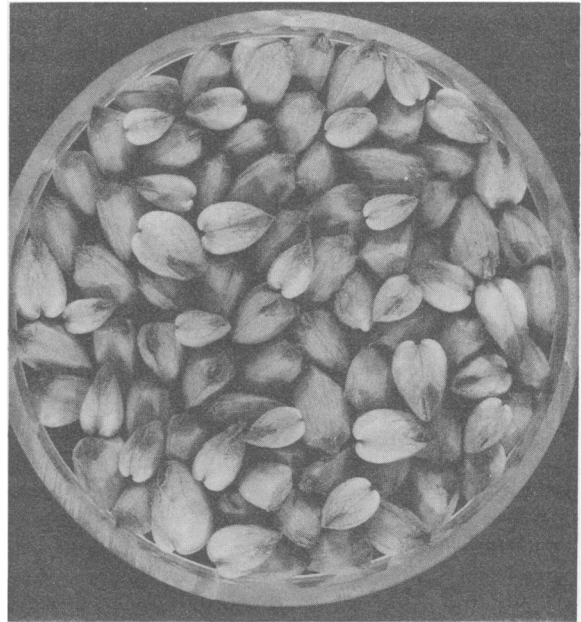
Fig. 11. Photograph of the *Mulinia lateralis* removed from the core pictured in Fig. 10. Diameter of the core is 10 cm; thus the clams are pictured in the actual density from the field.

Fig. 10. Photograph of undisturbed core taken from an exclosure in September 1974, in place since May, showing *Mulinia lateralis* and *Pectinaria gouldii* on the surface, and the numerous siphons of *Mulinia*. Inside diameter of the core is 10 cm. The *Mulinia* from this core are pictured in Fig. 11.

cages than in any other treatment set out and sampled on the following dates: November 1973 to May 1974, May to September 1974, May to November 1974, and May 1974 to February 1975.

From the experiments of 1973 (Fig. 12), it can be seen that *Mulinia* density is not affected by hogchokers, but is effectively controlled by crab predation. In 1974, crabs and spot were also effective in reducing *Mulinia* density (Fig. 13). As had happened with many other species, the greater the density of crabs, the less the density of *Mulinia* (Fig. 14).

The actual mechanism by which *Mulinia* populations were kept low may have varied from treatment to treatment. The hand treatments had significantly fewer *Mulinia* than the empty cages, but significantly more individuals than outside the cages (Fig. 13). This manual disturbance of the sediments may eliminate many *Mulinia* by crushing, burying, or dislodging the newly settled clams from the sediment so that they may be carried away by tidal currents. This hand treatment was less effective than the crabs or spot in eliminating *Mulinia*.

Spot may have eliminated many *Mulinia* both by actually eating them, and by physical disruption of sediments. Spot feed mainly in the top few millimetres of sediment (Stickney et al. 1975). *Mulinia* are one of the most common and abundant species in the stomachs of

spot collected from the lower York River in summer 1973. There was a mean of 11.2 *Mulinia* per spot stomach of the 10 fish examined. Some of these *Mulinia* were adult size (5–10 mm), but most were juveniles 1–3 mm long, in spite of the fact that juvenile *Mulinia* are rarely ever taken in benthic samples in summer. However, *Mulinia* do spawn and set during summer, as evidenced by their recruitment into exclosures during summer 1973 (Fig. 12). They do not survive in nature due to such heavy predation by spot and probably other species.

Blue crabs may also eliminate many *Mulinia* by their digging and burrowing activities. In addition, they were observed to have eliminated a cage full of large *Mulinia* by eating them.

To verify that blue crabs could actually dig up and eat *Mulinia*, several large (≈18 mm) *Mulinia* were put into an aquarium containing sediment from the study area and allowed to burrow into the sediment. A blue crab was then put into the aquarium and observed. Two different crabs were used on 2 different occasions. In both cases, the crabs found the *Mulinia*, as if stumbling on them while walking about, dug them up and ate them. Usually the crab crushed the clams with its chelae, often near the clam's siphons, then proceeded to use its mouthparts to scrape the tissue out of the valves. With 2 clams, however, the crab was able to insert the dactyl of one chela between the valves of the clam, then inserted the dactyl of the other chela, and pried open the valves, all in ≈15 s. The crab then ate the whole clam, even scraping the abductor muscles off both valves without breaking either valve.
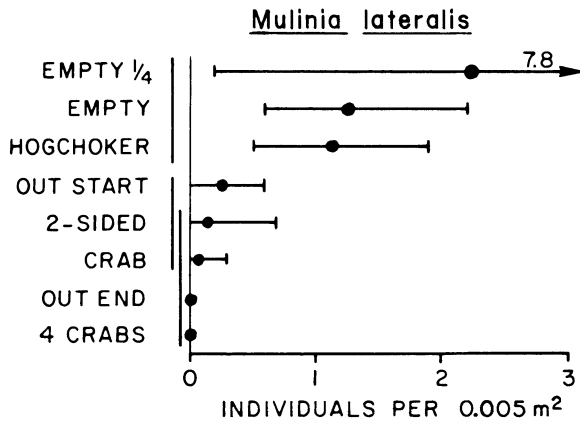
Mulinia lateralis

