

COMPETITION AND PREDATION IN MARINE SOFT-SEDIMENT COMMUNITIES

*W. Herbert Wilson*¹

Department of Zoology NJ-15, University of Washington, Seattle, Washington 98195

KEY WORDS: competition, predation, soft-sediment, infauna, succession

INTRODUCTION

One of the major goals of community ecology is to understand how interactions among the resident organisms affect their distribution and abundance. For terrestrial and rocky intertidal communities competition and predation clearly can play pivotal roles in community organization (28, 47, 84). The importance of biological processes in organizing marine soft-sediment communities is not as well understood (86), despite the fact that marine soft-sediments are the most common habitat on earth. As I argue below, paradigms of community organization based on other habitats seem to offer little insight into the structure of marine soft-sediment communities. Rather than attempting to explain the failure of such paradigms, I argue that soft-sediment habitats are sufficiently different from other communities that different paradigms are needed.

Soft-sediment communities are unusual in the rate at which the nature of the physical environment can change. Most sedimentary particles are smaller than the resident organisms (the infauna). The activities of the infauna can dramatically change the nature of the environment over time periods of hours or days. For instance, burrowing infauna may increase the porosity and erodability of the sediment (102). Subsurface deposit-feeders may alter the

¹Present address: Department of Biology, Colby College, Waterville, Maine 04901

vertical distribution of sediment grain sizes and change the spectrum of grain sizes by ingesting small sediment particles and egesting them as larger fecal pellets. The effects of infauna have dramatic and rapid effects on sediment biogeochemistry (2). Infaunal organisms live in, rather than on, the substratum, and their activities alter the fundamental nature of the habitat on very short temporal scales. These characteristics require a unique perspective into the nature of competitive interactions in these communities.

This review on the importance of competition and predation in structuring infaunal communities emphasizes experimental studies. Since the introduction of experimental methods to the study of soft-sediment communities (76, 103), the depth of understanding and the strength of inferences have increased greatly. The emphasis on experimental data necessitates a bias toward intertidal and shallow subtidal communities because experimental data from the deep sea have been difficult and expensive to collect.

COMPETITION

Direct Interactions

Because of the three-dimensional structure of soft-sediment habitats, vertical and horizontal partitioning of space is possible, reducing direct encounters of potential competitors with each other. Nevertheless, direct interactions are found most frequently between conspecifics or closely related species (141, 144). Agonistic interactions have been described among nereid polychaetes (104). Opheliid polychaetes apparently interact directly to maintain constant abundance per volume of sediment (112, 137). Levin (62) showed that the regular dispersion pattern of the spionid polychaete, *Pseudopolydora paucibranchiata*, is maintained by strong, direct, competitive interactions. Aggressive interactions of *P. paucibranchiata* with associated tube-building infauna result in significantly reduced foraging time for the latter species (63). Direct interactions of the polychaete *Nereis diversicolor* with the amphipod *Corophium volutator* led to declines of the amphipod (81). Croker & Hatfield (31) demonstrated strong direct effects (increased mortality and reduced reproductive effort) of one haustoriid amphipod on a second species; the inferior competitor is confined to the high intertidal zone in the field. Grant (45) demonstrated similar interactions of two haustoriids which led to vertical separation with the inferior competitor forced to occupy deeper, anoxic sediments in the presence of the superior competitor. Vertical zonation of bivalves in a California lagoon changed in apparent response to the removal of the thalassinid shrimp, *Callinassa californiensis*, implying competitive release (85). Deposit-feeding protobranch bivalves changed their position as a function of heterospecific density (64). Intertidal gastropod zonation is maintained by the displacement of *Hydrobia totteni* by *Ilyanassa obsoleta* (66). All

of these interactions occur among organisms that at least attempt to establish at the same depth in the sediment.

Exploitative Competition

SUSPENSION-FEEDERS Because direct competitive interactions are minimized by the three-dimensional nature of the habitat, indirect competitive mechanisms are to be expected. Peterson (87, 89, 90) has provided a wealth of experimental data on exploitative competition among suspension-feeding bivalves. Bivalves are advantageous research organisms because they can be easily marked and their growth can be accurately quantified. Identification of competitive effects can be measured through differences in growth as well as survivorship. The growth of *Sanguinolaria nuttallii* was reduced by 80% when these clams were confined with two other deep-dwelling bivalves, although no effects of a shallow-dwelling bivalve were evident on *S. nuttallii* growth. These results imply that competition for space is occurring. The interpretation of this interaction was confirmed by confining *S. nuttallii* with surrogates of the other deep-dwelling clams (valves of dead clams tied together and placed in life position in the sediment). The growth of *S. nuttallii* was depressed in the presence of the surrogate clams to an extent equal to the reduction of growth in the presence of living clams. A study of competition among two shallow-dwelling bivalves (*Protothaca staminea* and *Chione undatella*) involved the enclosure of these species at a range of densities (1/2X to 8X normal density) in the field (87). The growth rate of each species as well as the ratio of the dry weight of gonads to the dry weight of total soft parts, a measure of reproductive effort, declined as a negative function of intraspecific density. Density-dependent migration of *P. staminea* was documented. Over the two years of the study, few deaths could be attributed to competition. Interspecific interactions were usually not significant. Because the two bivalve species occupy the same depth stratum in the sediment, one infers that food is the limiting resource and that the two species differ somehow in the types of phytoplankton they consume. Experiments with Australian suspension-feeding bivalves (90) indicated that bivalves transplanted into the high intertidal grew less than conspecifics established lower in the intertidal zone. The depression of growth was not a linear function of immersion time, implying that there is density-dependent reduction of food as the tide rises. The observation that the phytoplankton can be depleted from the water column by the suspension-feeders in an intertidal mudflat (21) implies that competition for food may be occurring among suspension-feeders in a Maine mud flat.

The strength of competition may have a strong environmental component. When the bivalve *Macoma baltica* was maintained in a muddy sediment in the field, growth was found to be density-dependent, while conspecifics main-

tained in sand showed no density-dependence of growth (79). The difference may be related to the facultative feeding behavior of this bivalve; in muddy substrates, deposit-feeding predominates whereas suspension-feeding predominates in sandy substrates.

