Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay

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ABSTRACT: Abundances and size-frequency distributions of common epibenthic fish and crustaceans were compared among 3 depth zones (1–35, 35–70, 71–95 cm) of the Rhode River, a subestuary of Chesapeake Bay, USA. In the absence of submerged aquatic vegetation (SAV), inter- and intraspecific size segregation occurred by depth from May to October, 1989–1992. Small species (*Palaemonetes pugio, Crangon septemspinosa, Fundulus heteroclitus, F. majalis, Rhithropanopeus harrisii, Apeltes quadracus, Gobiosoma bosci*) were most abundant at water depths < 70 cm. Furthermore, the proportion of small individuals decreased significantly with depth for 7 of 8 species, with *C. septemspinosa* being the exception, exhibiting no size change with increasing depth. These distributional patterns were related to depth-dependent predation risk. Large species (*Callinectes sapidus, Leiostomus xanthurus*, and *Micropogonias undulatus*), known predators of some of the small species, were often most abundant in deep water (> 70 cm). In field experiments, mortality of tethered *P. pugio* (30 to 35 mm), small *F. heteroclitus* (40 to 50 mm), and small *C. sapidus* (30 to 70 mm) increased significantly with depth. We hypothesize that predation risk was size-dependent, creating the observed intra- and interspecific size differences among depth zones. For *C. septemspinosa*, burial may modify this size-dependency and create the unusual absence of intraspecific size increase with depth. Historically, *P. pugio* and *Fundulus* spp. (and other small species) were not restricted to shallow (< 70 cm) waters and were abundant in deeper SAV beds, which provided a structural refuge from predators. Since the recent demise of SAV in Chesapeake Bay, our results indicate many small species have shifted their distributions and now utilize primarily shallow water as an alternate refuge habitat.

INTRODUCTION

Non-vegetated sediments often dominate the bottom area of estuaries, and the extent of non-vegetated substrate has increased historically in many estuaries, especially during periods of rapid decline in the abundance of submerged aquatic vegetation (SAV) (e.g. Pérès & Picard 1975, Rasmussen 1977, Orth & Moore 1984, Muehlstein 1989, Shepherd et al. 1989). Despite a frequent prominence of non-vegetated sediments in estuaries, the importance of submerged aquatic vegetation to the structure and dynamics of animal communities has been emphasized (e.g. Orth et al. 1984 and references therein). In particular, the value of SAV as a refuge from predation has probably received most attention in both estuarine (e.g. Heck & Thoman 1981,

Peterson 1982, Summerson & Peterson 1984, Wilson et al. 1987, Rozas & Odum 1988, Bell & Pollard 1989) and freshwater systems (e.g. Werner et al. 1983, Holomuzki 1986, Mittelbach 1986, Foster et al. 1988, Savino & Stein 1989) (but see also Kemp et al. 1984 and Orth et al. 1984 for discussion of other roles of SAV). However, the importance of other (alternate) refuge habitats in estuaries is poorly resolved when SAV is absent or occurs in low abundance.

For Chesapeake Bay (USA), SAV has historically undergone great fluctuations in abundance and species composition, and is now scarce relative to the recent past (e.g. Bayley et al. 1978, Stevenson & Confer 1978, Orth & Moore 1984). Although SAV persists in large but diminished beds in the lower Bay, submerged vegetation is now nearly absent through-

out most of the upper Chesapeake Bay. An extensive literature documents the utilization of SAV by, and its importance to, the fauna of Chesapeake Bay (e.g. see review by Orth et al. 1984; also Heck & Thoman 1984, Kemp et al. 1984, Rozas & Odum 1987a, Sogard & Abele 1991). With the exception of documented declines in abundance of waterfowl and scallop populations (Stevenson & Confer 1978, Perry & Uhler 1988), data are not available which evaluate potential changes in abundance, habitat utilization, diet, size structure, and dynamics of animal populations due to declines in SAV; rather, the literature implies erroneously that the present-day ecology of Chesapeake Bay fauna is strongly associated with SAV.

This paper examines the distribution of highly mobile epibenthic fish and crustacean species, associated historically with SAV, in a non-vegetated subestuary of Chesapeake Bay. Specifically, we examined utilization of shallow water as a refuge from predators in the absence of SAV. Our goal was to characterize the composition and distribution of species in shallow water, and begin to evaluate the refuge value of shallow water.

Our study included the entire epibenthic community, and we focused intensively on mummichogs Fundulus heteroclitus, grass shrimp Palaemonetes pugio, and juvenile blue crabs Callinectes sapidus as model species likely to utilize shallow water as refuge. These 3 species are abundant in Chesapeake Bay (Heck & Orth 1980, Orth & Heck 1980, Heck & Thoman 1984, Everett & Ruiz 1993), and other estuaries along the Atlantic coast of North America (Nixon & Oviatt 1973, Welsh 1975, Valiela et al. 1977, Weinstein 1979, Roundtree & Abele 1992), where they are functionally important in estuarine food webs and community dynamics (Bell & Coull 1978, Virnstein 1979, Kneib 1985, 1988, Posey & Hines 1991, Eggleston et al. 1992). Besides their frequent association with SAV (e.g. Heck & Orth 1980, Orth & Heck 1980, Heck & Thoman 1984, Orth & van Montfrans 1987), all 3 species are often found in shallow (< 1 m) water and are known to utilize intertidal habitats with emergent vegetation (Kneib 1984a, b, Rozas & Hackney 1984, Rozas & Odum 1987c, Fitz & Wiegert 1991). Use of shallow water is thought to reduce their risk of predation (Boesch & Turner 1984, Kneib 1984b, Rozas & Hackney 1984, Rozas & Odum 1987b, McIvor & Odum 1988), providing a refuge just as SAV does for each of these species (Coen et al. 1981, Heck & Thoman 1981, Wilson et al. 1987, Rozas & Odum 1988). In laboratory experiments, Posey & Hines (1991) have further shown that grass shrimp prefer shallow water in the presence of fish predators, supporting the common belief that shallow water provides a refuge from predation for mobile epibenthic fauna. Our field data examine explicitly this relationship in

the absence of SAV by testing 2 general hypotheses: (1) habitat utilization is restricted to shallow rather than deeper waters in the presence of predators; and (2) the risk of predation increases with increasing water depth.

METHODS

Study sites. All field work was done at 2 study sites in the Rhode River (Fig. 1), a shallow subestuary of Chesapeake Bay with an average depth of 2 m and maximum depth of 4 m (Han 1974). Water temperature fluctuates seasonally between 2 and 30 °C, and salinity varies from 3 to 17 ppt (Hines et al. 1987a, pers. obs.); tidal amplitude is ca 0.5 m (Hines et al. 1985). Canning House Bay (CHB), the site of most work, is dominated by sand beaches with very little fringing marsh vegetation. Big Island (BI) has a shoreline with nearly continuous cover of Spartina patens. Although SAV occurred historically as late as the mid-1970s in the Rhode River (Southwick & Pine 1975), the subtidal substrate at both sites and the entire subestuary is now composed almost exclusively of non-vegetated fine sediments. While SAV was absent at CHB for the duration of this study (1989–1992), a few small patches (< 1 m²) of Ruppia maritima were found at BI in shallow water (< 50 cm depth) during 1990; SAV was absent at BI in 1991 and 1992. Drift algae (Ulva sp. and Enteromorpha sp.) were occasionally present at both sites during
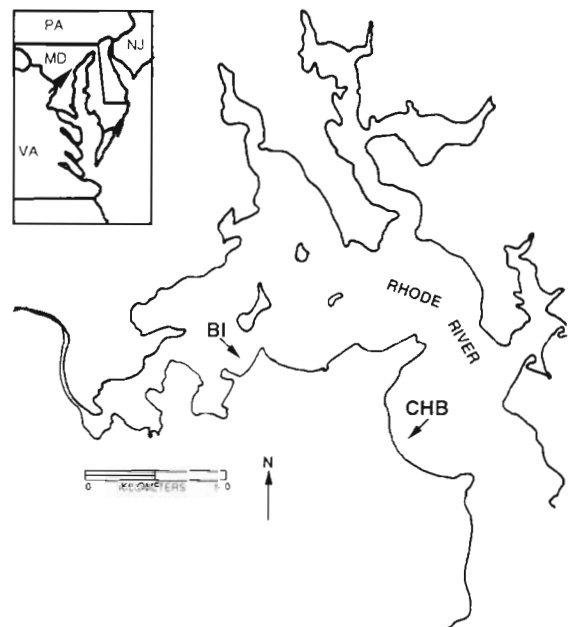

Fig. 1. Rhode River subestuary in Chesapeake Bay, Maryland, USA. Arrows indicate locations of Big Island (BI) and Canning House Bay (CHB) sites

summer months, and small amounts of the filamentous alga *Vaucheria* sp. were present between January and April.