FIG. 12. Density of *Mulinia lateralis* after cages had been in place 2 mo in 1973 (July to September). Means and 95% confidence limits. A vertical line between two treatments indicates a nonsignificant difference (*P* > .05) between the means.
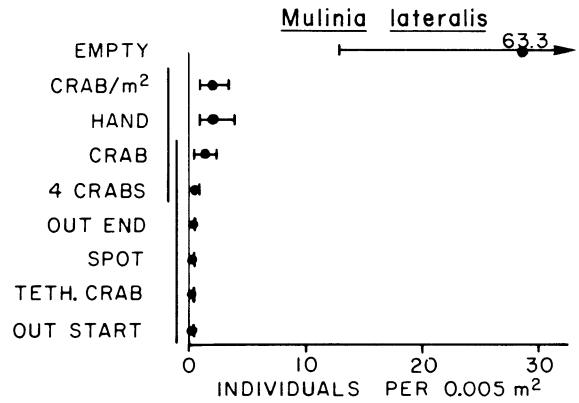
Mulinia lateralis

FIG. 13. Density of *Mulinia lateralis* after cages had been in place 2 mo in 1974 (May to July). Means and 95% confidence limits. A vertical line between 2 treatments indicates a nonsignificant difference (*P* > .05) between the means.

There is other evidence that blue crabs eliminated the *Mulinia* by actually eating them, not just by physically disturbing the sediment. The unplanned but fortuitous empty→crab treatment was a cage that had been empty for 2 mo (May to July 1974); then 2 small crabs (6–8 cm) somehow got into the cage. One was allowed to remain for the next 2 mo (July to September). In mid-July, I observed that this cage contained a dense population of large *Mulinia* (the density of *Mulinia* was 14,700/m² with a mean length of 13.4 mm in another empty cage set out in May and sampled in July). Four days later, I observed the 2 crabs and hundreds of empty and broken *Mulinia* shells in the cage. The crab that was allowed to remain grew considerably in the next 2 mo (to 13 cm carapace width). No *Mulinia* were found in samples from this cage in September 1974 (Fig. 15). In contrast,

the empty cage sampled at this time was so densely packed with *Mulinia* (7,950/m², 18.2-mm mean length) that some of the clams were lying on top of one another (Figs. 10, 11). Four days after this cage had been removed, exposing ≈2,000 clams to crab predation, the sediment surface was littered with empty and broken shells, and not one live *Mulinia* could be found.

In November 1974 and February 1975, empty cages also full of *Mulinia* were sampled. After the cage was removed and the samples taken, the cage was put back so that approximately half of the *Mulinia* were within the cage and half were outside the cage. At both of these times, crabs were not feeding in shallow parts of the estuary and nearly all clams survived both inside and outside the cages. In late April 1975, when crabs first started to appear, a few broken *Mulinia* shells were
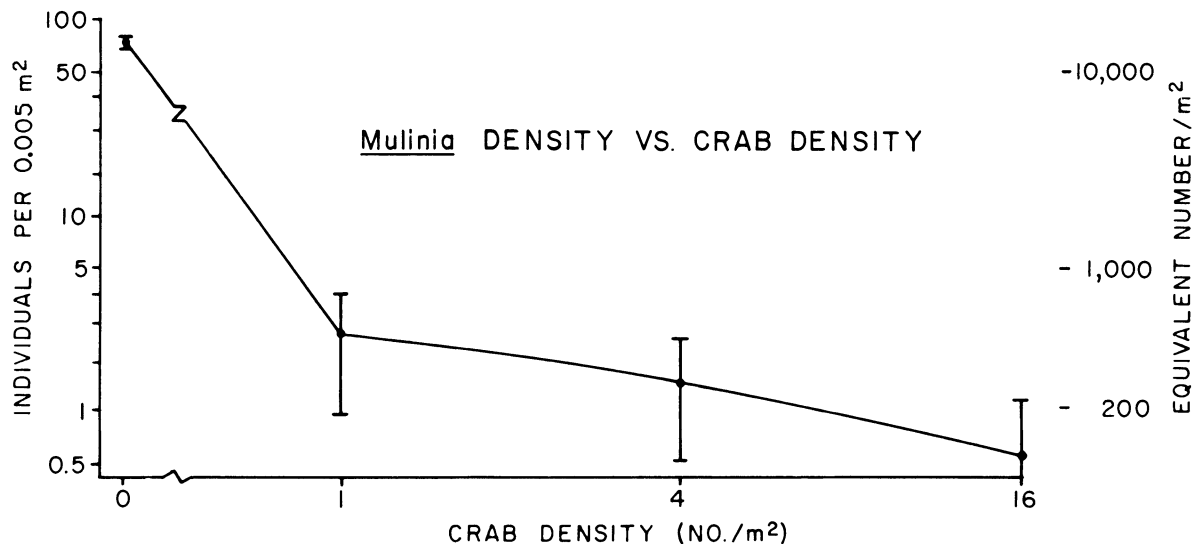