DEPOSIT-FEEDERS Characterization of the food resources for deposit-feeders is elusive (67). Except for differences in sizes of sediment grains ingested (124), little is known of the differential use, if any, of the various components of detritus by deposit-feeders. It is therefore impossible to enhance detritus levels in the field with any degree of confidence. As an alternative to varying food levels, soft-sediment ecologists have adopted the approach of varying densities of deposit-feeders, thereby influencing per capita resource levels. Even this approach is problematic because the feeding rate and density of deposit-feeders affect the growth of diatoms and bacteria in diverse ways; increased feeding of detritivores may enhance microfloral growth (11, 12, 30). Most of the organisms studied have been soft-bodied organisms whose growth is difficult to measure. The commonly measured responses of deposit-feeders to density are emigration rates and mortality.

For the deposit-feeding snail *Hydrobia ventrosa*, Levinton (65) showed that feeding and movement decreased as a function of increasing density and that floating, a means of dispersal, increased as density rose. Wilson (130) manipulated the densities of two species of co-occurring spionid polychaetes; the density of each species was varied independently over four experimental densities. Migration in and out of the experimental containers was strongly density-dependent; after eight weeks all containers had densities indistinguishable from ambient densities. Strong intraspecific effects were documented but interspecific effects were weak and usually not statistically significant. Ambrose (7) showed that emigration of a burrowing, deposit-feeding amphipod was density-dependent. Wilson (134) documented strong size-dependent emigration in the amphipod *Corophium volutator* with juveniles forced to emigrate from high adult densities.

Several efforts have been made to manipulate directly the detrital resource levels. Young & Young (146) added processed sewage sludge (Milorganite) to seagrass beds. Some species responded positively to Milorganite addition while others were unaffected. Dauer et al (32) added organic fertilizer to a subtidal site and documented no change in densities of members of the community, although the densities of some species in predator exclusion cages (at densities above control densities) did increase. However, it is not clear how long the enrichment persisted in the sediment. Wiltse et al (136) added urea to a salt marsh habitat in Massachusetts, which resulted in significant increases in sediment chlorophyll but no increase in infaunal abundance. The latter two studies can be cautiously interpreted to show that

detritus is not limiting in the two communities. However, the uncertainty about the nature of detrital resources and the effects of the experimental treatments brings into question the realism of the enrichments.

Sediment-Mediated Interactions

The rapidity with which the features of the sedimentary environment change as a function of biotic activity provides an additional means of interaction between infauna. Such sediment-mediated interactions are common in many infaunal communities. The effects of resident organisms on the sediment may render the sediment less habitable by other organisms. Such interactions were first explored by Rhoads & Young (103) who noted that sandy substrates tended to be dominated by suspension-feeders while mud substrates were dominated by deposit-feeders. Predicting that deposit feeders roil the sea bottom sufficiently to clog the filtering apparatus of suspension-feeding organisms (the trophic group amensalism hypothesis), Rhoads & Young showed that the growth of the bivalve *Mercenaria mercenaria* was, when grown near the bottom above a deposit-feeder community, significantly depressed relative to the growth of conspecifics grown at greater heights off the bottom. For the duration of the experiment (64 days), no significant mortality occurred. These data provide some support for the limitation of growth of suspension-feeders in sediments dominated by deposit-feeders. Woodin (138) shifted the focus from trophic group to mobility group; her functional groups were suspension-feeders, tube-building organisms, and bioturbators (sediment destabilizers). The effects of any group were predicted to be inimical to individuals from other functional groups. Tube-builders and bioturbators strongly alter the sedimentary environment; these functional groups are discussed below. Suspension-feeders typically have minimal effect on the nature of the sediment (141).

TUBE-BUILDERS Tube-building organisms, particularly when abundant, are predicted to retard the movement of burrowing organisms and to preempt space from large suspension-feeders (137, 138). In Washington state, Woodin (137) first demonstrated significant tube-builder effects when she noted that the larvae of tube-building polychaetes were confusing the surface of experimental cages with the sediment surface. As a result, the density of tube-builders, primarily three polychaetes, was significantly reduced inside the cages relative to unmanipulated control areas. Significantly greater numbers of a burrowing polychaete (*Armandia brevis*) were found in cages with low tube-builder density, compared to unmanipulated areas with high tube-builder density. Strong negative correlations existed between *A. brevis* abundance and combined tube-builder abundance. Laboratory experiments indicated that each *A. brevis* required a minimum volume of sediment. The

interaction seen in the field is therefore interpreted as competition for space. In areas of high tube-builder abundance, burrowers have less available sediment for burrowing and feeding. Hulberg & Oliver (34, 53) challenged this interpretation, claiming from experiments in California that the larvae of the *A. brevis* preferentially settle within cages, irrespective of tube-builder abundance. The laboratory experiments of Woodin support her interpretation rather than the alternative posed by Hulberg & Oliver. Tamaki (112) showed that the larvae of *Armandia* sp. did not preferentially settle in sediments taken from within a cage although the effects of flow were not examined. He did corroborate Woodin's finding of a minimum volume requirement for each worm, but he claimed that competition for food, rather than space, was limiting. It is difficult if not impossible to separate food from space as distinct resources for a mobile infaunal species.

Other efforts to document exclusion of other functional groups by tube-builders have met with mixed results. Reise (100) found a negative relationship between burrowing capitellid polychaetes and tubicolous spionid polychaetes in some predator-exclusion experiments. Brenchley (19) showed that eelgrass (*Zostera marina*) root-mats and dense tube-mats of mixed species composition acted additively to retard the movement of burrowing deposit-feeders. In most cases, the burrowers were able to penetrate the mat. Thus, her data do not provide evidence of exclusion. Measurement of lateral movement rather than vertical burrowing would have been enlightening. Wilson (131) found that tubicolous spionid polychaetes and tanaid crustaceans coexisted with a sediment-destabilizing bivalve in laboratory experiments. Weinberg (123) found conflicting effects of tube-builders on a suspension-feeding bivalve (*Gemma gemma*); a tubicolous spionid (*Polydora ligni*) had a negative influence on bivalve abundance while a tubicolous maldanid polychaete (*Clymenella torquata*) had a positive effect. The spread of an eelgrass (*Zostera marina*) bed was associated with declines in the abundance of a burrowing crustacean (*Callianassa californiensis*), presumably because the seagrass root-mat impeded burrowing (48). Lateral movement of the bivalve *Macoma secta* was influenced more by sedimentary properties than by the dense arrays of phoronid (*Phoronopsis viridis*) tubes (34, 106). A summary of the available data indicates that the tube-builders or root-mats may be associated with diminished numbers of mobile burrowers but that burrowers are never totally excluded.

