

# Importance of predatory infauna in marine soft-sediment communities

W. Herbert Wilson Jr.

Manomet Bird Observatory, Box 936, Manomet, Massachusetts 02345, USA  
and  
Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4J1, Canada

**ABSTRACT:** Ambrose (1984a) suggested that a 3-way interactive model should be applied to marine infaunal communities having the levels of epibenthic predators, predatory infauna and nonpredatory infauna. It is shown that the 3-level interactive model incorporates the implicit, unstated assumption that epibenthic predators preferentially prey on predatory infauna. A review of the literature reveals that this assumption is not true. The assumption of predatory infauna being more susceptible to epibenthic predation is challenged. Reanalysis of the caging studies analyzed by Ambrose with a more rigorous and conservative classification of predatory and nonpredatory infauna provides no support for the proposed model. The application of the proposed 3-level interactive model to marine infaunal communities is not justified.

## INTRODUCTION

Ambrose (1984a) claimed that predatory infauna should be considered separately from nonpredatory infauna in the investigation of soft-sediment community organization. He argued that a 3-level interactive model should be applied to infaunal communities. Epibenthic predators (crabs, fish, birds) are assumed to feed primarily on infaunal predators and to a lesser extent on nonpredatory infauna. Predatory infauna are assumed to feed upon the nonpredatory infauna.

The support for the model comes from Ambrose's analysis of the data from 7 caging studies performed in North America and Europe. He reasoned that, if the 3-way interactive model is appropriate, the exclusion of predators should have a greater positive effect on infaunal predators than on nonpredatory infauna. To test this prediction, the ratio of the abundance of nonpredatory infauna to the abundance of predatory infauna was calculated for each experiment in both predator exclusion and control treatments. If predatory infauna are preyed on more heavily than nonpredatory infauna, the computed ratios from caged areas should be higher than the ratios from control areas subject to epibenthic predation. Ambrose analyzed the 56 available experiments by computing the sign of the differ-

ence between caged and control ratios. The hypothesis of greater ratios in caged areas was tested with a 1-tailed sign test. He showed that the cage ratios were significantly greater than the control ratios for muddy-sand habitats and seagrass habitats but not for sand habitats. Based on this analysis, he advocated the 3-level interactive model for marine infaunal communities.

Ambrose's synthesis of previously reported work is laudable. However, I wish to raise a number of objections to his methodology and underlying assumptions. I believe that there is insufficient evidence to justify the application of the proposed 3-level interactive model to soft-sediment communities in general.

## MECHANISM OF PROPOSED INTERACTIONS

Ambrose suggests that the ratio of predatory infauna to nonpredatory infauna should be higher in caged areas compared to open control areas either because epibenthic predators prefer predatory infauna, or epibenthic predators prey equally upon both predatory and nonpredatory infauna but the nonpredatory infauna incur additional predation from the predatory infauna. In this section, I will show that the first

mechanism, preferential predation on nonpredatory infauna by epibenthic predators, is a requirement of the 3-level interactive model as proposed.

Let us consider for heuristic purposes a community of 10 epibenthic predators, 50 infaunal predators and 250 nonpredatory infaunal animals. Let the individual predation rates for both epibenthic predators and predatory infauna be 1.0 over the course of the simulated experiments. Table 1a gives calculations for both caged and open areas where epibenthic predators take only predatory infauna (preferential predation) and where epibenthic predators take predatory and nonpredatory infauna in strict proportion to their abundance (nonpreferential predation). To identify the extrema of the model, let us impose all of the predation from epibenthic predators before any infaunal predation is imposed. As seen in Table 1a, the preferential mechanism yields a decrease in the ratio of predatory to nonpredatory infauna in the presence of epibenthic predation whereas the nonpreferential mechanism produces equal ratios in open and caged areas. At the opposite extreme where we impose infaunal predation before any predation by epifauna, similar results obtain. Table 1a also presents the results of ratio calculations for a number of predation regimes in which

epibenthic and infaunal predation alternate. The results are consistent in that preferential predators depress the infaunal ratio whereas nonpreferential predators do not. Two regimes (E-R-I and I-R-E) incorporate a pulse of recruitment between the 2 pulses of predation; 100 nonpredatory infauna and 10 predatory infauna are added. Note that the proportional increase of nonpredatory infauna is higher than that of predatory infauna. The pulse of recruitment does not affect the results of the simulation. The preferential predation mechanism yields significantly lower ratios in open areas compared to caged areas. There is no difference in ratios under the nonpreferential predation mechanism.