FIG. 14. *Mulinia lateralis* density *versus* blue crab density in cages. Means (log scale) and 95% confidence limits of July 1974 data.
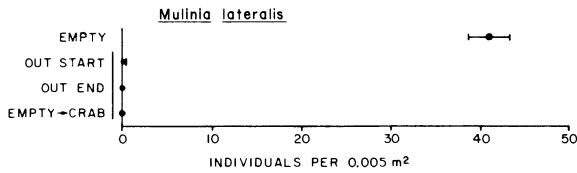
Mulinia lateralis

FIG. 15. Density of *Mulinia lateralis* after cages had been in place 4 mo in 1974 (May to September). Means and 95% confidence limits. A vertical line between 2 treatments indicates a nonsignificant difference ($P > .05$) between the means.

found outside these cages and 1 crab was observed carrying off a large *Mulinia*. By the middle of May, no live *Mulinia* could be found outside the cages, whereas most of the *Mulinia* inside the cages survived until August and some until September 1975, when the mesh of the cages corroded, holes appeared, and crabs were seen inside the cages.

At this time, the *Mulinia* were 16 mo old. Most were 22–23 mm; the largest was 26.3 mm, much larger than is ever found in natural habitats. J. Kraeuter (*personal communication*) has grown *Mulinia* in the laboratory to >30 mm in less than a year. Thus it appears that *Mulinia* is a favored food of blue crabs and that predation is probably the major factor controlling adult population size during warmer months. Peterson (1975) found a similar situation with respect to blue crab predation on intertidal *Mytilus edulis* in Barnegat Bay, New Jersey.

DISCUSSION

The effect of predation on a community depends partly on the intensity of the predation. Low-level predation pressure may increase species diversity by (1) reducing the density of dominant species, which allows the density of competitively inferior species to increase (Brooks and Dodson 1965, Paine 1966, 1969, Porter 1972); (2) reducing most species densities to a level below that regulated by competitive exclusion of species (Dayton and Hessler 1972, Roughgarden and Feldman 1975); or (3) creating patches with lowered densities at different stages of succession to a hypothetical "climax community" (Hutchinson 1961, Horn and MacArthur 1972, Levin and Paine 1974). Sufficiently severe predation pressure may decrease species diversity by reducing population densities of all species (Sammarco et al. 1974). Effects of predation may be most drastic in physically controlled environments, because the prey organisms must give adaptive priority to the physical regime, rather than to refinement of biological interactions (Sanders 1969, Slobodkin and Sanders 1969).

In the community studied here, and over the time spans examined (1–12 mo), increasing predation pressure caused a slight decrease in species diversity (number of species), and decreasing predation pressure below natural levels allowed a large increase in diversity, indicating that natural predation pressures are severe.

Although the physical stresses of the estuarine environment may be severe, they are not major factors limiting natural population densities of this community; predation does play a major role. In such a trophically simple community (detritus-based), Menge and Sutherland (1976) would have predicted competition, not predation, to be the dominant organizing interaction.

Density-dependent interactions

The theory of competitive exclusion (Gause 1934) predicts the elimination of one species by another if both compete for the same limited resource. However, predation can alter the outcome of competition between two competing species, allowing both species to coexist in a space in which only one could exist without predation (Slobodkin 1961, Brooks and Dodson 1965, Paine 1966, Cramer and May 1972, Porter 1972, Levin and Paine 1974, Roughgarden and Feldman 1975).

In the York River community studied here, densities of most species increased when protected from predators; no species decreased in density, suggesting a lack of competitive exclusion. It appears that competitive pressures are not very important in the regulation of population densities in this community. Resources are not limiting in these shallow sand communities in Chesapeake Bay.

In contrast to this situation, limitation by, and competition for, space and food has been demonstrated in intertidal marine benthic environments between barnacles (Connell 1961*a*, *b*), between deposit-feeding mud snails (Fenchel 1975), between tube-building and burrowing polychaetes (Woodin 1974), between a phoronid and a bivalve (Ronan 1975), and between infaunal bivalves (C. H. Peterson, *personal communication*). J. Committo (*personal communication*) found that intertidal infaunal population densities increased only slightly in response to decreased predation in exclosure cages in the Newport River estuary, North Carolina. These infaunal densities decreased later in the summer, both inside and outside exclosures.