Season and time-of-day. Field samples and experiments were restricted both to the warm season (April to October) and to daylight hours, when the dominant, mainly visual, predators are active in the subestuary (Hines et al. 1987b, 1990). Thus, all work coincided with the time when predation and its effects on mobile species was likely to be greatest.

Cylinder sampling methods. Densities of epifaunal species were measured in water up to 1 m deep using a rigid, open-ended cylinder. The sheet-metal cylinder was suspended above water on a boom, extending over the bow of a boat, and was dropped remotely onto a sampling site by pulling a release cord. The cylinder trapped pelagic and benthic species as it fell quickly through the water column and became embedded in the bottom sediments, while still extending above the water surface (e.g. Zimmerman et al. 1984). Water within the deployed cylinder was completely pumped out, using a suction dredge with a 1 mm mesh bag to retain water-borne animals (e.g. Orth & van Montfrans 1987). Animals remaining in the cylinder were removed from the sediment surface with dipnets, and the surface sediments were probed thoroughly for buried crabs. For each sample, all organisms were identified to species and counted, and a subsample (n > 20, when available) was measured for size.

Influence of cylinder size on density estimates. To select the cylinder size used, we compared the effect of 4 cylinder sizes (0.292, 0.659, 1.823, and 4.674 m^2) on estimates of animal density. Samples were taken (as above) with alternating cylinder sizes within a narrow depth range (43 to 65 cm) at CHB, on the same date (10 July 1990). With the initial data, the number of samples necessary to allow a test of independence among treatments (minimum expected value of 5 ind. treatment^{-1}; Sokal & Rohlf 1981) was estimated for blue crabs and required more small than large cylinder samples. We adjusted sample sizes to test for cylinder-size bias in blue crabs, because our goal was to test whether such highly mobile species were able to escape cylinders below a certain size, due to the increased edge:area ratio with decreasing size. Data for all other species were also collected for comparison.

Distribution patterns at Canning House Bay. Cylinder samples were taken to examine spatial and temporal (seasonal, annual) variation in abundance of common epibenthic species at CHB. Sampling compared abundances of epibenthic fish and crustaceans as a function of water depth within shallow waters (< 1 m depth and within 30 m of shore), using replicate cylinder samples (1.82 m^2), in each of 4 years: 1989 (July–August, October); 1990 (April, May, July,

August, October); 1991 (June, July, August); and 1992 (July, August). Samples were taken from depth zones (or strata), parallel to a shoreline approximately 1 km long. Sampling occurred haphazardly at all tidal levels, except that unusually high tides were avoided. Water depth was measured for each sample and used to define depth zones 1 to 3 (water depths of 1–35, 36–70, and 71–95 cm respectively). All samples for the 2 deepest zones were taken with a boat as described above. Samples in the shallow zone, within 2 m of shore, were often taken by manually tossing the cylinder from shore. On all dates, samples were taken in an alternating manner among depth zones.

The number of sample dates for each year, and the sample size within each depth zone by date, was variable. For 1990, samples were taken on 5 separate dates, over a 6 mo period, to provide seasonal information. Throughout our study, 4 to 12 replicate samples were taken for each date and zone, except in April 1990, when few animals were present and < 4 samples were taken for each zone.

Using the data from cylinder samples, relative abundances of common species were compared among depth zones. The frequent lack of homogenous variances, and absence of any variance at all for some dates and zones, violated assumptions necessary for comparison of densities by depth zone and time using parametric statistics (Sokal & Rohlf 1981) Instead, the proportional abundances of species among the 3 depth zones were calculated for each sample date and compared using Friedman ANOVAs and multiple comparisons (Siegel & Castellan 1988). Only dates for which a species was present were included in the analyses.

To portray temporal variation in abundance of common species, density (± SE) in the zone of highest abundance and unweighted means across all 3 zones are shown for each sample date. We performed no formal comparisons of abundance by time (season or year), or time × depth, because the data did not satisfy necessary assumptions for parametric statistics (as above).

Size distributions (all 3 depth zones combined) are presented for common epibenthic species, and, for many of these species, size composition was compared as a function of depth. For these purposes, data from all sampling dates were pooled, and each population was divided into 2 size classes. Size classes were chosen to separate young-of-the-year from older individuals or immature from sexually mature individuals based upon data from Chesapeake Bay (Schwartz 1965, Haefner 1976, Williams 1984, Hines et al. 1990, Ruiz & Hines unpubl. data). For species that were relatively rare in the 2 deepest zones (*Palaemonetes pugio, Crangon septemspinosa, Fundulus heteroclitus* and *F. majalis*), the shallow zone was subdivided into 2 equal

subzones (1–18, 19–35 cm) to provide better resolution in comparing sizes by depth. In addition, for 6 species, the 2 deepest zones were combined to provide an adequate sample size for statistical comparisons among zones. All distributions were compared using χ^2 analyses for each species by depth.

Distribution patterns at Big Island. Cylinder samples (1.82 m²) were also taken at BI to examine the generality of abundance patterns at CHB. In August 1990, replicate samples (n > 5) were taken from each of 3 depth zones (1–35, 36–70, and 71–95 cm) in an identical fashion to those at CHB. During sampling, small patches of *Ruppia maritima* were discovered and sampled in the shallow and mid depth zones (n = 3 for each), allowing comparison with adjacent non-vegetated substrate. For common species, abundances were compared among depth zones (non-vegetated areas) using χ^2 tests. The overall effect of vegetation on abundance was compared with a sign test, and the effect of depth and vegetation was compared for grass shrimp abundance using a 2-way ANOVA and *t*-tests.

Abundance of large predators. An otter trawl (3 m wide mouth, 5 cm mesh net body, 7 mm mesh cod end, and tickler chain) was used to estimate abundance of large fish and crustaceans at the CHB site, providing a measure that is independent of the cylinder samples and more likely to include rare species (because of an increase in area sampled relative to cylinder samples). Replicate (2 to 6) trawl samples were taken approximately monthly, within a week of cylinder sampling dates for 1990 and 1991. Trawl samples for each monthly period always included 2 sites adjacent to the area used for cylinder sampling; replicate samples were taken from these sites on 1 (May and November 1990) or 3 (all other dates) consecutive days. The trawl samples, taken perpendicular to shore, included a depth range from 0 to ca 100 cm. The trawl net was positioned on shore, to begin fishing immediately, and hauled 32 m offshore. The trawls sampled an approximate area of 96 m², but the exact area and depth range varied among trawls according to tidal conditions at the time of sampling. For each trawl, the catch was identified to species and counted, and a subsample (n = 20 when available) was measured to the nearest mm.