BIOTURBATORS Disruption of the sediment by animal activities (feeding, burrowing) is predicted to have negative effects on suspension-feeding and tube-building infauna. Depressed growth of suspension-feeders in the presence of bioturbating organisms was first shown for bivalves (103) and scleractinian corals (1). A suspension-feeding bivalve (*Sanguinolaria nuttallii*) increased after the experimental removal of a burrowing thalassinid shrimp,

Callianassa californiensis (85). Exclusion of epibenthic gastropods resulted in increases of spionid polychaetes (135) and oligochaetes and capitellid polychaetes (41). For tube-building organisms, removal of a mobile cockle (*Cerastoderma edule*) led to an increase in the tube-building amphipod crustacean, *Corophium volutator* (55). Brenchley (18) conducted a thorough laboratory analysis of the effect of sedimentation on a tube-building assemblage and showed that mortality of the tube-dwellers was a function of the size of the animal, presumably correlated positively with the ability to burrow through newly deposited sediment, as well as a function of the magnitude and frequency of the sedimentation episodes. Wilson (129) demonstrated a reduction of spionid polychaetes in areas of high sediment disturbance by the polychaete *Abarenicola pacifica*. A small spionid polychaete (*Pygospio elegans*) was reduced in the presence of *A. pacifica* relative to controls while a larger spionid (*Pseudopolydora kempii*) was unaffected. Laboratory experiments indicated that suffocation rather than emigration was the likely mechanism of reduced spionid abundances. However, emigration from intermediate levels of sediment disruption permitted local survival; despite emigration, mortality was great at high levels of bioturbation. Highsmith (49) demonstrated significant reductions in the abundance of tube-dwelling tanaids (*Leptocheilia dubia*) in the presence of burrowing sand dollars (*Dendraster excentricus*), providing an explanation for the patchy distribution of these two species in the field. The deposit-feeding bivalve, *Macoma balthica*, and a cockle, *C. edule*, caused a local reduction of the small spionid, *P. elegans*, but not a larger confamilial species (*Spio filicornis*) (101). Ronan (34, 106) showed that the thalassinid shrimp, *Callianassa californiensis*, disrupted the orientation of the tubes of the phoronid *Phoronopsis viridis* in California. In Oregon, the densities of most sedentary species were reduced in the presence of *C. californiensis* (92). Laboratory experiments indicated that tube-builders could coexist with a small, mobile clam (*Transennella tantilla*), indicating that the sediment disruption of the bivalve was insufficient to affect other members of the community (131).

The available data therefore indicate that animal-mediated sediment disturbance can have significant deleterious effects on suspension-feeders and tube-builders in infaunal communities. The result of such disturbance is a complex function of the sizes of the organisms and the magnitude and frequency of the sediment disturbance (94, 129). Presently, there is insufficient information to allow the formulation of a predictive model of the effect of bioturbators on other functional groups. A major barrier to such a model is the inadequacy of functional groupings (57). Depending on animal density, sediment microflora, and the strength of ambient flow, an assemblage of tube-builders may stabilize or destabilize sediments, with correspondingly divergent effects on other members of the infauna (38, 46, 57, 68).

Influence of Adults on Settling Larvae and Juveniles

ESTABLISHED COMMUNITIES In her expansion of the trophic group amensalism hypothesis (103), Woodin (138) presented the hypothesis that discrete, densely populated patches of infaunal invertebrates maintain their integrity by preventing the recruitment of larvae of other species. The mechanism of such adult-larval interactions is predicted to vary among functional groups: Bioturbators should suffocate larvae, suspension-feeders should filter larvae from the plankton, and tube-builders should exclude larvae by preemption of space and defecation on the sediment surface. Although exceptions are frequently seen to the predicted associations of functional groups (138), the concept of adult-larval interactions has had a pervasive influence in the study of marine infaunal communities. In the laboratory, Wilson (128) demonstrated that terebellid polychaetes significantly depress the survivorship of nereid polychaete larvae. Field experiments have met with mixed success in their support of the adult-larval hypothesis. Williams (126) showed reduced survivorship of clam spat (*Tapes japonica*) among high densities of conspecific adults to that in areas where adult clams were absent or at low density. Through field and laboratory experiments, Highsmith (49) showed that tanaid crustaceans (*Leptochelia dubia*) prey on the settling larvae of sand dollars (*Dendraster excentricus*). Negative effects of organisms on the settlement and survivorship of larvae or recently settled juveniles have been demonstrated for drifting algal mats (80), nereid polychaetes (3), spionid polychaetes (69, 100, 113, 123, 125, 129), a mixed polychaete assemblage (133), phoxocephalid amphipods (82, 83), pontoporeid amphipods (39), nassariid gastropods (54), and bivalves (15, 55). Intraspecific adult-larval interactions are demonstrably strong in a nereid polychaete (58) and a corophiid amphipod (134). Despite these observations and experimental support for the importance of adult-larval interactions, other data fail to support the hypothesis. Using microcosms, Maurer (74) was unable to demonstrate any effect of varying densities of venerid bivalves on larval recruitment. In field experiments, Hines et al (51) varied the densities of a suspension-feeding bivalve (*Mya arenaria*) and a deposit-feeding bivalve (*Macoma balthica*). Although they could demonstrate reduced larval abundances at high adult densities for both bivalves, the responses of the larvae of individual settling species were inconsistent. Positive effects of adult density were even documented for some species with planktonic larvae. Similarly, Commito (23) found that the infauna below mussel (*Mytilus edulis*) beds were not reduced; oligochaete abundance decreased in response to experimental removal of *M. edulis* (26).

Recently, Watzin (120–122) has identified meiofaunal predators, particularly turbellarians, as potent predators on settling infauna. She experimentally doubled the densities of meiofauna in experimental containers and compared settlement in those containers to settlement in cores of unmanipulated

meiofauna. Although ambient meiofaunal density served as a control rather than, for instance, half-normal density or absence of meiofauna, the strengths of the meiofauna-larval effects documented suggest that these interactions may be important determinants of macrofaunal settling success.

The present data indicate that adult-larval interactions are detectable in the field and in the laboratory. However, the mechanism of the interaction is typically not determined in field experiments. Field tests are unable to distinguish between avoidance of high densities of adults by larvae and increased mortality of settling larvae by ingestion or suffocation by established adults. Woodin (143) provided field data which show reduced settlement of larvae of a spionid polychaete (*Pseudopolydora kempii*) in the presence of an arenicolid polychaete (*Abarenicola pacifica*). Eckman (37) presented data showing that passive hydrodynamic effects from tubes or plant stalks may cause the accumulation of larvae. Similarly, Ertman & Jumars (40) showed that larvae may passively accumulate around projecting bivalve siphons. Our present level of understanding of these phenomena does not allow prediction of conditions where adult-larval interactions are important structuring forces in the community.