The reason for such a discrepancy between these other studies and mine is unclear. The greatest difference is that all of the above studies are intertidal as opposed to my subtidal study. Although not always true, the higher in the rocky intertidal zone, the less important is predation as a factor regulating population densities (Connell 1972). Such is also the case with blue crab predation on littorinid snails in a Florida salt marsh (Hamilton 1976). Perhaps this same gradient exists for soft-sediment communities. In the York River, all the major predators are restricted to water at least a few centimetres deep. Perhaps this limitation causes a discontinuity in the importance of predation between intertidal areas (where predators are infrequent) and subtidal areas (where predators are continually abundant during summer months).

Only at the extremely high population densities found in some exclosures did competitive exclusion appar-

TABLE 7. A comparison of densities ($\bar{x}$ per 0.005 m²) from replicates of exclosure cages, with and without dense concentrations of large *Mulinia lateralis* ($\bar{x}$ shell length = 13.4 mm). Data are from July 1974, when cages had been in place 2 mo

Parameters and taxa	With 76.0 *Mulinia* per core	With only 12.2 *Mulinia* per core
Total density	242.6	445.8
Number of species	17.0	21.6
Heteromastus filiformis	83.0	263.8
Streblospio benedicti	10.4	94.4
Glycinde solitaria	3.4	12.0
Spiochaetopterus oculatus	1.2	5.8
Scoloplos robustus	0.6	2.4
Acteon punctostriatus	1.2	6.4
Lyonsia hyalina	2.4	0.8
Mya arenaria	4.0	0
Tellina versicolor	0.2	1.8
Phoronis psammophila	2.2	6.6

TABLE 8. A comparison of infaunal densities in eelgrass, *Zostera marina*, beds with caged areas in the eelgrass (data mainly provided by R. J. Orth) and caged areas in bare sand from this study. Numbers from eelgrass are rarefied so that all data are reported as mean number per 0.005 m². All data are from 1974

	Mean density per 0.005 m²		
Parameter and taxa	Caged eelgrass	Uncaged eelgrass	Caged bare sand Jul-Sep-Nov mean
Total density	264.8	201.6	213.4
Number of species	20.1	19.0	17.7
Peloscolex gabriellae	41.4	41.1	53.0
Heteromastus filiformis	27.9	21.6	37.3
Streblospio benedicti	26.7	12.5	18.7
Spiochaetopterus oculatus	52.3	28.3	2.4
Nereis succinea	7.8	7.9	4.7
Polydora ligni	130.7	5.1	6.8
Glycinde solitaria	1.9	1.0	3.7

ently occur. For example, at a density of 140,000/m² in one exclosure, individuals of *Streblospio benedicti* were an average of only 3 mm apart and had almost totally overlapping feeding radii (the tentacular palps extend 10–20 mm along the sediment surface). In some exclosures, *Mulinia lateralis* were so dense that they could not all fit in a single layer (Figs. 10, 11), and apparently competed with one another for space as they grew (Fig. 9). In such great density, *Mulinia* apparently successfully competed with other species; densities of most other species except bivalves were much lower in exclosures with dense *Mulinia* than in exclosures with fewer *Mulinia* (Table 7). This exclusion of other species by *Mulinia* may have been due to (1) removal of settling larvae while filter feeding (predation) (Woodin 1976); (2) sediment instability caused by *Mulinia*'s active movements (amensalism) (Rhoads and Young 1970); or (3) occupying most of the available habitat space (competition). Such competitive success of the opportunistic *Mulinia* is contrary to the popularly held opinion that opportunistic species are poor competitors. Rather, it seems that they are poor avoiders of predation.

Some problems of interpretation

Effect of an empty cage.—It is difficult to distinguish the extent to which the increase of infaunal density and diversity in exclosures is caused by (1) exclusion of predators, (2) changes in currents and sediment stability, or (3) "trapping" of larvae. The exclusion of predators has been stressed above, but other factors may also be important.

The cages did affect sediment stability as shown by the increased silt-clay content and decreased movement of orange-painted sediment in the exclosures. However, some of this enhanced sediment stability may have been due to increased binding and stabilization of sediments by the dense populations of infaunal tube-building species (e.g., by *Streblospio benedicti*)

forming a "turf" (Buchanan 1963, Young and Rhoads 1971).

Orth (1977) has shown that eelgrass, *Zostera marina*, increases sediment stability, which is associated with an increase in infaunal density and species richness. Part of this increase in the infauna may be due to the partial exclusion of predators by the rhizome mat 1–2 cm below the sediment surface which would prevent digging by most predators. Infaunal density and species richness increased in eelgrass when predators were excluded; however, this increase was less than when predators were excluded from bare sand. Both eelgrass and exclosures in bare sand produced similar high-density, diverse infaunal communities (Table 8); both stabilize sediments and offer protection from predators.

Planktonic larvae may have preferentially set in cages in response to decreased current velocity, or to contact with the wire mesh, or to sediment changes. However, while cages may increase setting of larvae, their survival is not ensured—a predator would negate this effect. Results from the 2-sided control cage indicated that the main effect of the cage was the exclusion of predators; direct physical effects were minor.