Risk of predation. We used tethering to compare the relative risks of predation among depth zones for grass shrimp, mummichogs, and blue crabs at CHB. This technique has been a valuable experimental approach to assess predation pressure in the field for crabs, lobsters, fish, and snails (e.g. Heck & Thoman 1981, Watanabe 1984, McIvor & Odum 1988, Rozas & Odum 1988, Wilson et al. 1987). While tethering can significantly alter animal behavior and absolute rates of predation (e.g. Barshaw & Able 1990b, Smith 1990), it allows comparison of relative rates among experimental sites by controlling presumably for the effects of tethering.

In June 1991, tethered grass shrimp and mummichogs were placed in all 3 depth zones at CHB. Animals were collected the day of experiments and brought into the laboratory to attach tethers. For grass shrimp, monofilament line (0.45 kg test, 0.08 mm diameter) was tied around the abdomen, anterior to the first pleopods; this halter was then tied to a leader of 2.72 kg test monofilament. For mummichogs, a needle with attached nylon suture (0.017 mm diameter) was pushed through the epidermis and connective tissue just anterior to the dorsal fin; after removing the needle, the thread was tied into a loop that ran through the fish. Each tethered grass shrimp and mummichogs was tied individually (on a 20 cm line) to the end of a 50 cm steel rod buried horizontally in the sediment.

We used blue crabs in a similar tether experiment, including all 3 depth zones, at CHB in August 1989. A loop of monofilament (9.07 kg test) was tied around the crabs' antero-lateral spines to form a halter, which was tied to a coated steel leader (4.54 kg test; e.g. Smith 1990). The blue crabs were tethered individually (by a 0.75 to 1.00 m line) to a steel spike pushed vertically beneath the sediment.

To control for differences in predation risk due to size, only a narrow size range was used in experiments for shrimp (30 to 35 mm), mummichogs (40 to 50 mm), and blue crabs (30 to 70 mm). Shrimp and blue crabs were further restricted to intermolt individuals, to reduce any variation in behavior and predation risk due to molt stage.

For each species, tether experiments were run on multiple days, and within a period of 3 to 4 d, with all depth zones represented on each day. Within a depth zone, distance between tethered animals (2 m) prevented interactions among individuals. Based upon initial results, experiments with shrimp were run for 30 min, those with mummichogs were run for 90 min, and blue crab tethering experiments lasted 24 h. All individuals were scored as either live or eaten, based upon presence or absence respectively.

Our laboratory observations indicated that tethered animals (controls) did not escape their tethers and maintained apparently normal behavior, surviving the experimental period in the absence of predation. Despite prey ability to move quickly and perform escape behaviors within the confines of a tether, mortality rates of tethered animals were consistently higher than untethered animals when exposed to several predator species in the laboratory (Hines & Ruiz unpubl. data). Not surprisingly, predator species differed significantly in their consumption rates of both tethered and untethered prey in these preliminary experi-

Table 1. Fish and crustacean species caught in cylinder and trawl samples at CHB. Animals are grouped by relative abundance (see text for explanation). Means (± SE) of each species are shown for trawl samples (n = 52); –: species not sampled quantatitively by trawls, due to small size of individual animals. For cylinder samples (n = 243), abundance is shown as the mean (± SE) of unweighted means for all 3 depth zones on each sample date (n = 13)

Sample type:	Cylinder Mean abundance (SE)	Trawl Mean abundance (SE)
Common species		
Anchoa mitchelli bay anchovy	1.671 (0.772)	0.173 (0.071)
Apeltes quadracus four-spine stickleback	1.297 (0.881)	0.462 (0.222)
Callinectes sapidus blue crab	0.396 (0.057)	7.154 (0.866)
Crangon septemspinosa sand shrimp	4.325 (2.228)	– –
Fundulus heteroclitus mummichog	0.331 (0.101)	1.981 (0.605)
Fundulus majalis banded killifish	0.248 (0.086)	0.885 (0.270)
Gobiesox strumosus skilletfish	0.125 (0.077)	0.000 (0.000)
Gobisoma bosci naked goby	0.181 (0.084)	0.019 (0.019)
Leiostomus xanthurus spot	0.429 (0.341)	12.038 (4.909)
Menidia menidia Atlantic silverside	1.601 (0.396)	0.423 (0.251)
Micropogonias undulatus Atlantic croaker	0.020 (0.013)	1.115 (0.330)
Palaemonetes pugio grass shrimp	3.840 (1.350)	– –
Rhithropanopeus harrisii mudcrab	0.447 (0.203)	– –
Rare species		
Anguilla rostrata American eel	0.038 (0.023)	0.000 (0.000)
Brevoortia tyrannus Atlantic menhadden	0.004 (0.004)	0.308 (0.308)
Chasmodes bosquianus striped blenny	0.000 (0.000)	0.000 (0.000)
Cyprinodon variegatus sheepshead minnow	0.006 (0.004)	0.038 (0.038)
Limulus polyphemus horseshoe crab	0.020 (0.013)	0.038 (0.038)
Lucania parva rainwater killifish	0.004 (0.004)	0.000 (0.000)
Microgobias thalassinus green goby	0.030 (0.024)	0.000 (0.000)
Morone saxatilis striped bass	0.000 (0.000)	0.000 (0.000)
Paralichthys dentatus summer flounder	0.005 (0.005)	0.019 (0.019)
Pseudopleuronectes americanus winter flounder	0.000 (0.000)	0.038 (0.027)
Sygnathus fuscus northern pipefish	0.106 (0.033)	0.019 (0.019)
Synodus foetens inshore lizardfish	0.005 (0.005)	0.000 (0.000)
Trinectes maculatus hogchocker	0.015 (0.010)	0.154 (0.004)

ments. Thus, experimental results must be interpreted cautiously, because tethering may differentially affect vulnerability to various predators, which could change among depth zones.

RESULTS

Cylinder and trawl samples in the nearshore waters of the Rhode River subestuary contained 26 species, which we categorized into 2 groups: 13 common species and 13 rare species (Table 1). The distinction between common and rare species depended on whether mean abundance for any depth zone was greater or less than 1.0 ind. cylinder^{-1} on any sampling date. With the exception of Atlantic croaker, which exhibits extreme temporal variation in abundance and can be very abundant (below; see also Hines 1990), a similar classification would result from using total mean abundance across all dates and depths (Table 1). For both CHB and BI, distributional patterns were examined in detail for only common species, because rare species did not provide adequate data for further analysis.

Influence of cylinder size on density estimates

Cylinder size had a significant effect on density estimates for the four-spine stickleback *Apeltes quadracus* ($\chi^2 = 56.95$, df = 2, p < 0.001) and, when data for the 2 smallest cylinders were pooled, the blue crab *Callinectes sapidus* ($\chi^2 = 5.69$, df = 1, p < 0.05; Fig. 2). For both species, density increased 2- or 3-fold from the 2 smallest cylinders to the second largest cylinder (1.82 m^2), with no further increase when using the largest cylinder. Although other species were captured in these cylinder samples, abundances were inadequate (i.e. lacked an expected value of ≥ 5 cell^{-1} necessary for chi-square analysis) to test for significant differences among treatments.

Based upon these comparisons, the second largest cylinder (1.82 m^2) was used as a standard sampling
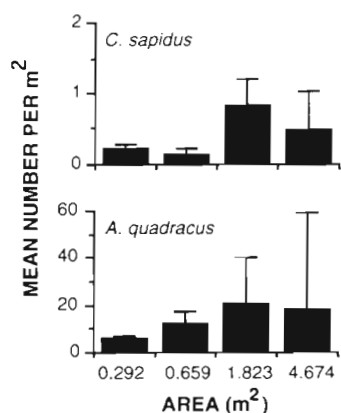
Fig. 2. *Callinectes sapidus* and *Apeltes quadracus*. Effect of cylinder size on density estimates at CHB. Density estimates (mean ± SE) are shown for samples taken with each of 4 different cylinder sizes (area = 0.292, 0.659, 1.823, 4.674 m²); no. of samples for each cylinder size are 16, 11, 8 and 8 respectively

unit. The 2 smallest cylinders underestimated abundance of highly mobile species, and use of the largest cylinder did not increase density estimates beyond those measured with the 1.82 m² cylinder.