Many epibenthic predators are warm-blooded animals; most are active, highly mobile organisms. It is therefore reasonable to expect that their metabolic rates and hence predation rates should be higher than those of infaunal predators. Let the predation rate for epibenthic predators be 3.0 over the course of our experiments while maintaining that rate at 1.0 for predatory infauna. Imposing the 6 predation regimes used in Table 1a, consistently lower infaunal ratios result in the presence of epibenthic predation which falls only on predatory infauna. However, under the

Table 1. Effect of preferential and nonpreferential predation by epibenthic predators on the ratio of predatory to nonpredatory infauna. In (a), individual predation rate for both epibenthic predators and infaunal predators is 1.0 over the course of the experiment. In (b), epibenthic predation rate is 3.0. Preferential epibenthic predators take only infaunal predators; nonpreferential epibenthic predators take predatory and nonpredatory infauna in strict proportion to their abundance. Cages exclude all epibenthic predators. A number of predation sequences are given. As an example, the regime  $\frac{1}{2}$ I-E- $\frac{1}{2}$ I refers to a sequence in which first half of the infaunal predators take predatory infauna, then all of the epibenthic predators take prey, then half of the remaining predatory infauna take prey. R in the sequence refers to a pulse of recruitment consisting of 10 predatory infauna and 100 nonpredatory infauna

Predation regime	Ratio of predatory to nonpredatory infauna			
	Preferential predation		Nonpreferential predation	
	Cage	Open	Cage	Open
<b>(a) Epibenthic predation rate = infaunal predation rate</b>				
E-I	0.250	0.190	0.250	0.250
I-E	0.250	0.200	0.250	0.250
$\frac{1}{2}$ E-I- $\frac{1}{2}$ E	0.250	0.195	0.250	0.255
$\frac{1}{2}$ I-E- $\frac{1}{2}$ I	0.250	0.195	0.250	0.251
$\frac{1}{3}$ E- $\frac{1}{3}$ I- $\frac{1}{3}$ E- $\frac{1}{3}$ I	0.250	0.193	0.250	0.250
$\frac{1}{4}$ I- $\frac{1}{4}$ E- $\frac{1}{4}$ I- $\frac{1}{4}$ E	0.250	0.198	0.250	0.250
E-R-I	0.207	0.167	0.206	0.207
I-R-E	0.200	0.167	0.200	0.200
<b>(b) Epibenthic predation rate = 3× infaunal predation rate</b>				
E-I	0.250	0.087	0.250	0.250
I-E	0.250	0.100	0.250	0.250
$\frac{1}{2}$ E-I- $\frac{1}{2}$ E	0.250	0.093	0.250	0.250
$\frac{1}{2}$ I-E- $\frac{1}{2}$ I	0.250	0.093	0.250	0.250
$\frac{1}{3}$ E- $\frac{1}{3}$ I- $\frac{1}{3}$ E- $\frac{1}{3}$ I	0.250	0.094	0.250	0.250
$\frac{1}{4}$ I- $\frac{1}{4}$ E- $\frac{1}{4}$ I- $\frac{1}{4}$ E	0.250	0.096	0.250	0.250
E-R-I	0.207	0.094	0.204	0.207
I-R-E	0.200	0.100	0.200	0.200

nonpreferential mechanism of epibenthic predation, the infaunal ratios do not differ between caged and open areas, contrary to Ambrose's claim. Incorporation of a pulse of recruitment (proportionately higher for nonpredatory infauna) does not alter the fact that preferential predators depress the infaunal ratio whereas nonpreferential predators do not.

