

Role of predatory infauna in structuring marine soft-bottom communities

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ABSTRACT: Present characterizations of interactions in marine soft-bottom communities classify fishes, crabs and birds (epibenthic predators) as predators, and infaunal species as prey. Many infaunal species, however, are themselves predators and act as prey for epibenthic predators and predators on other infauna – may function as intermediate predators. Data from 7 studies which employed cages to exclude epibenthic predators were used to test the hypothesis that predatory infauna do not become proportionally more abundant following exclusion of epibenthic predators. Predatory infauna became proportionally more abundant after epibenthic predators were excluded from muddy-sand and sea-grass habitats. This increase could be a consequence of preferential predation on predatory infauna by epibenthic predators, preferential predation on predatory infauna and predation by predatory infauna on other infauna, or equal predation on all infauna with additional predation by predatory infauna on other infauna. The result suggests that predatory infauna should be considered separately from non-predatory infauna when modeling interactions in soft-bottom communities and allows the prediction that prey species of predatory infauna may be less abundant in the absence than in the presence of epibenthic predators.

INTRODUCTION

Previous studies of marine soft-bottom community structure indicate that predation and/or disturbance by large, mobile epibenthic predators (such as bottom-feeding fishes, crabs and birds) are often important regulators of species abundance. Caging studies that exclude these predators from portions of the unvegetated bottom frequently result in large increases in the density of benthic infauna (see review by Peterson, 1979). As a result, our present characterization of interactions in these soft-bottom communities classifies fishes, crabs and birds as predators and infaunal species as prey. Many of the infauna, however, are themselves predators (e. g. nemertean and polychaete worms) and these groups also increase in the absence of epibenthic predators (Reise, 1977, 1978; Lee, 1978; Holland et al., 1980). These predatory infauna are capable of influencing the abundances of other infaunal species (Roe, 1976; Reise, 1979; Ambrose,

1982; Commito, 1982; Oliver et al., 1982). Expanding our present characterization of soft-bottom community structure by separating predatory and non-predatory infauna when modeling interactions in these communities may enable us to make new predictions concerning the outcome of interactions between epibenthic predators and infaunal species.

While predatory infauna and other infaunal species have been considered collectively as prey in models of soft-bottom community structure, differences in living habits between these 2 groups may make predatory infauna more available than other infauna as prey for epibenthic predators. Most predatory infauna do not form protective tubes (exceptions include the Onuphidae and Polyodontidae). Those that have protective burrows frequently extend large portions of their bodies onto the sediment surface or leave their burrows altogether (e. g. nereids, phyllococids) making themselves more susceptible to predation from epibenthic predators than are non-predatory infauna, many of which have protective tubes and burrows and rarely venture from them (e. g. capitellids, chaetopterids, maldanids). Shorebirds are common predators of predatory infauna (Recher, 1966; Bengtson and

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Svensson, 1968; Goss-Custard, 1977a, b; Goss-Custard et al., 1977; Schneider, 1978; Bryant, 1979; Hicklin and Smith, 1979; Kent and Day, 1983). Fishes and crabs are also important epibenthic predators (Virnstein, 1977, 1979) and both groups consume predatory infauna (Klawe and Dickie, 1957; Scarratt and Lowe, 1972; Wells and Steel, 1973; Stickney et al., 1975; Kravitz et al., 1976; Arntz, 1979; Elner, 1981; Kent and Day, 1983).

Predatory infauna may influence the abundance of other infauna by preying on adults, juveniles or larvae or by disturbing the sediment surface and reducing larval settlement and juvenile survivorship. Stomach analysis from members of 2 common predatory polychaete families, glycerids and nereids, show that they consume polychaetes, amphipods, isopods, gastropods and bivalves (Ockelmann and Vahl, 1979; Ambrose, 1982). Infaunal predatory amphipods and polychaetes have recently been shown to have a negative effect on larval settlement and juvenile survivorship (Ambrose, 1982; Commito, 1982; Oliver et al., 1982).

If predatory infauna are preferentially preyed upon by epibenthic predators or if predatory and non-predatory infauna are preyed upon equally but predatory infauna reduce the abundance of other infauna, then predatory infauna should become proportionally more abundant when epibenthic predators are excluded from the community. In this paper I test whether the ratio of the density of predatory infauna to the density of non-predatory infauna increases following the exclusion of epibenthic predators.