Distribution patterns at Canning House Bay

Abundance

The relative abundance for 9 of the 13 common species differed significantly among depth zones in the nearshore shallows (Fig. 3, Table 2). The results of multiple comparison tests were used to classify species according to 3 patterns of depth zonation. Shallow zone species, which had highest relative abundances in the shallow zone and significantly lower abundances in the mid and deep zones, included *Palaemonetes pugio*, *Crangon septemspinosa*, *Fun-*
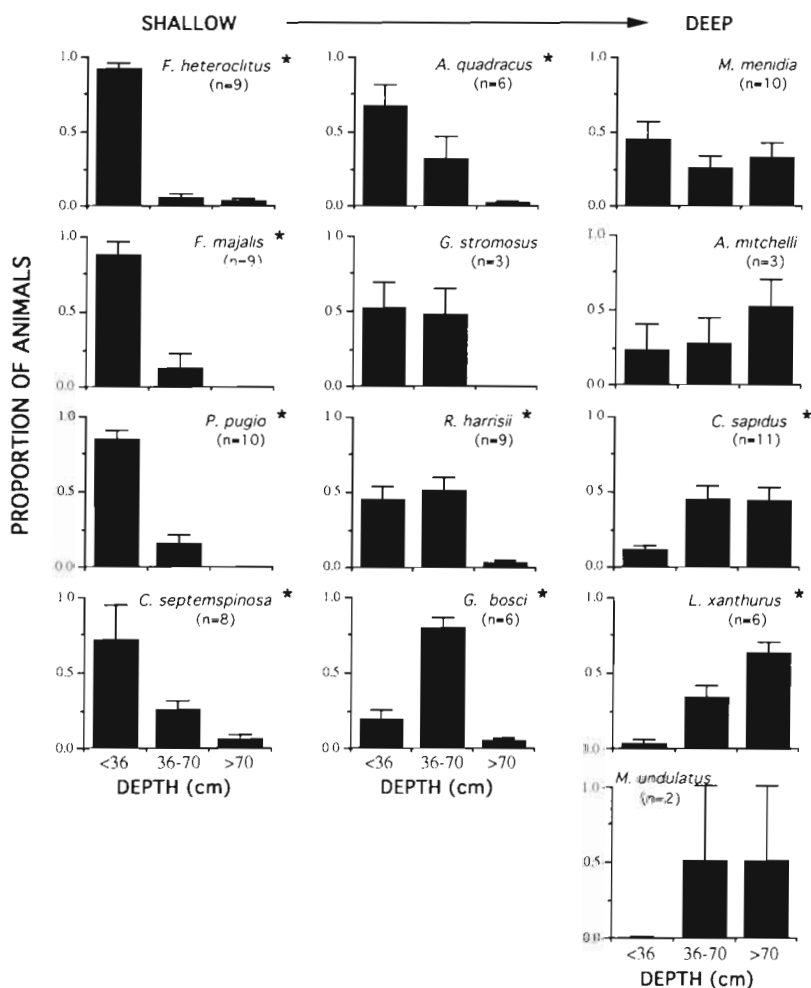

Fig. 3. Comparison of proportional abundance among 3 depth zones for common species (see Table 1) at CHB. Shown for each species is the proportional abundance (mean ± SE) among the 3 zones; data include only those sample periods (*n*) when the respective species was present. Species are arranged according to relative abundance in shallow to deep water; *significant differences among depth zones

Table 2. Classification of common species based upon distribution among 3 depth zones at CHB. Shown are results of Friedman 2-way ANOVAs (F_r, with number of depth zones k and sample dates N) which compare proportional abundance among depth zones (as shown in Fig. 3) for each species; zones not underscored by a continuous line are significantly different (p < 0.05) based on multiple comparisons. Species are classified into 3 groups (shallow, mid, and deep zone species) according to outcome of comparisons, and unclassified species showed no significant differences (ns) in abundance among depth zones. df = 2 for all comparisons

	F_r	k, N	p	Comparisons
Shallow zone species				
Crangon septemspinosa	11.45	3,10	< 0.01	1 2̲ 3̲
Fundulus heteroclitus	11.45	3,10	< 0.01	1 2̲ 3̲
Fundulus majalis	10.71	3,10	< 0.01	1 2̲ 3̲
Palaemonetes pugio	18.03	3,12	< 0.01	1 2̲ 3̲
Mid zone species				
Apeltes quadracus	9.25	3,6	< 0.01	1̲ 2̲ 3
Gobisoma bosci	17.39	3,7	< 0.01	1̲ 2̲ 3
Rhithropanopeus harrisii	11.23	3,11	< 0.01	1̲ 2̲ 3
Deep zone species				
Callinectes sapidus	10.84	3,12	< 0.01	1̲ 2̲ 3̲
Leiostomus xanthurus	8.33	3,6	< 0.05	1̲ 2̲ 3
Unclassified species				
Anchoa mitchelli	1.20	3,5	ns	
Gobiesox strumosus	4.67	3,3	ns	
Menidia menidia	0.95	3,10	ns	

dulus heteroclitus, and F. majalis (Fig. 3, Table 2). Relative to shallow zone species, the 3 mid zone species (Apeltes quadracus, Gobiosoma bosci, and Rhithropanopeus harrisii) exhibited a shift in relative abundance toward deeper water; their peak abundances were in either shallow or mid zones, and they still were rare in the deep zone. The relative abundances of all 3 species differed significantly among depth zones, but multiple comparisons showed significant differences (from mid to deep zones) for only G. bosci and R. harrisii (Table 2). Nevertheless, A. quadracus was classified as a mid zone species, because it was rare in the deep zone and exhibited an overall statistically significant difference in its distribution among zones. Finally, Callinectes sapidus and Leiostomus xanthurus were classified as deep zone species, displaying overall significant differences in relative abundances among zones with proportionally few individuals in the shallow zone (Fig. 3, Table 2). Multiple comparisons revealed a significant difference between shallow and deep zones for L. xanthurus and no significant differences for C. sapidus. However, unlike A. quadracus and other species, the data for C. sapidus were not heteroscedastic (Bartlett's test, p > 0.05) and allowed further analysis with a 1-way ANOVA, which revealed an overall significant difference ($F = 5.445$,

df = 1, p < 0.01) and a pairwise difference (Tukey HSD, p < 0.05) between the shallow zone and other 2 zones.

The distribution patterns for 4 of the common species were not classified by our statistical analyses (Table 2). Although Gobiesox strumosus and Micropogonias undulatus were almost completely absent from the deep and shallow zones respectively (Fig. 3), the small sample size and low statistical power for each could not detect significant differences among zones that probably existed. In contrast, no zonation was evident either graphically or statistically for Menidia menidia and Anchoa mitchelli.

The common species at CHB exhibited strong temporal variation in their overall abundances across all 3 zones and at the zone of highest density (Fig. 4). Temporal patterns were not analyzed formally, because the absence of most species on some dates (and frequent heterogeneous variances) prohibited the use of many common statistical procedures. Instead, we chose to simply display the variation in abundance among sample dates over the 4 yr period of study. From these data we draw 2 main conclusions. First, in examining the data for 1990, there is evidence of a seasonal interaction in the zonation pattern described above. Shallow and mid zone species were absent in April 1990, and some of these species were not detected until July or August. When present, these species showed a strong pattern of depth zonation (Fig. 3). By contrast, blue crabs and spot were present in April samples, and the latter was not detected in August and October. Second, year-to-year changes occurred in the species composition of this community and abundance of species present. This annual variation was most extreme for Atlantic croaker and skilletfish, which were only present in cylinder samples for 2 or 3 dates, respectively, out of the entire 13 sampling dates. Data from trawl samples (below) provide a better measure of the large year-to-year variation in croaker abundance (see also Hines et al. 1990).