SUCCESSION Following a disturbance that clears a soft-sediment habitat, colonization may be quite rapid and proceed with an early pulse of opportunistic species, followed by the arrival of species whose abundance remains relatively constant (70, 71). The successional models of Connell & Slatyer (29) have provided a theoretical framework for soft-sediment succession. The models presume that early colonists may have a negative (inhibition model), a positive (facilitation model), or no effect (tolerance model) on subsequent recruits. Three major successional studies in soft-sediment habitats have been conducted in light of these theories. Zajac & Whitlatch (149, 150) followed the colonization of defaunated sediment at three tidal heights in Connecticut. Succession did not vary as a function of tidal height. Recruitment did not vary consistently as a function of the number of residents, and hence their data are most consistent with the tolerance model of succession. Gallagher et al (43) examined succession on a smaller scale on an estuarine flat in Washington as a function of several common species on the flat (polychaetes, bivalves, crustaceans) as well as simulated tubes. They monitored the dynamics of eight species over five manipulations. Twenty-four of the treatment \times recruiting species combinations showed no effect of the experimental treatment, 11 showed a positive effect, and only one showed a negative influence. Although "facilitation" appears in the title of their paper, the tolerance model is most applicable to their successional dynamics. Ambrose (3) followed succession in defaunated sediments in Maine. Later recruitment varied inversely with the density of established juveniles. These studies demonstrate that all three models of succession may be operative. The

data available are insufficient to allow predictions of the type of successional dynamics in a given habitat.

PREDATION

Methodology

Experimental analyses of the effects of predation in infaunal communities have generally involved the exclusion or enclosure of suspected predators. Comparison to unmanipulated areas allows the investigator to assess the strength of the predators. However, cages baffle currents, potentially altering sedimentation rates and the supply of phytoplankton. Some workers assess the effects of cages by comparing the sediments inside and outside of cages (16, 17, 41, 52, 97). Lack of significant differences is taken to mean that hydrodynamic artifacts are unimportant and that any effect of cages is due to exclusion of predators. An alternative method is the emplacement of partial cages (sides only, roof only, half cage) which are designed to mimic the hydrodynamic effects of cages but allow unrestricted access to predators. Any differences between unmanipulated areas and partial cages can be attributed to hydrodynamic artifact. In practice, differences between control areas and partial cages are not detected (4, 96, 111, 134–136, 140). Despite the apparent success of cages at excluding predators without inducing significant hydrodynamic artifact, there is widespread distrust of caging experiments. Working in a high energy environment, Hulberg & Oliver (53) show that the shape of cages has dramatic effects on the outcome of exclusion experiments; this work implies that hydrodynamic artifacts are large. Eckman (36) and Gallagher et al (43) show that even single tubes protruding above the sediment surface may have strong effects on local abundances of organisms. They argue that a cage is bound to have strong hydrodynamic effects. The controversial aspect of caging experiments is therefore the adequacy of partial cages as controls. Until a study of cages and partial cages is performed in a flume in a variety of flow conditions, controversy will continue over the interpretation of caging experiments. Virnstein (115, 116) offers sage advice, urging that the results of caging experiments be augmented with observational data, gut content analysis, or laboratory experiments before acceptance of predation as the process producing any experimental differences. Frid & James (42) caution that lateral migration in and out of cages may confound results. Field enclosures of predators are of limited value in my view because of altered behavior of mobile predators when their movement is restricted.

Epibenthic Predation

A number of experiments involving exclusion of epibenthic predators resulted in increases of infauna relative to unmanipulated controls (4, 16, 17, 32, 41, 52, 58–61, 76, 78, 88, 110, 111, 114, 136). Epibenthic predation had

minimal impact in several studies (14, 15, 44, 72, 73, 97). Specific epibenthic predators that have been identified as significant influences include: gastropods (88, 135), horseshoe crabs (17, 140), portunid crabs (114, 140), other decapod crustaceans (78, 117, 145–147), fish (56, 60, 61, 93, 114), and shorebirds (108, 109). Several workers have used different kinds of exclusions to separate out the effects of different predators. Using cages with differing mesh size, Reise (100) claimed that small predators (shore crabs, shrimp, gobies) have a stronger effect on infaunal abundance than do larger predators (flatfish and birds). Woodin (140) used metal stakes to exclude horseshoe crabs (*Limulus polyphemus*) from experimental areas at an intertidal flat in Virginia; this experiment permitted her to separate the strong predator effect of portunid crabs from the weaker horseshoe crab effect. Using full exclusion cages and cages whose sides were attached to floats that lifted off the bottom when the tide was in, Quammen (96) was able to separate the effects of fish (excluded only from the full cages) from the effects of shorebirds (excluded from both types of cages). Fish were found to be of minor importance, while the effect of shorebirds depended on the habitat. She also demonstrated significant effects of a shore crab. Wilson (134) used full cages and roofs to separate the effects of fish and shorebirds in the Bay of Fundy; both types of predators had significant influences on infaunal density and demography.

For studies in which significant effects of epibenthic predation are detected, two patterns consistently emerge. The first is the obvious increase in infaunal abundance and biomass in response to the exclusion of epibenthic predators. The second effect contradicts the predictions of the intermediate disturbance hypothesis which predicts that at low levels of predation, species diversity should decline as a competitive dominant monopolizes the habitat (86). The consistent pattern in epibenthic exclusions is that diversity either increases or remains unaltered. No study has documented a disproportionate rise in abundance of a competitive dominant. The effect is not unexpected because competitive exclusion rarely occurs in soft-sediment communities (see above). Overgrowth interactions which are the chief source of competitive mortality in hard-substrate marine communities do not occur among infaunal organisms (86).

Infaunal Predators

Predatory infauna, primarily nemerteans and polychaetes, have received considerably less attention than epibenthic predators. However, the existing data indicate that infaunal predators may have strong impacts on community structure. The best analyzed example of infaunal predation has been conducted at intertidal sites in Maine. The predatory polychaete, *Glycera dibranchiata*, preys on the polychaete, *Nereis virens*; experimental exclusion of *G. dibranchiata* results in enhanced survivorship of *N. virens* (3, 4). In turn,

N. virens significantly reduces the abundance of the amphipod *Corophium volutator* (4, 22). Commito & Schrader (27) found that the addition of *N. virens* to a community where *C. volutator* is absent resulted in an increase in abundance of other infauna, rather than the predicted decrease due to prey switching by *N. virens*. They postulated that *N. virens* may be removing an intermediate predator, probably the polychaete *Nephtys incisa*, which preys on the infauna.