METHODS

I used data from 7 studies which employed cages to exclude large epibenthic predators from portions of the soft bottom (Naqvi, 1968; Young et al., 1976; Commito, 1976; Reise, 1977, 1978; Lee, 1978; Holland et al., 1980; Summerson, 1980) to test the prediction that the density ratio of predatory infauna to the remaining infauna increases following the exclusion of epibenthic predators. No attempt was made to analyze the raw data from every caging study ever conducted. The studies were chosen because they represent a broad range of habitats and because their data was accessible. A total of 56 separate exclusion experiments in 3 different habitats, sand, muddy-sand, and grass beds, were conducted in these studies. Cage artifacts (alteration of the physical and biological environment in addition to the desired exclusion of predators) are common in caging experiments in soft sediments (Virnstein, 1978). To control for cage artifacts some researchers construct cage controls, partial cages

which theoretically allow free access by epibenthic predators while mimicking the effects cages have on the environment. When possible, I used the densities from cage controls to compute ratios used in the comparisons with caged areas (Lee, 1978; Summerson, 1980). In the studies where cage controls were not used (Naqvi, 1968; Young et al., 1976; Reise, 1977, 1978; Holland et al., 1980) or where cage artifacts were shown to be unimportant (Commito, 1976), data from uncaged portions of the bottom were used in the comparisons.

I excluded from the analysis all epifaunal species. The decision to exclude a species was based on information in Abbott (1974) for mollusks, Bousfield (1973) and Myers (1970) for amphipods, Fauchald and Jumars (1979) and Pettibone (1963) for polychaetes, and Barnes (1974) for other species or groups. I excluded epifaunal animals because they frequently settle on cage walls and tops and occasionally fall into cages during cleaning and sampling (Virnstein, 1978; Summerson, 1980), thereby increasing densities of some species under cages for reasons other than the exclusion of predators.

I next divided the fauna into predatory and non-predatory species. There is considerable ambiguity regarding the exact diet of many infaunal species. Polychaetes in particular appear to possess very flexible feeding habits (Fauchald and Jumars, 1979) which undoubtedly change with age, season, habitat, and infaunal densities. Few species may be obligate predators. Occasional predatory behaviour, however, may be all that is required for these species to have a significant affect on the densities of other infaunal species. I used the review by Fauchald and Jumars (1979) to separate polychaetes which are at least occasionally predators, both carnivores and omnivores, from other feeding types. Nemertean are entirely carnivorous preying primarily on amphipods, polychaetes and bivalves (Barnes, 1974; McDermatt, 1976; Roe, 1976). Some gastropods are infaunal and predaceous and I consulted Abbott (1974) to identify these species.

Each period of exclusion yielded 2 ratios of predatory to non-predatory infauna, 1 from the cage treatment and 1 from the uncaged control. As all experiments had at least 2 replicates for treatment and control, I used the mean density of all replicates in computing the ratios. Treating each experiment as a data point I applied a sign test (Sokal and Rohlf, 1969) to the sign of the difference in ratios between caged and uncaged areas. If no consistent difference between the ratios from the 2 areas exists then the number of times the ratio increases (positive sign) and decreases (negative sign) when epibenthic predators are excluded will be approximately equal. All differences of zero are omitted in the sign test. I employed a one-tailed test

because the alternate hypothesis is that the ratios are greater from caged areas than from uncaged areas. Experiments were separated on the basis of habitat (sand, muddy-sand, grass) and separate analyses were done for each habitat and all habitats combined. A table of binomial probabilities was used for sand and grass habitats and the normal approximation was used for the larger samples (greater than 20) from the muddy-sand habitat and when all habitats were combined (Sokal and Rohlf, 1969).

RESULTS

Ratios of density of predatory to non-predatory infauna and sign of the difference in ratios between caged and uncaged areas are presented in Table 1. Results of the sign test show that the ratio of predatory to non-predatory infauna increased following the exclusion of epibenthic predators in muddy-sand and grass habitats (Table 2). The sign test is also significant when all habitats are analyzed together. In these cases, there was an increase in the proportion of predatory infauna when epibenthic predators were excluded. In sandy habitats the ratios of predatory to non-predatory infauna did not increase in the absence of epibenthic predators (Tables 1 and 2).