Size

Size-frequency distributions of the common species from cylinder samples at CHB indicate a fundamental difference in sizes of organisms by depth. Interspecifically, the deep zone species (and also Micropogonias undulatus, which was unclassified but never occurred in the shallow zone) were represented by more large individuals than shallow and mid zone spe-
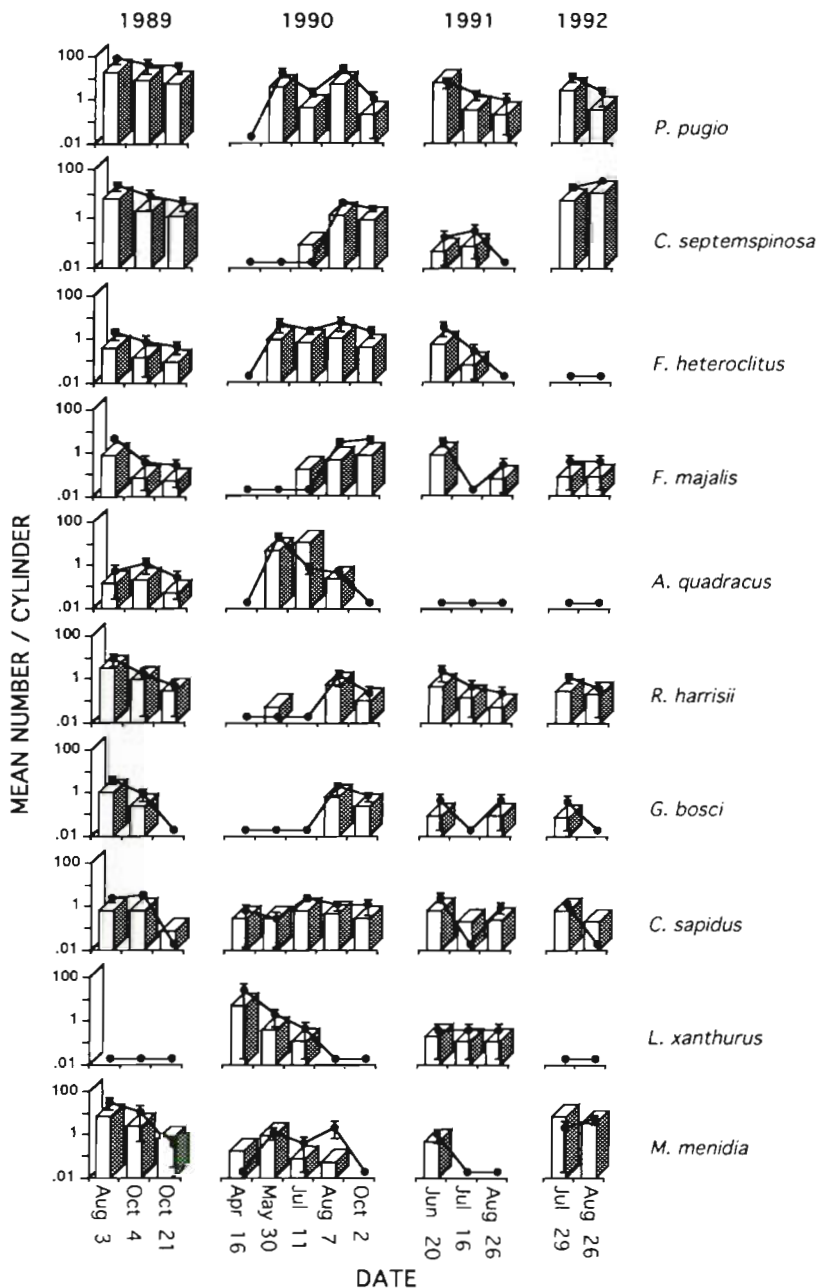
Fig. 4. Temporal variation in abundance of shallow, mid, and deep zone species (see Table 1) at CHB. Average abundances across all depth zones (= unweighted means) are shown with histograms, and abundances (means ± SE) at zone of peak abundance are depicted by (•). Mean values are plotted on a log scale for each sample period during 4 yr (1989–1992)

(Fig. 5, Table 4); the exception was *Crangon septemspinosa*, for which size composition did not differ with depth. Such intraspecific size comparisons were not made for some of the common species, because they lacked: sufficient sample sizes (*Gobiesox strumosus*, *Micropogonias undulatus*); dispersion among zones (*Gobisoma bosci*); or more than one age/size class (*Anchoa mitchelli*, *Leiostomus xanthurus*).

Distribution patterns at Big Island

The relative abundance of species among depth zones for non-vegetated areas at BI was similar to that observed at CHB. As at CHB, grass shrimp and both *Fundulus* species had their peak densities in the shallowest zone, departing significantly from uniform distributions (shrimp: $\chi^2 = 56.40$, df = 1, p < 0.001; mummichogs: $\chi^2 = 12.28$, df = 1, p < 0.01; banded killifish: $\chi^2 = 12.95$, df = 1, p < 0.01). Other species at BI were not abundant enough in cylinder samples for statistical analyses, but their patterns of distribution appeared similar to those at CHB. In particular, blue crabs were most abundant in the deep zone, and four-spine stickle-backs were present in all zones and most abundant in the mid zone.

Each of the common species had a higher abundance in SAV compared to non-vegetated habitat of the same depth zone (Fig 6). Treating each zone × species combination as an independent paired sample, all 14 of the pairs had their highest abundance in SAV, representing a highly significant difference among habitats (Sign Test after Snedecor & Cochran 1978: $\chi^2 = 12.07$, df = 1, p < 0.001) Moreover, the decline seen with increasing depth for non-vegetated habitat appeared to be

cies, showing a tendency for the largest species to occur in the deepest zone (Table 3). Intraspecifically, the relative abundance of large (i.e. mature or 1+ yr class) individuals increased significantly with increasing depth for *Palaemonetes pugio*, *Fundulus heteroclitus*, *F. majalis*, *Rhithropanopeus harrisii*, *Apeltés quadracus*, *Menidia menidia*, and *Callinectes sapidus*

reversed or diminished for all of these species (Fig. 6) This interaction appeared most pronounced for *Palaemonetes pugio*. A 2-way ANOVA revealed a significant effect of vegetation and the interaction of vegetation × depth on abundance, and *t*-tests found a significant effect of vegetation in both zones and of depth for only non-vegetated habitat (Table 5).

Table 3. Size distributions of common species at CHB. For all dates combined, distributions are presented as percent of the total number of a species within indicated size category

	<5	5–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	81–90	91–100	101–110	111–120	>120	n
Shallow zone species															
Palaemonetes pugio	–	–	12.0	32.6	40.0	15.4	–	–	–	–	–	–	–	–	992
Crangor septemspinosa	–	–	13.4	70.7	13.5	2.4	–	–	–	–	–	–	–	–	843
Fundulus heteroclitus	–	1.7	31.7	14.2	5.0	1.7	3.3	12.5	15.8	10.8	3.3	–	–	–	120
Fundulus majalis	–	–	17.5	20.4	23.3	15.5	11.6	–	–	3.9	1.9	3.9	1.0	1.0	103
Mid zone species															
Apeltes quadracus	–	–	–	39.3	58.0	1.4	0.9	–	–	0.4	–	–	–	–	219
Gobisoma bosci	–	1.7	55.2	24.2	8.6	6.9	1.7	1.7	–	–	–	–	–	–	58
Rhithropanopeus harrisii	60.9	35.5	3.6	–	–	–	–	–	–	–	–	–	–	–	110
Deep zone species															
Callinectes sapidus	–	–	13.9	19.0	16.8	10.2	4.4	5.1	9.5	5.8	7.3	1.4	2.9	3.7	137
Leiostomus xanthurus	–	–	7.1	50.0	4.8	11.9	9.5	2.4	–	4.8	2.4	–	4.8	2.4	42
Unclassified species															
Anchoa mitchelli	–	–	0.7	34.3	58.6	5.7	0.7	–	–	–	–	–	–	–	140
Gobiesox strumosus	–	3.8	11.5	19.2	42.3	23.0	–	–	–	–	–	–	–	–	26
Menidia menidia	–	–	10.5	21.0	22.6	14.2	13.9	11.0	4.7	1.1	0.8	–	0.2	–	381
Micropogonias undulatus	–	–	–	–	–	–	–	20.0	–	40.0	–	20.0	20.0	–	5