Effect of a predator.—It is also difficult to determine the reasons for the decrease of infauna due to a predator: (1) predation on adults (implicitly stressed above), (2) predation on newly set larvae, (3) decreased sediment stability caused by the foraging activities of the predators, or (4) physical disruption of tubes and burrows.

The cage probably alters currents or sediment properties in such a way that induces planktonic larvae to set preferentially within the cage. However, the subsequent survival of these recently set juveniles is determined by the presence or absence of predators. The unanswered question is whether the cage increases sediment stability which in turn allows an increase of in-

fauna, or whether the cage excludes predators which allows an increase of infauna which stabilizes sediment. To better differentiate the biological and physical aspects, more careful analyses of sedimentary parameters and predators' feeding activities are necessary.

Effect of cage size.—Differences in the infauna in different-sized cages with crabs were probably due to the different crab densities rather than to different cage sizes. The size of cages was varied in order to vary crab densities, rather than directly varying the number of crabs in the standard size cage; otherwise cannibalism would have been a problem. Thus both the size of the cage and the area over which a crab could roam were different for each crab density. Therefore, part of the effect of the different crab densities may have been due to cage size. However, the results can be explained by mechanisms involving increased crab density, and empty cages of 2 different sizes were not different from one another for number of species, total density or individuals of most species (Figs. 3, 4).

Effect of cage mesh size.—Although cages excluded most large predators, many smaller individuals of many predatory species undoubtedly had free passage through the 12-mm mesh of the cages. Naqvi (1968) concluded that 6-mm mesh cages offered more protection from predators in Alligator Harbor, Florida, than 12-mm or 24-mm mesh cages. In the York River area I studied, small blue crabs of the new year class are very abundant throughout the summer (P. Haefner, *personal communication*). Young et al. (1976) postulated that smaller decapod crustaceans which could move in and out of cages through the mesh may be more important predators on the infauna in the Indian River, Florida, than the larger mobile predators studied here. My preliminary data from the Indian River show that *Callinectes sapidus*, xanthids, alpheids, penaeids, and palaemonids did increase in abundance in exclosures. However, in the area of the York River studied here, the larger individuals of blue crab, spot and hogchoker were effectively caged in or out, and these larger individuals of blue crabs and spot are apparently the major predators on the infauna.

IMPLICATIONS

Species populations in the community studied are not resource limited as has been found in other marine communities, both on hard substrates (Dayton 1971, Connell 1972) and in soft sediments (Woodin 1974, C. H. Peterson, *personal communication*). Predation pressures and physical disturbances are severe in this community and keep population levels far below the carrying capacity of the environment. Dayton and Hessler (1972) proposed a similar role for predation in the deep sea. At these lowered densities, competitive interactions, both inter- and intraspecific, are relatively unimportant. Physical factors, such as sediment instability (Aller and Dodge 1974, Orth 1977), changes in salinity and temperature (Boesch et al. 1976b), and high

turbidity, together with severe predation pressures stress the community. The community structure is not controlled by processes operating exclusively within the benthos; rather, this infaunal community is controlled by factors external to the infauna. In this community, the patterns of species occurrence and density are disproportionately affected by the activities of at least 2 species of high trophic status. The blue crab *C. sapidus* and the spot *L. xanthurus* together fit this definition of "foundation species" (Paine 1969, Dayton 1975).

A corollary of the conclusion that predators are important to the benthic community studied is that this community is important to the predators. Secondary productivity is probably very high with 2 or 3 generations per year for many species and an average biomass of 7 g/m² (wet weight) (Virnstein 1975). Large individuals of many species are cropped by predators and never grow to their maximum attainable size. For example, in exclosures *Mulinia lateralis*, *Lyonsia hyalina* and *Pectinaria gouldii* grew to a much larger size in only a few months than is ever found in natural sediments outside cages. These very rapid growth rates combined with absence of large individuals implies that, for many species, there is >1 generation per year. The annual turnover rate of the macrobenthos of Kiel Bight in the Baltic Sea is 1 to several times the mean biomass, most of which is consumed by commercially fished species (Arntz and Brunswig 1975).

A similar relationship probably exists in Chesapeake Bay, except that growth and production rates in Chesapeake Bay are greater than in the Baltic and other northern areas. Growth rates for bivalves in the Baltic (Muus 1973) are much slower than found in this study. For example, 2-yr-old *Mya arenaria* are only 28 mm long in the southern Baltic (Munch-Petersen 1973), 20 mm in the Bay of Fundy (Newcombe 1935), but 68 mm in Chesapeake Bay (J. Lucy, *personal communication*). Mature *Mulinia lateralis* (10–15 mm) are 1–2 yr old in Long Island Sound (Calabrese 1969); this size is attained in only 2 mo in Chesapeake Bay (Fig. 9A). Cephalic plate width (a standard measure of overall size) of *Pectinaria hyperborea* in St. Margaret's Bay, Nova Scotia, 1 yr after setting was 4 mm (Peer 1970), 3 mm for *Pectinaria californiensis* in Puget Sound (Nichols 1975), ≈5 mm for *Pectinaria gouldii* after 4 mo in Barnegat Bay, New Jersey (Busch and Loveland 1975), but >7 mm in Chesapeake Bay in 4 mo (this study). Although growth rates of these 3 species are not necessarily comparable, all attain a similar maximum size. Both Nichols (1975) and Peer (1970) reported an annual production to mean biomass ratio of 4.3 for *Pectinaria*. Turnover ratios would be greater in Chesapeake Bay due to faster growth and low population densities, thus providing a potentially larger food supply for bottom-feeding fishes and crabs.