The success of the preferential predation mechanism and the failure of the nonpreferential predation mechanism can be understood by consideration of direct and indirect effects. Under the preferential mechanism, nonpredatory infauna are positively affected indirectly by the removal of predatory infauna by epibenthic predators. When epibenthic predation is removed by caging, this positive effect no longer obtains for the nonpredatory infauna and their numbers fall disproportionately, leading to an increase in the ratio of predatory to nonpredatory infauna. Under the nonpreferential mechanism of epibenthic predation, the indirect positive effect is counterbalanced because most of the epibenthic predation falls on the more abundant nonpredatory infauna. The likelihood of demonstrating a significant increase in the ratio of predatory to nonpredatory infauna depends on the magnitude of the positive indirect effect of epibenthic predation on nonpredatory infauna by removal of predatory infauna. This effect will be maximized when all epibenthic predation falls on the predatory infauna. This effect will always obtain whether the rates of intrinsic increase of nonpredatory infauna are equal or different from those of predatory infauna. If nonpredatory infauna recruit more quickly, then nonpreferential epibenthic predators will take even higher numbers of the nonpredatory infauna and fewer of the predatory infauna, subjecting the nonpredatory infauna to even stronger direct effects from the predatory infauna. From this analysis, I conclude that epibenthic predation must fall preferentially on the predatory infauna if the 3-level interactive model is to be supported. Epibenthic predation falling equally on the 2 levels of infauna will not produce significantly different infaunal ratios.

#### EVIDENCE FOR PREFERENTIAL PREDATION BY EPIBENTHIC PREDATORS

Ambrose argues that predatory infauna may be more susceptible to epibenthic predation than nonpredatory infauna because they are more active at the sediment surface. However, some infaunal predators are always found beneath the sediment surface such as the nemertean *Cerebratulus lacteus* (McDermott 1976) and the polychaete *Glycera dibranchiata* (Klawe & Dickie 1957). Some phyllodocid polychaetes and nemerteans which are found on the sediment surface produce a

copious mucus which is repellent to a number of fish species (Prezant 1980). Furthermore, tubicolous, non-predatory infauna frequently leave their tubes or burrows (Fauchald & Jumars 1979, Fish & Mills 1979, Boates 1980, Harris & Morgan 1984). It is not valid to assume that predatory infauna are subject to higher levels of epibenthic predation than nonpredatory infauna merely based on presumed differences in motility of the 2 groups.

Gut analyses of epibenthic predators fail to support the assumption of preferred ingestion of predatory infauna. Although many of the shorebird references cited by Ambrose (1984a) in support of preferential predation on infaunal predators by shorebirds do report known predatory infauna in shorebird diets (Recher 1966, Bengston & Svensson 1968, Goss-Custard 1977a, b, Goss-Custard et al. 1977, Bryant 1979, Hicklin & Smith 1979), I find no evidence of preferential predation on predatory infauna.

The literature lacks evidence for preferential predation on predatory infauna by fish and crabs. Virnstein (1979) lists the 18 most abundant infaunal species collected during caging experiments and assesses their relative responses to the exclusion of fish and crab predation. The only predator among these species is the polychaete *Glycera dibranchiata* which increased in the absence of epibenthic predation but not to the extent of many of the nonpredatory, non-opportunistic infaunal species (e.g. *Mya arenaria* and *Lyonisia hyalina*). Ambrose cites a number of references on the diets of predatory fish and crabs (Klawe & Dickie 1957, Scarratt & Lowe 1972, Wells & Steele 1973, Stickney et al. 1975, Kravitz et al. 1976, Arntz 1979). Klawe & Dickie (1957) report that *Glycera dibranchiata* was found only once in a fish stomach. Among these references, only Arntz (1979) provides data which can be used to show preferential ingestion of an infaunal predator. Plaice and rockling show selection for the polychaetes *Nephtys* spp. but the preference disappears if one excludes the biomass of 2 deep-dwelling bivalves which are not accessible prey for either plaice or rockling. The remaining studies list species of predatory infauna which are eaten but are not preferred prey. Hence, analysis of the diets of epibenthic predatory fails to support the assumption of greater susceptibility of predatory infauna to epibenthic predators.