Similar to CHB, an apparent increase in size occurred with depth for 3 of the common shallow zone species (*Palaemonetes pugio*, *Fundulus heteroclitus* and *F. majalis*). Statistical comparison of these patterns is complicated by the low abundance at particular depth subzones, or for particular size groups (creating expected values below the recommended level of 5; Sokal & Rohlf 1981). To allow comparisons, depth subzones were combined for *P. pugio*, and a significant difference existed when comparing the size structure between the shallowest subzone (0–18 cm) and deeper water ($\chi^2 = 56.14$, df = 2, p < 0.001). For both *Fundulus* species combined, size structure was also significantly different among the 3 zones ($\chi^2 = 32.56$, df = 2, p < 0.001).

Abundance of large predators

Trawl samples at CHB were composed of 16 species (Table 1), which exhibited seasonal and annual variation in abundance and mean size (Fig. 7). The most abundant species included *Fundulus heteroclitus*, *F. majalis*, *Leiostomus xanthurus*, and *Callinectes sapidus*, and all of these were present from May to October. During the summer, abundance of the first 3 declined, while abundance of blue crabs remained relatively stable. *Trinectes maculatus*, *Pseudopleuronectes americanus* and *Paralichtys dentatus* were least abundant and often absent in monthly trawl samples. *Micropogonias undulatus* exhibited the highest interannual variation, being absent in trawl and cylinder samples for 3 yr (1989, 1990, 1992) and present in all monthly samples for 1991.

For 3 of the most common fish species (*Fundulus majalis*, *Leiostomus xanthurus* and *Micropogonias undulatus*), trawl samples early in the season contained relatively small individuals compared to mid-late summer (Fig 7). Both the *F. heteroclitus* and *Callinectes sapidus* populations exhibited little directional change in mean size from May to October; however, the latter decreased in size in November, when new recruitment occurred and larger crabs may have moved out of the subestuary (e.g. Hines et al. 1987b, 1990).

Overall, estimates of species composition and relative abundance of large, epibenthic predators were consistent between trawl and cylinder samples at CHB (Table 1). While a few rare species were added with trawl samples, trawl and cylinder samples both indicate that the *Fundulus* spp., *Leiostomus xanthurus*, *Callinectes sapidus*, and (in 1 yr) *Micropogonias undulatus*, due to their size and abundance, were the predators of potential importance to shallow zone species.
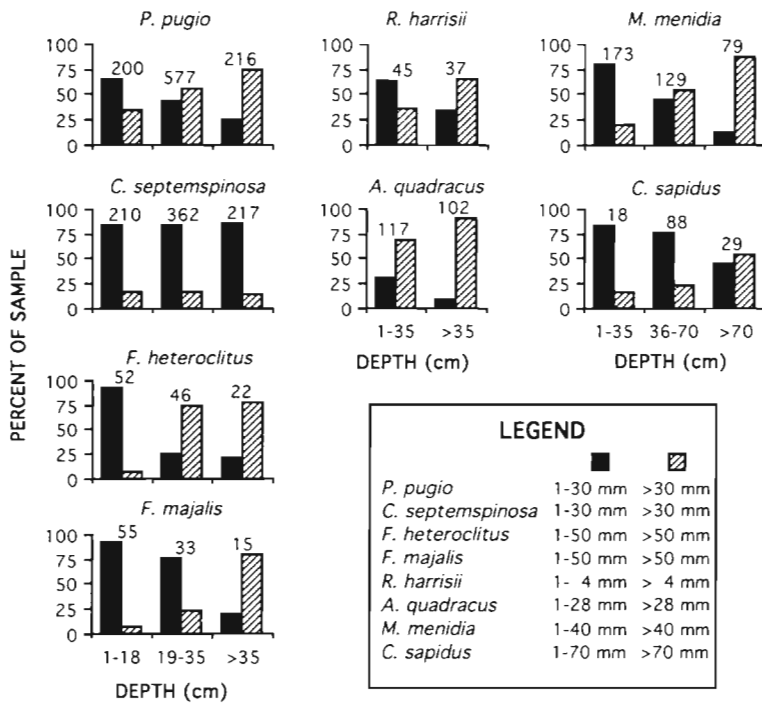
Fig. 5. Size composition of shallow zone species (see Table 4) by depth at CHB. Histograms show the percentage of 2 size classes occurring in each depth zone. Data are pooled from samples taken in all 4 yr (1989–1992). For each species, sample sizes are indicated within depth zones

Table 4. Comparison of size composition by depth for 8 common species at CHB. Shown are results of chi-square analyses. ns: not significant at $p > 0.05$

Species	χ^2	df	p
Palaemonetes pugio	65.72	2	< 0.001
Crangon septemspinosa	1.19	2	ns
Fundulus heteroclitus	53.84	2	< 0.001
Fundulus majalis	34.91	2	< 0.001
Rhithropanopeus harrisii	6.98	1	< 0.01
Apeltes quadracus	14.44	1	< 0.001
Menidia menidia	101.23	2	< 0.001

Risk of predation

Survival of tethered grass shrimp, mummichogs, and small blue crabs differed significantly among depth zones: $\chi^2 = 34.37$, df = 2, $p < 0.001$ for *Palaemonetes pugio*; $\chi^2 = 17.57$, df = 2, $p < 0.001$ for *Fundulus heteroclitus*; $\chi^2 = 15.57$, df = 2, $p < 0.001$ for *Callinectes sapidus*. For each species, mortality (> 80 %) in the deepest (60–80 cm) zone was much greater than that (20 to 45 %) in the shallowest (15–20 cm) zone. One interpretation of these experiments might be that they reflect differential effects (interaction) of tethering on vulnerability to various predator species, which may change

composition with depth. However, nearly all potential predators large enough to consume the tethered prey were absent from the shallowest zone, and composition of these predators did not change appreciably between the mid and deep zones (Fig. 3, Table 2). In addition, for small intermolt blue crabs the major source (> 90 %) of mortality in the Rhode River is cannibalistic large blue crabs, rather than a suite of species (Smith 1990). Thus, we surmise that the large differences in mortality among zones, in combination with the observed corresponding changes in predator depth distributions, support the hypothesis that shallow water provides a refuge from predation in the absence of SAV.