Hayne and Ball (1956) found that, although the standing crop of bottom fauna in ponds decreased in the

presence of bottom-feeding fishes, the rate of production of the bottom fauna increased. They reported the average production of bottom fauna during a growing season to be ≈17× the standing crop, when fish were present. In the absence of fish, the production decreased to zero at a higher level of standing crop. Arntz (1971) also found that the production of benthic fauna in the Kiel Bight (Baltic Sea) was greater in areas of low standing crop. Thus, the heavily preyed-upon infauna of shallow sandy areas studied here may be more important in terms of crab and fish food production than the higher density, but less preyed-upon, infauna of grass beds. In grass beds, predators may prey more heavily on epifauna than infauna (Orth 1977, Young and Young 1977).

Because food and space are not limiting, resources are underutilized and a much greater biomass could be maintained. If protected from predators, much larger crops of infaunal bivalves could be reared as food for man, as is done for epifaunal oysters.

In summary, such shallow water infaunal communities are highly stressed; species populations are not resource limited, but rather are predator controlled, and these communities are an important food source for predatory species important to man.

The degree of importance attributed to predators as determined by this study could not have been determined by other than experimental methods. Any merely correlative, nonmanipulative studies could not have determined the effects of increasing or decreasing predation pressure; proper controls are simply not available.

LITERATURE CITED

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

Arntz, W. E. 1971. Biomasse und Produktion des Macrobenthos in den tieferen Teilen der Kieler Bucht im Jahr 1968. Kiel. Meeresforsch. 27:36–72.

Arntz, W. E., and D. Brunswig. 1975. An approach to estimating the production of macrobenthos and demersal fish in a western Baltic *Abra alba* community. Merentutkimuslaitoksen Julk. Havsforskningsinst. Skr. 239:195–205.

Blegvad, H. 1928. Quantitative investigations of bottom invertebrates in the Limfjord 1910–1927 with special reference to the plaice food. Rep. Danish Biol. Stn. 34:33–52.

Boesch, D. F. 1971. Distribution and structure of benthic communities in a gradient estuary. Ph.D. thesis, College of William and Mary, Williamsburg, Virginia. 120 p.

——. 1973. Classification and community structure of macrobenthos in the Hampton Roads area, Virginia. Mar. Biol. 21:226–244.

——. 1974. Diversity, stability and response to human disturbance in estuarine ecosystems, p. 109–114. *In* Proc. First Int. Congr. Ecol., The Hague. Center for Agricultural Publishing and Documentation, Wageningen.

——. 1977. A new look at the zonation of benthos along the estuarine gradient, p. 245–266. *In* B. C. Coull [ed.] Ecology of marine benthos. Univ. South Carolina Press, Columbia.

Boesch, D. F., R. J. Diaz, and R. W. Virnstein. 1976a. Effects of Tropical Storm Agnes on soft-bottom macrobenthic communities of the James and York estuaries and the lower Chesapeake Bay. Chesapeake Sci. 17:246–259.

Boesch, D. F., M. L. Wass, and R. W. Virnstein. 1976b. The dynamics of estuarine benthic communities, p. 177–196. *In* M. L. Wiley [ed.] Estuarine processes, Vol. 1. Uses, stresses, and adaptation to the estuary. Academic Press, New York.

Brooks, J. L., and S. I. Dodson. 1965. Predation, body size and composition of plankton. Science 150:28–35.

Buchanan, J. B. 1963. The bottom fauna communities and their sediment relationships off the coast of Northumberland. Oikos 14:154–175.

Busch, D. A., and R. E. Loveland. 1975. Tube-worm-sediment relationships of *Pectinaria gouldii* (Polychaeta: Pectinariidae) from Barnegat Bay, New Jersey, USA. Mar. Biol. 33:255–264.

Calabrese, A. 1969. The early life history and larval ecology of the coot clam, *Mulinia lateralis* (Say) (Mactridae: Pelecypoda). Ph.D. thesis, Univ. Connecticut, Storrs. 101 p.

——. 1970. Reproductive cycle of the coot clam, *Mulinia lateralis* (Say), in Long Island Sound. Veliger 12:265–269.

Castagna, R. M. 1955. A study of the hogchoker *Trinectes maculatus* (Bloch and Schneider) in the Walkulla River, Florida. M. S. thesis, Florida State Univ., Tallahassee. 23 p.