There are limited additional examples of the influence of infaunal predators. Roe (105) showed that a nemertean predator (*Paranemertes peregrina*) removed 14–35% of the population of a nereid polychaete each year. Reise (98) attributed a decrease in spionid polychaetes to the increased survivorship of infaunal predators within epibenthic predator exclusion cages. Schubert & Reise (110) showed that experimental additions of the predatory polychaete, *Nephtys hombergii*, resulted in significant declines of two burrowing polychaetes. Gut analyses of *N. hombergii* confirmed that these two polychaetes were the major prey items. Rönn et al (107) showed that enhancement of *Nereis diversicolor* resulted in the decrease of chironomid larvae in an oligohaline estuary. Ambrose (5) noted increased emigration by the burrowing amphipod *Rhepoxynius abronius* after the introduction of the predatory infaunal polychaete *Nephtys caeca*.

Commito & Ambrose (24, 25) surveyed the literature for evidence of infaunal predators. Ambrose (6) suggested that infaunal predators should be inserted into the current two-level model of community dynamics (epibenthic predators-infauna). Wilson (132) showed that this model requires that epibenthic predators preferentially remove infaunal predators; otherwise the advantage to the nonpredatory infauna of a decrease in epibenthic predation is exactly counterbalanced by an increase in infaunal predation. Nonetheless, both authors agree (8) that infaunal predation is likely to be of widespread importance in many infaunal communities and deserves more attention.

Browsing Predation

Some predators remove only a portion of their prey. The major prey item of flatfish in the Wadden Sea are spionid palps and bivalve siphons (118). Despite the prevalence of regeneration of body parts in infaunal organisms (91, 127, 146), the importance of browsing predation in the field is poorly understood. Laboratory experiments have demonstrated that the removal of portions of polychaetes results in decreased defecation (proportional to feeding) and tube-building (142) and reduced fecundity (148), although the polychaete *Arenicola marina* tolerates weekly tail amputation with no measurable loss in growth rate (10). While most structures lost to browsing predators are exposed at the sediment surface, some infaunal predators remove portions of prey from below the sediment surface (131). Meiofaunal

predators may remove portions of small macrofauna (121). Browsing predation may indirectly affect mortality. As browsing predators remove the tips of siphons of deep-dwelling bivalves, the bivalves are forced to move toward the sediment surface to make contact with the overlying water, making them more susceptible to digging predators (50).

Complex Trophic Interactions

Multiple levels of predation with complex interactions are being documented in infaunal communities. The *Glycera dibranchiata*-*Nereis virens*-*Corophium volutator* interaction described above (3, 4) provides one such case. The abundance of *C. volutator* is enhanced by the presence of *G. dibranchiata* which preys on *N. virens*, a major predator of *C. volutator*. Kneib & Stiven (61) demonstrate that the size of the predators may have important ramifications on prey abundance. Using enclosures of three different sizes of the killifish *Fundulus heteroclitus* in a North Carolina salt marsh, they showed that infaunal abundances were highest in the presence of large killifish and least in the presence of small fish or no fish. Their postulate, subsequently confirmed (59), was that large killifish prey on an intermediate predator, the shrimp *Palaemonetes pugio*. Small killifish are too small to prey on the intermediate predator. Later experiments in a Georgia salt marsh (60) documented the reduction of *P. pugio* by the killifish, but only an infaunal sea anemone increased when *P. pugio* abundance declined. The anemone benefits from the presence of a higher level predator. Two levels of predators are frequently documented in seagrass beds (77, 78, 117). Exclusions of fish lead to increased survivorship of decapod crustaceans (shrimp and brachyuran crabs) which reduce infaunal abundance significantly.

The importance of size-selection by predators has received little attention by soft-sediment ecologists. Kent & Day (58) showed that flounder and sandpipers preferentially prey upon large individuals of a nereid polychaete, *Ceratonereis pseudoerythraensis*. In the absence of epibenthic predation, adult nereids cannibalize smaller worms. Wilson (134) demonstrated that size-selective predation by shorebirds and fish on adults of the amphipod *Corophium volutator* ameliorated competition between adults and juveniles; in the absence of predators, juveniles were forced to emigrate from the vicinity of their parents' burrows.

Refuges from Predation

It is apparent that some environmental features confer protection for infauna from predation. Sediment type affects the digging ability of portunid crabs and hence the susceptibility of infaunal bivalves to crab predation (9). Oyster-shells confer protection from digging predators (33). Seagrasses provide a deterrent to digging predators (88, 99, 100, 117). Predator exclusions in

seagrass beds generally produce little increase in infaunal abundance, indicating their efficacy as refuges (111), while cages in adjacent unvegetated areas result in infaunal abundances similar to those observed within seagrass beds. Concentrations of tubes of onuphid polychaetes which project above the sediment surface confer a refuge from digging predators (69, 139, 140). Several workers have shown that shallow-dwelling species are more susceptible to epibenthic predation than are deeper-dwelling species (13, 52, 75, 114).

CONCLUSIONS

A recurrent theme in this review is that, although we may understand the mechanisms of a particular competitive or predatory interaction, we lack the ability to generate a priori predictions of the effects of those processes. It must be appreciated that the understanding of infaunal communities has progressed rapidly in the past twenty years. Nevertheless, a unifying theory of soft-sediment community structure does not appear attainable at our present level of understanding. The great variety of sediments inhabited and modified by infaunal organisms have only begun to be studied experimentally. The distributions of infaunal organisms and the outcomes of their biological interactions are clearly affected by the nature of the physical environment (9, 20, 79) and the hydrodynamic regime (37). Experiments similar to those reviewed above performed in different habitats will provide greater insight into environment-infauna interactions. Such data alone will not, however, lead to a unified theory. I conclude by describing what I perceive to be fundamental gaps in our knowledge of how competition and predation operate in marine infaunal communities.