DISCUSSION

Shallow water as refuge habitat

Large, highly mobile fish and crustaceans are often found in the shallow, and especially intertidal, areas of estuarine habitats (e.g. Reise 1978, deVlas 1979, Peterson 1979, Peterson & Quammen 1982, Rozas & Hackney 1984). Many of these animals maintain a relatively constant depth by moving with the ebb and flow of tides that results in inter- and intraspecific size segregation by depth (e.g. Macer 1967, Gibson 1973, Kuipers 1973, Kneib 1984b, 1987, Bishop & Kahn 1991); these patterns are often attrib-

Table 5. *Palaemonetes pugio*. Comparison of grass shrimp abundance by depth and habitat type (presence or absence of SAV) at BI. Results of 2-way ANOVA (depth × habitat) and of separate t-tests for effects of habitat within each depth zone, and of depth within each habitat type. df = 1 in all cases; ns: not significant at $p > 0.05$

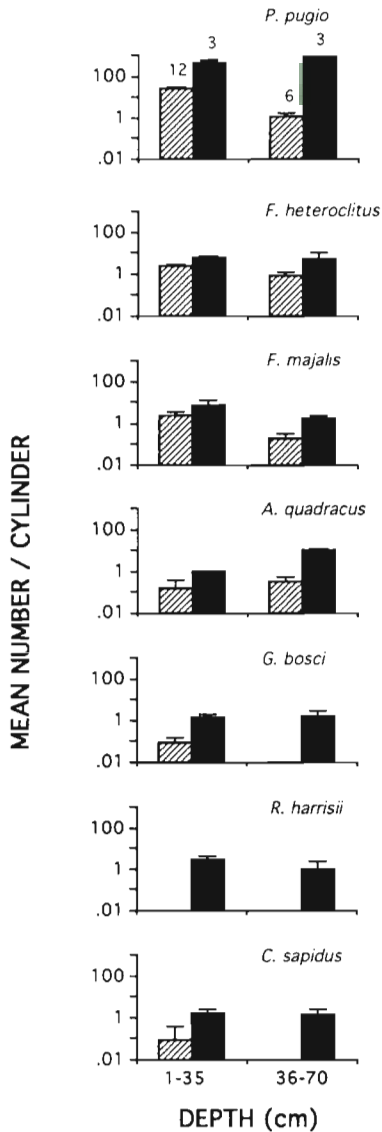| 2-way ANOVA Factor	F-ratio	p
Depth	0.80	ns
Habitat	71.88	< 0.001
Depth × Habitat	6.17	< 0.05
t-tests By habitat	t	p
Depth zone 1	15.22	< 0.001
Depth zone 2	3.74	< 0.01
By depth zone	t	p
SAV present	1.64	ns
SAV absent	2.99	< 0.01

Fig. 6. Comparison of densities by depth and substrate for common species (see Table 1) at BI, August 1990. In the presence (solid histograms) and absence (diagonally shaded histograms) of SAV, mean density ± SE is shown by depth zone for each species; no. of cylinder samples are indicated at top

Fig. 7 Seasonal and annual variation in abundance and size for large epibenthic species (see Table 1) in shallow water trawl samples at CHB. Mean abundance ± SE (histograms; 2 trawls for May and November, and 6 trawls per other sample dates) and mean size ± SE (•; sample size varies according to availability) is shown for each sample date by species

uted to depth- and size-dependent differences in the risk of predation (e.g. Boesch & Turner 1984, Rozas & Odum 1987b, c, McIvor & Odum 1988, Gibson 1986). In particular, risk of predation in shallow water estuaries is thought to diminish with both decreasing water depth and increasing individual size. As a result, larger individuals should experience a greater refuge in size from predators than smaller individuals, allowing the largest animals to exploit depths that are too risky for smaller ones.

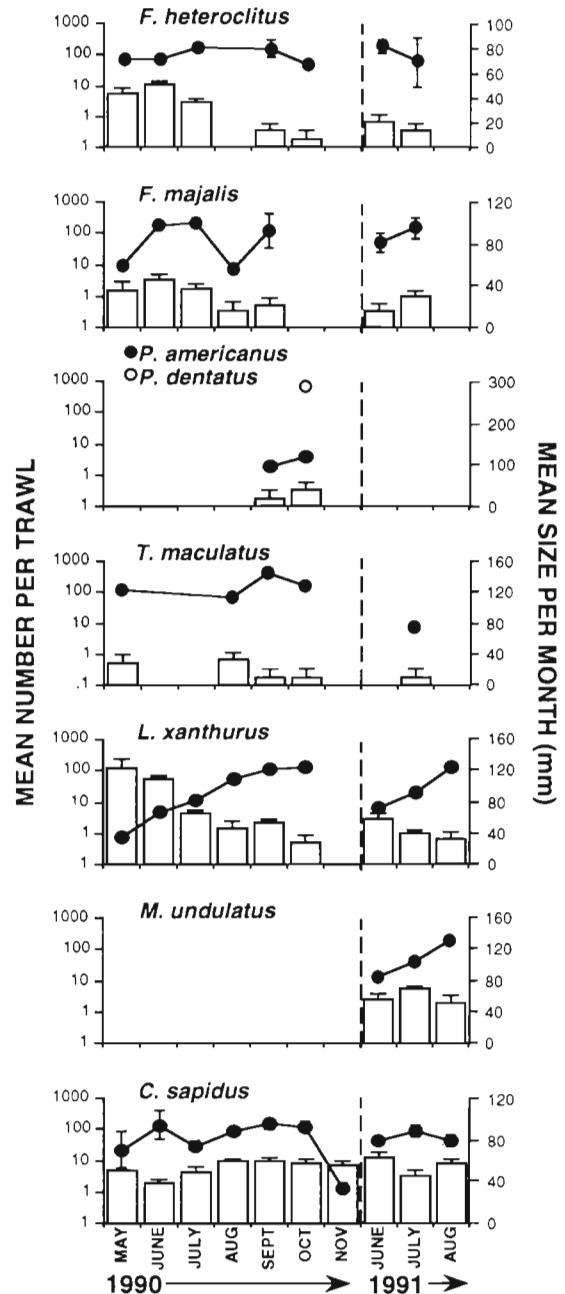Strong support for this model of depth- and size-dependent risk of predation exists for some benthic marine invertebrates on rocky shores (e.g. Connell 1972, Underwood 1979) and fish in freshwater habitats (e.g. Fraser & Emmons 1984, Power et al. 1985, Schlosser 1987, 1988a, b, Harvey et al. 1988, Werner & Hall 1988, Harvey 1991)(see also review by Lima & Dill 1990 on predation risk and prey behavior). For estua-
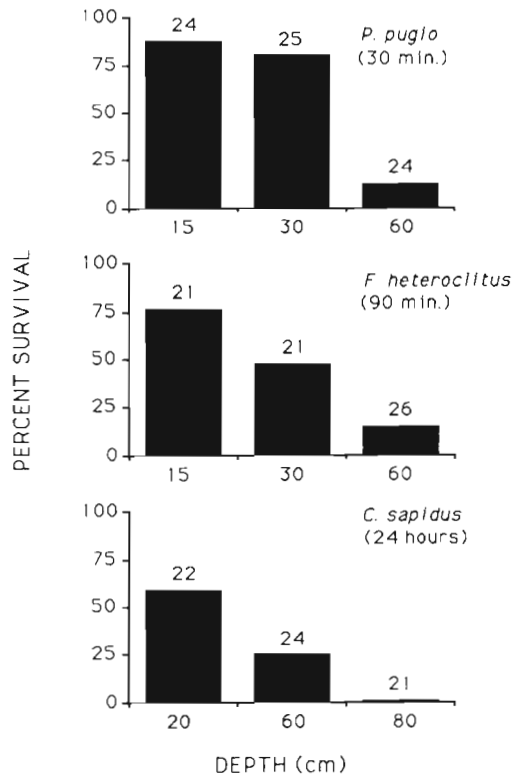
Fig. 8. *Palaemonetes pugio, Fundulus heteroclitus,* and *F. majalis.* Depth-specific survival of tethered grass shrimp (30 min), small mummichogs (90 min), and small blue crabs (24 h) at CHB. For grass shrimp and mummichogs, percent survival of tethered animals is shown at 15, 30, and 60 cm depths (June 1991); survival of blue crabs is shown at 10, 60, and 80 cm depths (August 1989). Sample sizes shown at top of each histogram

rine habitats, predation risk decreases for snails and mangrove crabs with increasing vertical height (i.e. decreasing depth and duration of submersion) on emergent vegetation (Hamilton 1976, Vaughn & Fisher 1988, Wilson 1989). In addition, McIvor & Odum (1988) found that risk of predation for *Fundulus heteroclitus* was less at a shallow site with SAV compared to a deeper, non-vegetated site. However, hypotheses about the independent effect of depth on predation risk have not been tested experimentally in the field for estuarine epifaunal communities.