#### RATIO ANALYSIS

Objections can be raised to Ambrose's criteria for classifying infauna into predatory and nonpredatory species. He claims that 'occasional predatory behaviour may be all that is required for these (omnivorous) species to have a significant effect on the

densities of other infauna'. Yet, there is a dearth of information on the importance of infaunal predation, even for obligate predators. Roe (1976) documented a 14 to 35 % reduction of the preferred prey species of a nemertean. Reise (1978) presented correlative evidence for a weak effect of nemerteans and infaunal anemones on other infauna. Commito (1982) and Ambrose (1984b) show significant predation by a nereid polychaete on the amphipod *Corophium volutator*. All of these studies concern strict predators. I can find no examples of putative omnivorous species demonstrating any significant predatory effect. It is not yet resolved whether infaunal predation is a primary organizing process in marine infaunal communities. Until the question is answered, it is necessary to allow only known predators into the ratio analysis as infaunal predators. The purpose of the analysis should be to try to reject the alternative hypothesis, the 3-way interactive model, not to confirm it. A liberal definition of predatory infauna invites Type I errors, errors which should be minimized in such an analysis.

It is necessary to exclude small predatory infauna which cannot ingest or kill adult nonpredatory infauna. Adult infauna are operationally defined as all organisms which will be retained by the sieve size used in a given study. Organisms such as syllid polychaetes necessitate this size criterion. A syllid feeds by puncturing its prey with a chitinized tooth and removing the soft parts with its pumping pharynx (Fauchald & Jumars 1979). Most are small (<10 mm long) and are incapable of swallowing an adult macrofaunal organism. Infaunal syllids may well have significant effects on meiofauna and recently settled juveniles of macrofauna. However, predation on juveniles will affect both predatory and nonpredatory infauna. It is not trivial to note that predatory infauna must pass through a vulnerable larval/juvenile stage.

Similar arguments apply to phoxocephalid amphipods which are potent predators on settling stages of infauna (Oliver et al. 1982) but not capable of consuming adult macrofauna.

I have recalculated the ratios of predatory to non-predatory infauna for 4 of the studies used by Ambrose (Naqvi 1968, Young & Young 1977, Reise 1978, Holland et al. 1980) using a more restrictive and conservative definition of infaunal predator. These 4 studies were chosen *a priori* for reanalysis because they are available in the primary literature for readers who wish to compare our analyses. Two of the theses used by Ambrose wholly (Lee 1978) and partly (Summerson 1980) concern sand habitats where Ambrose's analysis showed that the 3-level model is not appropriate.

Based on my arguments above, I require that an infaunal predator be a strict predator and that it be capable of ingesting adult nonpredatory infauna. In Naqvi (1968), *Glycera dibranchiata* and *G. americana*, *Eulalia sanguinea*, the 4 eunicean polychaetes and the nemerteans *Cerebratulus lacteus* and *Lineus socialis* are admissible as infaunal predators. *Nephtys buccera* is considered a deposit-feeder based on its overwhelming abundance and size. *Synsyllis longigularis* is too small to be a predator on adult macrofauna.

From Young & Young (1977), only nemerteans are considered infaunal predators. The syllid *Exogone dispar* is excluded on the basis of size and deposit-feeding habits (Fauchald & Jumars 1979).

From Reise (1978), the following organisms are considered to be infaunal predators: the nemerteans *Amphiporus lactifloreus*, *Tetrastemma melanocephalum* and *Lineus viridis*, and the polychaetes *Eteone longa*, *Phyllodoce mucosa*, *Nereis virens* and *Nephtys hombergi*. The omnivorous *Nereis diversicolor* is excluded. The 2 phyllodocid polychaetes are included even though recent evidence (Zajac 1985) indicates

Table 2. Source of data, densities of predatory and nonpredatory infauna, their ratios in caged and control areas and the differences and sign of those ratios. All data are from muddy-sand habitats