Chanley, P., and J. D. Andrews. 1971. Aids for identification of bivalve larvae of Virginia. Malacologia 11:45–119.

Clifford, H. T., and W. Stephenson. 1975. An introduction to numerical classification. Academic Press, New York. 229 p.

Connell, J. H. 1961a. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology 42:783–794.

——. 1961b. Effect of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. Ecol. Monogr. 31:61–104.

——. 1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. Ecol. Monogr. 40:49–78.

——. 1972. Community interactions on marine rocky intertidal shores. Annu. Rev. Ecol. Syst. 3:169–192.

——. 1975. Some mechanisms producing structure in natural communities, p. 460–490. *In* M. L. Cody and J. M. Diamond [eds.] Ecology and evolution of communities. Belknap Press, Cambridge, Mass.

Copeland, B. J. 1970. Estuarine classification and responses to disturbances. Trans. Am. Fish. Soc. 99:826–835.

Cramer, N. F., and R. M. May. 1972. Interspecific competition, predation and species diversity: A comment. J. Theor. Biol. 34:289–293.

Dayton, P. K. 1971. Competition, disturbance and community organization: The provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41:351–389.

——. 1975. Experimental evaluation of ecological dominance in a rocky intertidal community. Ecol. Monogr. 45:137–159.

Dayton, P. K., and R. R. Hessler. 1972. The role of disturbance in maintaining diversity in the deep sea. Deep-Sea Res. 19:199–208.

Dovel, W. L., J. A. Mihursky, and A. J. McErlean. 1969. Life-history aspects of the hogchoker, Trinectes maculatus, in the Patuxent River estuary, Maryland. Chesapeake Sci. 10:104–119.

Fager, E. W. 1957. Determination and analysis of recurrent groups. Ecology 38:586–595.

Fenchel, T. 1975. Factors determining the distribution patterns of mud snails (Hydrobiidae). Oecologia 20:1–7.

Folk, R. L. 1968. Petrology of sedimentary rocks. Hemphill's, Austin, Texas. 170 p.

Gause, G. F. 1934. The struggle for existence. Williams and Wilkins, Baltimore. 163 p.

Grassle, J. F., and J. P. Grassle. 1974. Opportunistic life histories and genetic systems in marine benthic polychaetes. J. Mar. Res. 32:253–284.

Hamilton, P. V. 1976. Predation on Littorina irrorata (Mollusca: Gastropoda) by Callinectes sapidus (Portunidae). Bull. Mar. Sci. 26:403–409.

Hayne, D. W., and R. C. Ball. 1956. Benthic productivity as influenced by fish predation. Limnol. Oceanogr. 1:162–175.

Hildebrand, S. F., and W. C. Schroeder. 1928. The fishes of Chesapeake Bay. Bull. U. S. Bur. Fish. No. 53 Pt. 1 (Reprinted 1972, for Smithsonian Inst. by T. F. H. Publ., Inc., Neptune, New Jersey). 388 p.

Holland, A. F., R. G. Zingmark, and J. M. Dean. 1974. Quantitative evidence concerning the stabilization of sediments by marine benthic diatoms. Mar. Biol. 27:191–196.

Horn, H. S., and R. H. MacArthur. 1972. Competition among fugitive species in a harlequin environment. Ecology 53:749–752.

Huggett, R. J., R. W. Virnstein, and D. F. Boesch. 1975. A chemical and biological survey of the lower Potomac River in the vicinity of Piney Point, Maryland. Virginia Inst. Mar. Sci. Tech. Doc. No. 425. Final Report to Steuart Petroleum Company. 16 p.

Hutchinson, G. E. 1961. The paradox of the plankton. Am. Nat. 95:137–146.

Illowsky, J. E., and J. Colvocoresses. 1975. Fish and major decapods, Section III, p. 336–462. In Yorktown Power Stn. Ecol. Study. Spec. Sci. Rep. No. 76. Virginia Inst. Mar. Sci., Gloucester Point, Virginia.

Levin, S. A., and R. T. Paine. 1974. Disturbance, patch formation and community structure. Proc. Natl. Acad. Sci. 71:2744–2747.

Levinton, J. S. 1970. The paleoecological significance of opportunistic species. Lethaia 3:69–78.

Lie, U. 1974. Distribution and structure of benthic assemblages in Puget Sound, Washington, USA. Mar. Biol. 26:203–223.

Menge, B. A. 1976. Organization of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. Ecol. Monogr. 46:355–393.

Menge, B. A., and J. P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition and temporal heterogeneity. Am. Nat. 110:351–369.

Munch-Petersen, S. 1973. An investigation of a population of the soft clam (Mya arenaria L.) in a Danish estuary. Medd. Danmarks Fisk. Havunders. N. S. 7(3):47–73.

Muus, K. 1973. Setting, growth and mortality of young bivalves in the Oresund. Ophelia 12:79–116.