DISCUSSION

Increase in proportion of predatory infauna could be a consequence of (1) preferential predation on these predatory infauna by epibenthic predators; (2) preferential predation on predatory infauna and predation by predatory infauna on other infauna; (3) equal predation on predatory and non-predatory infauna with additional predation by predatory infauna on other infaunal species; or (4) competition between predatory and non-predatory infauna with predatory infauna out-competing non-predatory infauna. These processes cannot be separated by comparing ratios of predatory to non-predatory infauna. Regardless of the mechanism, these results support the proposal that predatory infauna be considered separately from other infaunal species in models of soft-bottom community structure. The exclusion of epibenthic predators affects predatory and non-predatory infauna differently. Furthermore, as predators of other infauna and prey for epibenthic predators, predatory infauna may be an important link between epibenthic predators and certain infaunal species. Competition between predatory and non-predatory infauna is an unlikely explanation for the increase in the proportion of predatory infauna because Peterson (1979) showed that species richness

increased and in most cases evenness increased or remained unchanged following the exclusion of epibenthic predators.

The increase in the proportion of predatory infauna following the exclusion of epibenthic predators occurred despite several factors favoring increases in the abundances of non-predatory infauna under exclusion cages. First, because cages reduce the rate of water flow they will accumulate fine sediment and organics (Virnstein, 1978), which favor deposit-feeding species. Cage controls were used in only a few studies. While some predatory infauna may also be deposit feeders (e.g. some species of nereids; Fauchald and Jumars, 1979) and thus be attracted, other deposit-feeding species are more numerous than these predators and will probably be attracted to a greater degree. Second, the life-history characteristics of many of the non-predatory infauna make them more likely than predatory infauna to settle and reach high densities under cages. Most predatory infauna have a more restricted reproductive period than opportunistic species whose larvae are present in the water column for large portions of the year (McCrary, 1969; Rasmussen, 1973; Grassle and Grassle, 1974). The caging studies covered all seasons of the year and no attempt was made to analyze the results by season because sample sizes would have been unacceptably small. As a result, settlement into cages is more likely for species other than predatory infauna. Opportunistic species sometimes account for the largest absolute increases under cages (Virnstein, 1979; Holland et al., 1980), a result of these species' high reproductive rates.

It is not possible to determine the reasons for the failure of predatory infauna to increase in abundance relative to the remainder of the infauna under cages in sandy habitats (Table 2). Possibilities include reduced efficiency of predatory infauna, greater efficiency of epibenthic predators in reducing the abundance of non-predatory infauna and greater cage artifacts in sand habitats compared to muddy-sand and grass habitats. Alternatively, the sample size for sandy habitats may be too small to test adequately the prediction.

Total densities of infauna in grass beds are not affected by caging (Young et al., 1976; Orth, 1977; Reise, 1977, 1978; Young and Young, 1977; Virnstein, 1978; Summerson, 1980). Orth (1977) and Reise (1977) hypothesize, and Peterson (1982) demonstrated that the dense root mat in grass beds protects infaunal organisms from predation. Many physical and biological factors may be responsible for higher infaunal densities in grass beds than in the nearby unvegetated bottom (Thayer et al., 1975, 1980; Orth, 1977; Reise, 1977). To some degree, however, grass beds may be considered as natural predator exclusion experiments

Table 1. Source of data, ratio of density of predatory infauna to density of non-predatory infauna in samples from caged and control areas, and sign of difference in ratios between cage and control. Each pair of ratios represents 1 period of exclusion