Source	Predatory infauna		Nonpredatory infauna		Cage	Control	Difference
	Control	Cage	Control	Cage			
Naqvi (1968)	55	53	257	747	0.071	0.214	-0.143
Reise (1978)							
Table 7	1	39	149	3420	0.011	0.007	+0.004
Table 8	5	20	823	3312	0.006	0.006	0
Table 9	0	5	477	4932	0.001	0.000	+0.001
Holland et al. (1980)							
Nov	487.5	510.3	9045.1	14984.4	0.034	0.054	-0.020
Mar	643.6	1453.8	32056.1	31922.8	0.046	0.020	+0.026
May	843.1	2102.3	40919.8	59753.0	0.035	0.021	+0.014
Jul	492.7	8453.3	6963.8	72006.8	0.017	0.071	+0.046
Aug	109.4	164.2	5529.2	5803.4	0.028	0.020	+0.008

Table 3. Source of data, densities of predatory and nonpredatory infauna, their ratios in caged and control areas and the differences and sign of those ratios. All data are from seagrass habitats

Source	Predatory infauna		Nonpredatory infauna		Cage	Control	Difference
	Control	Cage	Control	Cage			
Young & Young (1977)							
Haulover	116	0	5009	6899	0.000	0.023	-0.023
Linkport	71	0	2321	3312	0.000	0.031	-0.031
St. Lucie	92	111	1346	1035	0.107	0.068	+0.039
Reise (1978)							
Table 16	11	35	1440	1537	0.023	0.008	+0.015
Table 17	15	17	1533	1577	0.011	0.010	+0.001
Table 18a	0	0	981	820	0.000	0.000	0
Table 18b	0	0	981	1011	0.000	0.000	0
Table 19	32	69	1986	1527	0.045	0.016	+0.029
Table 20	16	20	3327	2711	0.007	0.005	+0.002

that these predators take only portions of their polychaete prey and hence may not induce mortality.

From the muddy-sand site in Holland et al. (1980), only the phyllodocids *Eteone longa* and *E. heteropoda*, the rare amphinomid *Pseudeurythoe paucibranchiata* and the nemertean *Micrura leidyi* are classified as infaunal predators. The goniadid *Glycinde solitaria* is excluded on the basis of its small size.

The re-analyses of these data are shown in Table 2 (muddy-sand habitat) and Table 3 (seagrass habitat). For the muddy-sand sites, the (cage-control) statistic is positive in 6 of the 9 cases. However, 3 of these cases have differences of less than 0.01 and are best interpreted as not significantly different from 0.00. The differences for the remaining 3 experiments are never greater than 0.046. In 2 cases, the abundance of predatory infauna fails to be higher in predator exclusion treatments as should be the case if epibenthic predators are preying upon the predatory infauna.

From the seagrass habitat (Table 3), 5 of the 9 experiments have positive differences between caged and control ratios. However, 2 of these (Reise 1978, Tables 17 and 20) show no difference in the number of predatory infauna between caged and open areas; the 3-way interactive model requires that infaunal predators be more abundant in the absence of epibenthic predation. Three of the differences between ratios are less than 0.015 and should not be considered different from 0.00. Only 2 of the differences can be considered significantly greater than 0.00. Even here, the differences are not large as is suggested by the depiction of the 3-way interactive model (Ambrose 1984a, Fig. 1).

## DISCUSSION

I do not deny the possible importance of infaunal predation in determining the distribution and abun-

dance of other infauna. This area of research is promising and more experimental data are needed. The best example to date of the importance of infaunal predation is the *Glycera dibranchiata* - *Nereis virens* - *Corophium volutator* community analyzed convincingly by Commito (1982) and Ambrose (1984b). However, Ambrose (1984b) was able to demonstrate no significant effect of epibenthic predators after 10 wk and only a weak although significant effect after 20 wk. Observations of feeding by gulls (Ambrose 1986) showed that gulls remove 0.04 % of the population of large *N. virens* over the course of a tide. This rate extrapolates to 6.8 % of the population of large *N. virens* over the period of June to October. Given that the 95 % confidence intervals for large *N. virens* are  $\pm 190$  %, 67.1 % and 30.4 % of the means for high, middle and low intertidal stations, respectively (Ambrose 1986), removal of 6.8 % of *N. virens* is not statistically detectable. Hence, in the community where infaunal predators have the strongest effect yet demonstrated, the 3-level interactive model is at best weakly applicable. It is becoming apparent that complex trophic interactions occur in infaunal communities (e.g. Commito 1982, Kneib & Stiven 1982, Ambrose 1984b, Commito & Shrader 1985). However, until it is demonstrated that epibenthic predators take infaunal predators preferentially and that infaunal predators significantly affect nonpredatory infauna, a 2-level model of epibenthic predators and infauna should have primacy as the best general description of marine soft-sediment communities.