For competitive interactions, mortality is clearly relatively uncommon in infaunal communities. Experiments with hard-bodied invertebrates for which growth and reproduction could be quantified (87, 89, 90) are much more sensitive to competitive effects. Experiments in which the growth of populations of soft-bodied invertebrates can be monitored will be of great interest. The nature of the food of deposit-feeders is a major stumbling-block for any investigator seeking to understand exploitative competition among deposit-feeders. The microscopic analyses of sediments developed by Watling (119) seem promising. Finally, more attention needs to be given to spatial patterns. The proper spatial scale on which observations and experiments are made needs to be determined a priori by direct observation. Often the biologically relevant scale may be on the order of mm (35, 36, 40, 43, 130) whereas a typical sample (e.g., 0.01 m²) is far too coarse to detect the biologically relevant patterns. Finally, further analysis of the sizes of interacting individuals seems to hold great promise for predicting the outcome of competitive encounters.

Predation is a more straightforward and better understood process in that its measurement, the disappearance of organisms, is easier to observe and to quantify. Although some infaunal communities are structured by predation, little effort has been given to understanding the behavior of predators on infaunal organisms in relation to established foraging theories (95). More data on size-selective foraging and on habitat choice would be most welcome. The mobility of many epibenthic predators and the difficulty of understanding their population dynamics are serious roadblocks to a predictive theory. Nevertheless, sufficient data on predator-prey relationships exist to begin their consideration in light of optimal foraging theory.

ACKNOWLEDGMENTS

I gratefully acknowledge the following scientists for valuable discussion and/or comments on the manuscript: W. Ambrose, B. Brown, A. H. Hines, C. H. Peterson, W. Sousa, and S. Woodin.

Literature Cited

1. Aller, R. C., Dodge, R. E. 1974. Animal-sediment relations in a tropical lagoon Discovery Bay, Jamaica. *J. Mar. Res.* 32:209-30
2. Aller, R. C., Yingst, J. Y. 1985. Effects of the marine deposit-feeders *Heteromastus filiformis* (Polychaeta), *Macoma balthica* (Bivalvia), and *Tellina texana* (Bivalvia) on averaged sedimentary solute transport, reaction rates, and microbial distributions. *J. Mar. Res.* 43:615-45
3. Ambrose, Jr., W. G. 1984. Influence of residents on the development of a marine soft-bottom community. *J. Mar. Res.* 42:633-654
4. Ambrose, Jr., W. G. 1984. Influences of predatory polychaetes and epibenthic predators on the structure of a soft-bottom community in a Maine estuary. *J. Exp. Mar. Biol. Ecol.* 81:115-45
5. Ambrose, Jr., W. G. 1984. Increased emigration of the amphipod *Rhepoxynius abronius* (Barnard) and the polychaete *Nephtys caeca* (Fabricius) in the presence of invertebrate predators. *J. Exp. Mar. Biol. Ecol.* 80:67-75
6. Ambrose, Jr., W. G. 1984. Role of predatory infauna in structuring marine soft-bottom communities. *Mar. Ecol. Prog. Ser.* 17:109-15
7. Ambrose, Jr., W. G. 1986. Experimental analysis of density dependent emigration of the amphipod *Rhepoxynius abronius*. *Mar. Behav. Physiol.* 12:209-16
8. Ambrose, Jr., W. G. 1986. Importance of predatory infauna in marine soft-bottom communities: reply to Wilson. *Mar. Ecol. Prog. Ser.* 32:41-45
9. Arnold, W. S. 1984. The effects of prey size, predator size, and sediment composition on the rate of predation of the blue crab, *Callinectes sapidus* Rathbun, on the hard clam, *Mercenaria mercenaria* (Linné). *J. Exp. Mar. Biol. Ecol.* 80:207-19
10. Bergman, M. J. N., Van der Veer, H. W., Karczmarski, L. 1988. Impact of tail-nipping on mortality, growth and reproduction of *Arenicola marina*. *Nether. J. Sea Res.* 22:83-90
11. Bianchi, T. S., Levinton, J. S. 1981. Nutrition and food limitation of deposit-feeders. II. Differential effects of *Hydrobia totteni* and *Ilyanassa obsoleta* on the microbial community. *J. Mar. Res.* 39:547-56
12. Bianchi, T. S., Rice, D. L. 1988. Feeding ecology of *Leitoscoloplos fragilis*. II. Effects of worm density on benthic diatom production. *Mar. Biol.* 99:123-31
13. Blundon, J. A., Kennedy, V. S. 1982. Refuges for infaunal bivalves from blue crab, *Callinectes sapidus* (Rathbun), predation in Chesapeake Bay. *J. Exp. Mar. Biol. Ecol.* 65:67-81
14. Boates, J. S., Smith, P. C. 1979. Length-weight relationships, energy content and the effects of predation on *Corophium volutator* (Pallas) (Crustacea: Amphipoda). *Proc. Nova Scotia Inst. Sci.* 29:489-99