Source	Ratio of predatory to non-predatory infauna		Sign of difference Cage – Control	Source	Ratio of predatory to non-predatory infauna		Sign of difference Cage – Control	
	Cage	Control			Cage	Control		
	Sand				Muddy-Sand			
Lee (1978)	.146	.172	–	Reise (1977)	.001	.002	–	
	.131	.145	–					
Summerson (1980)	.114	.159	–	Holland et al. (1980)	.180*	.116	+	
	.156	.215	–		.290*	.018	+	
	.356	.269	+		.068	.090	–	
			.063		.036	+		
Holland et al. (1980)	.160	.110	+		.046	.028	+	
	.005	.010	–		.358	.011	+	
	.011	.004	+		.112	.084	+	
	.120	.249	–					
	Muddy-Sand				Grass			
Naqvi (1968)	.735	.616	+	Young et al. (1976)	.075	.151	–	
Commito (1976)	.443	.330	+		.104	.357	–	
	.485	.444	+		.085	.124	–	
	.567	1.38	–		.018	.355	–	
	.817	.190	+		.309	.154	+	
	.151	.149	+		.384	.056	+	
	.387	.789	–		.277	.186	+	
	.282	.300	–		.268	.407	–	
	.249	.122	+		.309	.228	+	
	.182	.159	+		.223	.223	0	
	.256	.412	–		.165	.150	+	
	.257	.457	–		.345	.187	+	
	.250	.303	–					
	.104	.638	–		Reise (1978)	.015	.004	+
.400	.000	+	.022	.005		+		
.048	.041	+	.004	.002		+		
	.139	.119	+	(1977)	.020	.004	+	
	.308	.071	+					
	.235	.154	+	Summerson (1980)	.251	.096	+	
Reise (1978)	.012	.007	+		.255	.128	+	
	.014	.014	0		.420	.397	+	
	.011	.002	+					

* These data actually come from a muddy habitat but are included here because no other data from a truly muddy habitat are available

Table 2. Habitat, number of experiments where the ratio of predatory to non-predatory infauna was larger from caged than control areas, total number of experiments and significance level of 1-tailed sign test

Habitat	Number of experiments where ratio is larger from caged than control area	Total number of experiments	Significance level
Sand	3	9	ns*
Muddy-sand	20	29	p < 0.05
Grass	13	18	p < 0.05
All habitats	36	56	p < 0.025

* ns: not significant (p > 0.05)

(Peterson, 1979) and can be predicted to have a greater proportion of predatory infauna than nearby unvegetated areas.

This prediction is true in at least 2 cases. Summerson (1980) found that 26% (by number of individuals) of the infauna in grass beds were predaceous compared to 16% in the surrounding sand. Thayer et al. (1980) found the average percentage of predatory infauna in 3 grass beds to be 48%, compared to 22% in unvegetated sand. High percentages of predatory infauna are possible because of the flexible feeding habits of predatory polychaetes (Fauchald and Jumars, 1979), which make up the majority of the predatory infauna in these habitats. While predatory infauna may receive more protection in grassbeds than in unvegetated habitats, the results of comparing ratios of predatory to non-predatory infauna between caged and uncaged areas in grass beds (Table 2) indicate that predatory infauna are still being preyed upon by epibenthic predators. The greater relative abundance of predatory infauna in grass beds than in unvegetated habitats also suggests that predation by these predators on non-predatory infauna may be a more important organizing force in vegetated habitats than in unvegetated ones.

Recent work (Reise, 1979; Ratcliffe et al., 1981; Ambrose, 1982; Commito, 1982; Oliver, et al. 1982) shows that predatory infauna are capable of reducing the abundance of other infaunal organisms. *Nereis diversicolor* has been shown to reduce the abundance of juvenile cockles in the field (Reise, 1979) and *Macoma balthica* spat in the laboratory (Ratcliffe et al., 1981). In experiments which measured colonization of sediment from which all organisms had been removed and infaunal predatory polychaetes selectively added, Commito (1982) and Ambrose (1982) found that *Nereis virens* reduced the abundance of a number of infaunal taxa. Oliver et al. (1982) demonstrated that several species of phoxocephalid amphipods reduce infaunal densities by predation and/or disturbance. This experimental evidence supports the contention that the increase in the proportion of predatory infauna following the exclusion of epibenthic predators was partially the result of predatory infauna reducing the abundance of other infauna.