*Acknowledgements.* W. G. Ambrose, Jr., J. Grant, R. T. Kneib and S. A. Woodin made valuable criticisms and comments on the manuscript. Although I do not share all of their views, I am grateful for them. The author was supported during the preparation of this manuscript by a NATO Postdoctoral Fellowship.

## LITERATURE CITED

- Ambrose, W. G., Jr. (1984a). Role of predatory infauna in structuring marine soft-bottom communities. *Mar. Ecol. Prog. Ser.* 17: 109-115
- Ambrose, W. G., Jr. (1984b). Influence of predatory polychaetes and epibenthic predators on the structure of a soft-bottom community in a Maine estuary. *J. exp. mar. Biol. Ecol.* 81: 115-145
- Ambrose, W. G., Jr. (1986). Estimate of removal rate of *Nereis virens* (Polychaeta: Nereidae) from an intertidal mudflat by gulls (*Larus* spp.). *Mar. Biol.* 90: 243-247
- Arntz, W. E. (1979). Predation by demersal fish and its impact on the dynamics of macrobenthos. In: Tenore, K. R., Coull, B. C. (ed.) *Marine benthic dynamics*. University of South Carolina Press, Columbia, p. 121-129
- Bengston, S. A., Svensson, B. (1968). Feeding habits of *Calidris pusilla* L. and *C. minuta* in relation to the distribution of marine shore invertebrates. *Oikos* 19: 152-157
- Boates, J. S. (1980). Foraging semipalmated sandpipers *Calidris pusilla* L. and their major prey *Corophium volutator* (Pallas) on the Starrs Point mudflat, Minas Basin. M. Sc. thesis, Acadia University, Wolfville
- Bryant, D. M. (1979). Effects of prey density and site characteristics on estuary usage by overwintering waders (Charadrii). *Estuar. coast. Shelf Sci.* 9: 369-384
- Commito, J. A. (1982). The importance of predation by infaunal polychaetes in controlling the structure of a soft-bottom community in Maine, USA. *Mar. Biol.* 68: 77-81
- Commito, J. A., Shrader, P. B. (1985). Benthic community response to experimental additions of the polychaete *Nereis virens*. *Mar. Biol.* 86: 101-107
- Fauchald, K., Jumars, P. A. (1979). The diet of worms: a study of polychaete feeding guilds. *Oceanogr. mar. Biol. A. Rev.* 17: 193-284
- Fish, J. D., Mills, A. (1979). The reproductive biology of *Corophium volutator* and *C. arenaria* (Crustacea: Amphipoda). *J. mar. biol. Ass. U.K.* 59: 355-368
- Goss-Custard, J. D. (1977a). Optimal foraging and the size selection of worms by redshank, *Tringa totanus* (L.), in relation to prey density. *Anim. Behav.* 25: 10-29
- Goss-Custard, J. D. (1977b). The energetics of prey selection by redshank, *Tringa totanus* (L.), in relation to prey density. *J. Anim. Ecol.* 46: 1-19
- Goss-Custard, J. D., Jones, R. E., Newberg, R. E. (1977). The ecology of the Wash. I. Distribution and diet of wading birds (Charadrii). *J. appl. Ecol.* 46: 1-19
- Harris, G. J., Morgan, E. (1984). Entrainment and the circatidal rhythm of the estuarine amphipod *Corophium volutator* (Pallas) to non-tidal cycles of inundation and exposure in the laboratory. *J. exp. mar. Biol. Ecol.* 80: 235-245
- Hicklin, P. W., Smith, P. C. (1979). The diets of five species of migrant shorebirds in the Bay of Fundy. *Proc. Nova Scotian Inst. Sci.* 29: 483-488