15. Bonsdorff, E., Mattila, J., Rönn, C., Öosterman, C.-S. 1986. Multi-dimensional interactions in shallow soft-bottom ecosystems; testing the competitive exclusion principle. *Ophelia, Suppl.* 4:37-44
16. Bottom, M. L. 1984. Effects of Laughing Gull and shorebird predation on the intertidal fauna at Cape May, New Jersey. *Est. Coast. Shelf Sci.* 18:209-20
17. Bottom, M. L. 1984. The importance of predation by horseshoe crabs, *Limulus polyphemus*, to an intertidal sand flat community. *J. Mar. Res.* 42:139-61
18. Brenchley, G. A. 1981. Disturbance and community structure: an experimental study of bioturbation in marine soft-bottom environments. *J. Mar. Res.* 39:767-90
19. Brenchley, G. A. 1982. Mechanisms of spatial competition in marine soft-bottom communities. *J. Exp. Mar. Biol. Ecol.* 60:17-33
20. Brown, B. 1982. Spatial and temporal distribution of a deposit-feeding polychaete on a heterogeneous tidal flat. *J. Exp. Mar. Biol. Ecol.* 65:213-27
21. Carlson, D. J., Townsend, D. W., Hilyard, A. L., Eaton, J. F. 1984. Effect of an intertidal mudflat on plankton of the overlying water column. *Can. J. Fish. Aquat. Sci.* 41:1523-28
22. Commito, J. A. 1982. Importance of predation by infaunal polychaetes in controlling the structure of a soft-bottom community in Maine, USA. *Mar. Biol.* 68:77-81
23. Commito, J. A. 1987. Adult-larval interactions: predictions, mussels and cocoons. *Est. Coast. Shelf Sci.* 25:599-606
24. Commito, J. A., Ambrose, Jr., W. G. 1985. Multiple trophic levels in soft-bottom communities. *Mar. Ecol. Prog. Ser.* 26:289-93
25. Commito, J. A., Ambrose, Jr., W. G. 1985. Predatory infauna and trophic complexity in soft-bottom communities. *Proc. Eur. Mar. Biol. Symp., 19th, Cambridge, 1985*, 323-33
26. Commito, J. A., Boncavage, E. M. 1989. Suspension-feeders and coexisting infauna: an enhancement counterexample. *J. Exp. Mar. Biol. Ecol.* 125:33-42
27. Commito, J. A., Shrader, P. B. 1985. Benthic community response to experimental additions of the polychaete *Nereis virens*. *Mar. Biol.* 86:101-107
28. Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42:710-23
29. Connell, J. H., Slatyer, R. O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Natur.* 111:1119-44
30. Connor, M. S., Teal, J. M., Valiela, I. 1982. The effect of feeding by mud snails, *Ilyanassa obsoleta* (Say), on the structure and metabolism of a laboratory benthic algal community. *J. Exp. Mar. Biol. Ecol.* 65:29-45
- 30a. Coull, B. C., ed. 1977. *Ecology of Marine Benthos*. Columbia: Univ. S. Carolina Press. 467 pp.
31. Croker, R. A., Hatfield, E. B. 1980. Space partitioning and interactions in an intertidal sand-burrowing amphipod guild. *Mar. Biol.* 61:79-88
32. Dauer, D. M., Ewing, R. M., Tourtellotte, G. H., Harlan, W. T., Sourbeer, J. W., Barker, H. R. Jr. 1982. Predation, resource limitation and the structure of benthic infaunal communities of the lower Chesapeake Bay. *Int. Revue ges. Hydrobiol.* 67:477-89
33. Dauer, D. M., Tourtellotte, G. H., Ewing, R. M. 1982. Oyster shells and artificial worm tubes: the role of refuges in structuring benthic communities of the lower Chesapeake Bay. *Int. Revue ges. Hydrobiol.* 67:661-77
34. Dayton, P. K., Oliver, J. S. 1980. An evaluation of experimental analyses of population and community patterns in benthic marine environments. In *Marine Benthic Dynamics*, ed. K. R. Tenore, B. C. Coull, pp. 93-120. Columbia, Univ. S. Carolina Press. 451 pp.
35. DeWitt, T. H., Levinton, J. S. 1985. Disturbance, emigration, and refugia: how the mud snail, *Ilyanassa obsoleta* (Say), affects the habitat distribution of an epifaunal amphipod, *Microdeutopus gryllotalpa* (Costa). *J. Exp. Mar. Biol. Ecol.* 92:97-113
36. Eckman, J. E. 1979. Small-scale patterns and processes in a soft-substratum, intertidal community. *J. Mar. Res.* 37:437-57
37. Eckman, J. E. 1987. Hydrodynamic processes affecting benthic recruitment. *Limnol. Oceanogr.* 28:241-57
38. Eckman, J. E., Nowell, A. R. M., Jumars, P. A. 1981. Sediment destabilization by animal tubes. *J. Mar. Res.* 39:361-74
39. Elmgren, R., Ankar, S., Marteleur, B., Ejdung, G. 1986. Adult interference with postlarvae in soft sediments: the *Pontoporeia-Macoma* example. *Ecology* 67:827-36
40. Ertman, S. C., Jumars, P. A. 1988. Effects of bivalve siphonal currents on

- the settlement of inert particles and larvae. *J. Mar. Res.* 46:797-813
41. Frid, C. L. J., James, R. 1988. The role of epibenthic predators in structuring the marine invertebrate community of a British coastal salt marsh. *Nether. J. Sea Res.* 22:307-14
 42. Frid, C. L. J. 1989. The role of recolonization processes in benthic communities, with special reference to the interpretation of predator-induced effects. *J. Exp. Mar. Biol. Ecol.* 126: 163-71
 43. Gallagher, E. D., Jumars, P. A., Trueblood, D. D. 1983. Facilitation of soft-bottom benthic succession by tube builders. *Ecology* 64:1200-16
 44. Gee, J. M., Warwick, R. M., Davey, J. T., George, C. L. 1985. Field experiments on the role of epibenthic predators in determining prey densities in an estuarine mudflat. *Est. Coast. Shelf Sci.* 21:429-48
 45. Grant, J. 1981. Dynamics of competition among estuarine sand-burrowing amphipods. *J. Exp. Mar. Biol. Ecol.* 49:255-65
 46. Grant, J., Bathmann, U. V., Mills, E. L. 1986. The interaction between benthic diatom films and sediment transport. *Est. Coast. Shelf Sci.* 23:225-38
 47. Harper, J. L. 1977. *Population Biology of Plants*. New York: Academic. 892 pp.
 48. Harrison, P. G. 1987. Natural expansion and experimental manipulation of seagrass (*Zostera* spp.) abundance and the response of infaunal invertebrates. *Est. Coast Shelf Sci.* 24:799-812
 49. Highsmith, R. C. 1982. Induced settlement and metamorphosis of sand dollar (*Dendraster excentricus*) larvae in predator-free sites: adult sand dollar beds. *Ecology* 63:329-37
 50. Hines, A. H., Posey, M. H. 1989. Complex trophic interactions in estuarine food webs: jargon, concepts and examples. *Am. Zool.* 29:27A
 51. Hines, A. H., Posey, M. H., Haddon, P. J. 1989. Effects of adult suspension- and deposit-feeding bivalves on recruitment of estuarine infauna. *Veliger* 32:109-19
 52. 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.* 57:221-35
 53. Hulberg, L. W., Oliver, J. S. 1980. Caging manipulations in marine soft-bottom communities: importance of animal interactions or sedimentary habitat modifications. *Can. J. Fish. Aquat. Sci.* 37:1130-39
 54. Hunt, J. H., Ambrose, W. G. Jr., Peterson, C. H. 1987. Effects of the gastropod, *Ilyanassa obsoleta* (Say), and the bivalve *Mercenaria mercenaria* (L.), on larval settlement and juvenile recruitment of infauna. *J. Exp. Mar. Biol. Ecol.* 108:229-40
 55. Jensen, K. T. 1985. The presence of the bivalve *Cerastoderma edule* affects migration, survival and reproduction of the amphipod *Corophium volutator*. *Mar. Ecol. Prog. Ser.* 25:269-77
 56. Joyce, A. A., Weisberg, S. B. 1986. The effects of predation by the mummichog, *Fundulus heteroclitus* (L.), on the abundance and distribution of the salt marsh snail, *Melampus bideniatus* (Say). *J. Exp. Mar. Biol. Ecol.* 100: 295-306
 57. Jumars, P. A., Nowell, A. R. M. 1984. Effects of benthos on sediment transport: difficulties with functional grouping. *Cont. Shelf Res.* 3:115-30
 58. Kent, A. C., Day, R. W. 1983. Population dynamics of an infaunal polychaete: the effect of predators and an adult-recruit interaction. *J. Exp. Mar. Biol. Ecol.* 73:185-203
 59. Kneib, R. T. 1985. Predation and disturbance by grass shrimp, *Palaemonetes pugio* Holthuis, in soft-substratum benthic invertebrate assemblages. *J. Exp. Mar. Biol. Ecol.* 93:91-102
 60. Kneib, R. T. 1988. Testing for indirect effects of predation in an intertidal soft-bottom community. *Ecology* 69:1795-1805
 61. 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* 63:1518-32
 62. Levin, L. A. 1981. Dispersion, feeding behavior and competition in two spionid polychaetes. *J. Mar. Res.* 39:99-117
 63. Levin, L. A. 1982. Interference interactions among tube-dwelling polychaetes in a dense infaunal assemblage. *J. Exp. Mar. Biol. Ecol.* 65:107-19
 64. Levinton, J. S. 1977. See Ref. 30a, pp. 191-227
 65. Levinton, J. S. 1979. The effect of density upon deposit-feeding populations: movement, feeding and floating of *Hydrobia ventrosa* Montagu (Gastropoda: Prosobranchia). *Oecologia* 43:27-39
 66. Levinton, J. S., Stewart, S., DeWitt, T. H. 1985. Field and laboratory experiments on interference between *Hy-*