Considering the effects of predatory infauna when modeling interactions in soft-bottom communities may help explain the paradox which exists between the results of analogous experiments in rocky intertidal and soft-bottom communities (Peterson, 1979). In the rocky intertidal, predation increases species diversity within communities by reducing competition among prey species and preventing dominant competitors from monopolizing a limiting resource and excluding other species from the community (Paine, 1966). There is no evidence for competitive exclusion by dominant

species following the exclusion of predators in soft-bottom systems. Competitive exclusion may fail to occur following the removal of epibenthic predators either because appropriate mechanisms of interference and exploitation competition are ineffective or because densities are kept below the carrying capacity of the environment by adult-larval interactions (Peterson, 1979). These arguments are based on a view of the soft-bottom system composed of only epibenthic predators and infaunal prey. Exclusion experiments in the soft-bottom community have failed to eliminate predatory infauna and may even have caused the density of these predators to increase. Predation from predatory infauna within exclusion cages may help explain the failure of a competitive dominant to become established in response to the removal of epibenthic predators from the soft-bottom community.

I propose a 3-level interactive model for soft-sediment marine systems (Fig. 1) similar to the trophic model for lake systems. In lakes, the top trophic level is occupied by vertebrate predators (fish or salamanders), the second level by invertebrate predators (calanoid copepods and cryptic midge larvae) and the third by

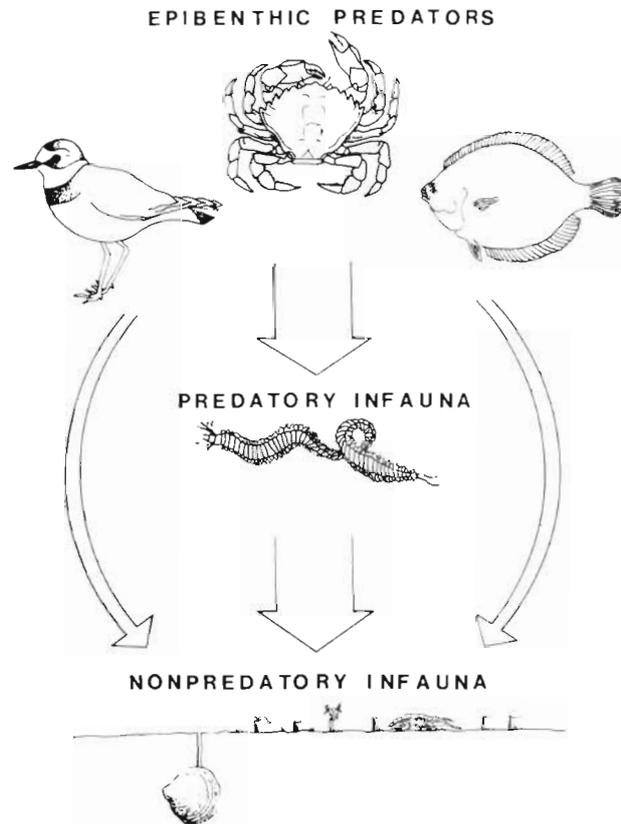


Fig. 1. Diagram of proposed 3-level interactive model. Curved arrows: interactions between epibenthic predators and non-predatory infauna. Broad arrows: relations which may be particularly important in predicting the outcome of interactions in soft-bottom communities

small herbivores and the juveniles of larger herbivores (Brooks and Dodson, 1965; Dodson, 1970, 1974). In the soft-sediment marine system the mechanism of interaction between the 3 levels I propose, epibenthic predators, predatory infauna, and non-predatory infauna, may not be confined to predation. Certain epibenthic predators, such as the blue crab *Callinectes sapidus* and the horseshoe crab *Limulus polyphemus*, may be responsible for much mortality through disturbance as well as by predation. Some predatory infauna may also disturb the sediment surface during their feeding and bury newly settled larvae, juveniles, and adults. Regardless of the mechanisms of interaction between the levels, the separation of infauna into predatory and non-predatory species allows the prediction tested in this paper that predatory infauna become proportionally more abundant following the removal of epibenthic predators. The addition of predatory infauna as intermediaries between epibenthic predators and non-predatory infauna leads to the prediction, not tested here, that prey species of predatory infauna may actually be less abundant in the absence than in the presence of epibenthic predators. These predictions are impossible with the conventional model which considers only epibenthic predators and infaunal species.

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