- Holland, A. F., Mountford, N. K., Hiegel, M. H., Kaumeyer, K. R., Mihursky, J. A. (1980). Influence of predation on infaunal abundance in upper Chesapeake Bay, USA. *Mar. Biol.* 57: 221-235
- Klawe, W. L., Dickie, L. M. (1957). Biology of the blood worm *Glycera dibranchiata* Ehlers and its relation to the blood worm fishery of the maritime provinces. *Bull. Fish. Res. Bd Can.* 115: 1-37
- Kneib, R. T., Stiven, A. E. (1982). Benthic invertebrate responses to size and density manipulations of the common mummichog, *Fundulus heteroclitus*, in an intertidal salt marsh. *Ecology* 63: 1518-1532
- Kravitz, M. J., Percy, W. G., Guinn, M. P. (1976). Food of the five species of co-occurring flatfishes on Oregon's continental shelf. *Fish. Bull. U.S.* 74: 984-990
- Lee, H. (1978). Predation and opportunism in tropical soft-bottom communities. Ph.D. thesis, Univ. of North Carolina, Chapel Hill
- McDermott, J. J. (1976). Predation of the razor clam *Ensis directus* by the nemertean worm *Cerebratulus lacteus*. *Chesapeake Sci.* 17: 299-301
- Naqvi, S. M. (1968). Effects of predation on infaunal invertebrates of Alligator Harbor, Florida. *Gulf Res. Rep.* 2: 313-321
- Oliver, J. S., Oakden, J. M., Slattery, P. N. (1982). Phoxocephalid amphipod crustaceans as predators on larvae and juveniles in marine soft-bottom communities. *Mar. Ecol. Prog. Ser.* 7: 179-184
- Prezant, R. S. (1980). An antipredation mechanism of the polychaete *Phyllodoce mucosa* with notes on similar mechanisms in other potential prey. *Fish. Bull. U.S.* 77: 605-616
- Recher, H. F. (1966). Some aspects of the ecology of migrant shorebirds. *Ecology* 47: 393-407
- Rsie, K. (1978). Experiments of epibenthic predation in the Wadden Sea. *Helgoländer Meeresunters.* 31: 55-101
- Roe, P. (1976). Life history and predator-prey interactions of the nemertean *Paranemertes peregrina* Coe. *Biol. Bull. mar. biol. Lab., Woods Hole* 150: 80-106
- Scarratt, D. J., Lowe, R. L. (1972). Biology of rock crab (*Cancer irroratus*) in Northumberland Strait. *J. Fish. Res. Bd Can.* 29: 1561-1566
- Stickney, R. R., Taylor, G. L., White, D. B. (1975). Food habits of five species of young southeastern United States estuarine Sciaenidae. *Chesapeake Sci.* 16: 104-114
- Summerson, H. C. (1980). The effects of predation on the marine benthic invertebrate community in and around a shallow subtidal seagrass bed. M.S. thesis, Univ. of North Carolina, Chapel Hill
- Virnstain, R. W. (1979). Predation on estuarine infauna: response patterns of component species. *Estuaries* 2: 69-86
- Wells, B., Steele, D. H. (1973). Intertidal feeding of winter flounder (*Pseudopleuronectes americanus*) in the Bay of Fundy. *J. Fish. Res. Bd Can.* 30: 1374-1378
- Young, D. K., Young, M. W. (1977). Community structure of the macrobenthos associated with seagrass of the Indian River estuary, Florida. In: Coull, B. C. (ed.) *Ecology of marine benthos*. University of South Carolina Press, Columbia, p. 359-382
- Zajac, R. N. (1985). The effects of sublethal predation on reproduction in the spionid polychaete *Polydora ligni* Webster. *J. exp. mar. Biol. Ecol.* 88: 1-20