The strong depth- and size-related distribution patterns observed for fish and crustaceans at CHB and BI appear to exist in other areas of the Rhode River, and in estuaries of Virginia and North Carolina. In censusing local grass shrimp abundance by depth at multiple sites along the Rhode River (Ruiz & Everett unpubl. data), we have routinely found strong depth zonation in summer months that is consistent with data presented in this study. Over the past 12 yr, monthly trawls and frequent underwater observations further indicate that grass shrimp and small killifish (*Fundulus* spp.)

were consistently rare in deep (2 to 4 m) portions of the Rhode River (Hines unpubl. data). Similar depth-restricted distributions exist for grass shrimp and small killifish in non-vegetated portions of North Carolina estuaries (Townsend 1991, Innis 1992). Finally, in a 1992 survey of non-vegetated habitat at the confluence of Virginia's York and Mattaponi Rivers, densities of grass shrimp and small (<35 mm) blue crabs also exhibited similar differences by depth (R. Everett, U.S. Fish & Wildlife Service, pers. comm.).

The refuge provided for grass shrimp, small killifish, and small blue crabs by shallow water most likely resulted from differences in the abundance of predators and, perhaps, the ability of predators to capture prey among depth zones. Spot, croaker, blue crabs, and large (>60 mm) mummichogs are known predators of grass shrimp and small killifish (Schmelz 1964, Nixon & Oviatt 1973, Heck & Thoman 1981, Kneib 1982, West & Williams 1986, Fitz 1990, Posey & Hines 1991, Everett & Ruiz 1993) that were commonly present during this study. Cannibalistic blue crabs are the major predator of other blue crabs in the Rhode River (Smith 1990, Hines & Ruiz unpubl. data). All of these predator species were least abundant in the shallow zone. Avoidance of the shallow zone by predators may result from increased risk from avian and mammalian predators, decreased foraging ability, or increased physiological stress due to elevated temperature or reduced oxygen levels relative to deeper water (e.g. Jenni 1969, Valiela et al. 1977, Gibson 1982, 1986, Kneib 1982, Rozas & Hackney 1984, Rozas & Odum 1987b), but the underlying mechanisms which generate these predator distributions are unclear.

Although the observed distributions of grass shrimp and small killifish may result from the simultaneous influence of many factors (e.g. variation in food availability, sediment characteristics, oxygen, and temperature), their selection of shallow zone habitat appears driven primarily by its refuge value. This is supported by observations of diurnal and seasonal variation in distributions at the Rhode River. First, grass shrimp disperse out of the shallow zone at night (Ruiz unpubl. data), suggesting that daytime distributions are limited by activities of their visual predators (e.g. Culp et al. 1991; see also Lima & Dill 1990 for review on effects of light intensity on predator activity and prey distribution). Second, grass shrimp and killifish both occur outside the shallow zone in winter and early spring (Ruiz & Everett unpubl. data), coinciding with a time when predators are relatively low in abundance (see also Hines et al. 1990) or very small in size.

In contrast to the other shallow zone species, *Crangon septemspinosa* were often found in the mid and deep zones. Predation risk as a function of depth was not measured for this species. The predators of *C.*

septemspinosa, and the relative abundance of predators among depth zones, were likely to be similar to those of grass shrimp due to size similarity of the 2 species. However, the common habit of burial may allow *C. septemspinosa* to utilize the deep zone more often than other shallow zone species, which bury much less frequently than the former (pers. obs.). Specifically, burial may reduce the risk of predation experienced by surface-dwelling species, operating just as depth of burial does for some invertebrates in soft-sediment communities (e.g. Virnstein 1979, Zwarts & Wanink 1989, Barshaw & Abele 1990a).

The mid zone species probably experienced a similar depth gradient in predation risk to that observed for the shallow zone species, due to similarity in sizes. However, the 2 groups may differ in their utilization of structure, which can modify predation risk (e.g. Heck & Thoman 1981, Peterson 1982, Mittelbach 1986, Savino & Stein 1989). Although SAV and oyster bars were absent at CHB, small twigs and branches (2 to 6 cm diameter) were occasionally present in the shallow and mid zones, and were very rare in deeper water. *Rhithropanopeus harrisii, Apeltes quadracus*, and *Gobisoma bosci* are often associated with structures such as SAV, oyster reefs, wood pilings, and woody debris (Wells 1961, Orth & Heck 1980, Heck & Thoman 1984, Lippson & Lippson 1984, Williams 1984, Rozas & Odum 1987a, Everett & Ruiz 1993). The fish species utilize such habitat structure to establish mating territories and nest sites (Hildebrand & Schroeder 1972, Lippson & Lippson 1984, FitzGerald & Wootton 1986), and, therefore, may be more dependent on structure compared to shallow zone species. Mudcrabs may also be especially dependent upon structure, as refuge, due to their low mobility.

Historical importance of nearshore shallows

Historically, SAV and oyster reefs have provided structural refuge from predation in deeper water (> 1 m) for many epibenthic species in estuaries (e.g. Coen et al. 1981, Heck & Thoman 1981, Dauer et al. 1982, Arnold 1984, Heck & Wilson 1987, Rozas & Odum 1988). Recent declines in SAV abundance for Chesapeake Bay, and elsewhere (see 'Introduction'), undoubtedly caused many significant changes to estuarine ecosystem function, including changes in population and community characteristics of associated fauna (e.g. Heck & Thoman 1984, Orth et al. 1984, Muehlstein 1989). With few exceptions (Stauffer 1937, Rasmussen 1977, Stevenson & Confer 1978, Perry & Uhler 1988), these changes have not been examined quantitatively. The long-term decline in Chesapeake Bay oyster reefs (Sindermann 1968), also an important

habitat for many animal species (Wells 1961, Bahr & Lanier 1981, Lippson & Lippson 1984), accentuates the potential for changes in population and community processes due to SAV declines alone.

Our study indicates a shift in depth distribution has occurred for epifaunal crustaceans and fish with changes in available habitat structure. In the presence of SAV, past studies found that *Palaemonetes pugio* and *Fundulus* spp. were common in waters > 1 m depth (e.g. Heck & Orth 1980, Orth & Heck 1980, Heck & Thoman 1984, Heck et al. 1989). However, in the absence of SAV, these species are now restricted primarily to a shallow (< 35 cm) depth zone along the shoreline. This shift in distribution is further illustrated by the differences in densities that we found among depth zones at BI, with and without SAV. Similarly, other species commonly associated with SAV or oyster bars > 1 m deep (*Crangon septemspinosa, Rhithropanopeus harrisii, Apeltes quadracus* and *Gobisoma bosci*; Wells 1961, Heck & Orth 1980, Orth & Heck 1980, Heck & Thoman 1984) were most abundant in depths < 70 cm at our study site. The nearshore shallows provide both refuge from predation and an important structural habitat created by woody debris (Everett & Ruiz 1993). Whether the role of woody debris in Chesapeake Bay is a recent change following the demise of SAV and oyster reefs is not clear.

We predict that many other attributes of animal populations have been impacted by the demise of SAV and oyster habitats. Based upon the disparity in animal densities between vegetated and non-vegetated sediments (e.g. Orth et al. 1984, Ferrell & Bell 1991), the absolute abundance of some species may have declined with the loss of SAV. Furthermore, accompanying a shift in habitat utilization, changes in the demography of populations may have occurred (e.g. Mittelbach 1986, Werner 1986). Given the functional importance of grass shrimp and killifish, both as predators and prey in the Chesapeake Bay community, any of these changes may have cascading effects (sensu Carpenter et al. 1985) on many community processes (e.g. Posey & Hines 1991). Quantitative exploration of these consequences is still in its infancy.

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