Naqvi, S. M. Z. 1968. Effects of predation on infaunal invertebrates of Alligator Harbor, Florida. Gulf Res. Rep. 2:313–321.

Newcombe, C. I. 1935. Growth of Mya arenaria L. in the Bay of Fundy region. Canadian J. Res. 13: 97–137.

Nichols, F. H. 1975. Dynamics and energetics of three deposit-feeding benthic invertebrate populations in Puget Sound, Washington. Ecol. Monogr. 45:57–82.

Orth, R. J. 1975. Destruction of eelgrass, Zostera marina, by the cownose ray, Rhinoptera bonasus, in the Chesapeake Bay. Chesapeake Sci. 16:205–208.

———. 1977. The importance of sediment stability in seagrass communities, p. 281–300. In B. C. Coull [ed.] Ecology of marine benthos. Univ. South Carolina Press, Columbia.

Pacheco, A. L. 1962a. Age and growth of spot in lower Chesapeake Bay, with notes on distribution and abundance of juveniles in the lower York River system. Chesapeake Sci. 3:18–28.

———. 1962b. Movements of spot, Leiostomus xanthurus, in the lower Chesapeake Bay. Chesapeake Sci. 3:256–257.

Paine, R. T. 1966. Food web complexity and species diversity. Am. Nat. 100:65–75.

———. 1969. A note on trophic complexity and community stability. Am. Nat. 103:91–93.

———. 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia 15:93–120.

Peer, D. L. 1970. Relation between biomass, productivity, and loss to predators in a population of a marine benthic polychaete Pectinaria hyperborea. J. Fish. Res. Board Canada 27:2143–2153.

Peterson, C. H. 1975. Space utilization and community organization in two New Jersey intertidal systems. Bull. Ecol. Soc. Am. 56(2):47.

Porter, J. 1972. Predation by Acanthaster and its effect on coral species diversity. Am. Nat. 106:487–492.

Rhoads, D. C., and D. K. Young. 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. J. Mar. Res. 28:150–178.

Ronan, T. E., Jr. 1975. Structural and paleoecological aspects of a modern marine soft-sediment community: An experimental field study. Ph.D. thesis, Univ. California, Davis. 220 p.

Roughgarden, J., and M. Feldman. 1975. Species packing and predation pressure. Ecology 56:489–492.

Sammarco, P. W., J. S. Levinton, and J. C. Ogden. 1974. Grazing and control of coral reef community structure by Diadema antillarum Philippi (Echinodermata: Echinoidea): A preliminary study. J. Mar. Res. 32:47–53.

Sanders, H. L. 1960. Benthic studies in Buzzards Bay III. The structure of the soft-bottom community. Limnol. Oceanogr. 5:138–153.

———. 1969. Benthic marine diversity and the stability-time hypothesis. Brookhaven Symp. Biol. 22:71–81.

Slobodkin, L. B. 1961. Growth and regulation of animal populations. Holt, Reinhart and Winston, New York. 184 p.

Slobodkin, L. B., and H. L. Sanders. 1969. On the contribution of environmental predictability to species diversity. Brookhaven Symp. Biol. 22:82–95.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry. W. H. Freeman and Co., San Francisco. 776 p.

Stickney, R. R., G. L. Taylor, and D. B. White. 1975. Food habits of five species of young southeastern United States estuarine Sciaenidae. Chesapeake Sci. 16:104–114.

Sutherland, J. P. 1974. Multiple stable points in natural communities. Am. Nat. 108:859–873.

Thorson, G. 1957. Bottom communities. In J. W. Hedgpeth [ed.] Treatise on marine ecology and paleoecology. Vol. 1. Ecology. Geol. Soc. Am. Mem. 67:461–534.

Virnstein, R. W. 1975. Benthic macroinvertebrates, Section II, p. 290–335. In Yorktown Power Stn. Ecol. Study. Spec. Sci. Rep. No. 76. Virginia Inst. Mar. Sci., Gloucester Point, Virginia.

Wass, M. L. et al. 1972. A checklist of the biota of lower Chesapeake Bay. Virginia Inst. Mar. Sci. Spec. Sci. Rep. No. 65. 290 p.

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

———. 1976. Adult-larval interactions in dense infaunal assemblages: Patterns of abundance. J. Mar. Res. **34**:25–41.

Young, D. K., and D. C. Rhoads. 1971. Animal-sediment relations in Cape Cod Bay, Massachusetts I. A transect study. Mar. Biol. **11**:242–254.

Young, D. K., M. A. Buzas, and M. W. Young. 1976. Species densities of macrobenthos associated with seagrass: A field experimental study of predation. J. Mar. Res. **34**:577–592.

Young, D. K., and M. W. Young. 1977. Community structure of the benthos associated with seagrass of the Indian River estuary, Florida, p. 359–382. *In* B. C. Coull [ed.] Ecology of marine benthos. Univ. South Carolina Press, Columbia.