- drobia totteni* and *Ilyanassa obsoleta* (Gastropoda) and its possible relation to seasonal shifts in vertical mudflat zonation. *Mar. Ecol. Prog. Ser.* 22:53-58
67. Lopez, G. R., Levinton, J. S. 1987. Ecology of deposit-feeding animals in marine sediments. *Q. Rev. Biol.* 62:235-60
 68. Luckenbach, M. W. 1986. Sediment stability around animal tubes: the roles of hydrodynamic processes and biotic activity. *Limnol. Oceanogr.* 31:779-87
 69. Luckenbach, M. W. 1987. Effects of adult infauna on new recruits: implications for the role of biogenic refuges. *J. Exp. Mar. Biol. Ecol.* 105:197-206
 70. McCall, P. L. 1977. Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. *J. Mar. Res.* 35:221-66
 71. McCall, P. L. 1978. See Ref. 125a. pp. 191-219
 72. Mahoney, B. M. S., Livingston, R. J. 1982. Seasonal fluctuations of benthic macrofauna in the Apalachicola estuary, Florida, USA: the role of predation. *Mar. Biol.* 69:207-13
 73. Mattila, J., Bonsdorff, E. 1989. The impact of fish predation on shallow soft bottoms in brackish waters (SW Finland): an experimental study. *Nether. J. Sea Res.* 23:69-81
 74. Maurer, D. 1983. The effect of an infaunal suspension feeding bivalve *Mercenaria mercenaria* (L.) on benthic recruitment. *Mar. Ecol.* 4:263-74
 75. Myers, J. P., Williams, S. L., Pitelka, F. A. 1980. An experimental analysis of prey availability for sanderlings (Aves: Scolopacidae) feeding on sandy beach crustaceans. *Can. J. Zool.* 58:1564-74
 76. Naqvi, S. M. Z. 1966. Effects of predation on infaunal invertebrates of Alligator Harbor, Florida. *Fla. Scient.* 29:313-21
 77. Nelson, W. G. 1979. An analysis of structural pattern in an eelgrass (*Zostera marina* L.) amphipod community. *J. Exp. Mar. Biol. Ecol.* 39:231-64
 78. Nelson, W. G. 1981. Experimental studies of decapod and fish predation on seagrass macrobenthos. *Mar. Ecol. Prog. Ser.* 5:141-49
 79. Ólafsson, E. B. 1986. Density dependence in suspension-feeding and deposit-feeding populations of the bivalve *Macoma balthica*: a field experiment. *J. Anim. Ecol.* 55:517-26
 80. Ólafsson, E. B. 1988. Inhibition of larval settlement to a soft bottom benthic community by drifting algal mats: an experimental test. *Mar. Biol.* 97:571-74
 81. Ólafsson, E. B., Persson, L.-E. 1986. The interaction between *Nereis diversicolor* O. F. Müller and *Corophium volutator* Pallas as a structuring force in a shallow brackish sediment. *J. Exp. Mar. Biol. Ecol.* 103:103-17
 82. 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.* 7:179-84
 83. Oliver, J. S., Slattery, P. N. 1985. Effects of crustacean predators on species composition and population structure of soft-bodied infauna from McMurdo Sound, Antarctica. *Ophelia* 24:155-75
 84. Paine, R. T. 1966. Food web complexity and species diversity. *Am. Natur.* 100:65-75
 85. Peterson, C. H. 1977. Competitive organization of the soft-bottom macrobenthic communities of southern California lagoons. *Mar. Biol.* 43:343-59
 86. Peterson, C. H. 1979. Predation, competitive exclusion, and diversity in the soft-sediment benthic communities of estuaries and lagoons. In *Ecological Processes in Coastal and Marine Systems*, ed. R. J. Livingston, 244-64. New York: Plenum. 477 pp.
 87. Peterson, C. H. 1982. The importance of predation and intra- and interspecific competition in the population biology of two infaunal suspension-feeding bivalves, *Protothaca staminea* and *Chione undatella*. *Ecol. Monogr.* 52:437-75
 88. Peterson, C. H. 1982. Clam predation by whelks (*Busycon* spp.): experimental tests of the importance of prey size, prey density, and seagrass cover. *Mar. Biol.* 66:159-70
 89. Peterson, C. H., Andre, S. V. 1980. An experimental analysis of interspecific competition among marine filter feeders in a soft-sediment environment. *Ecology* 61:129-39
 90. Peterson, C. H., Black, R. 1987. Resource depletion by active suspension feeders on tidal flats: influence of local density and tidal elevation. *Limnol. Oceanogr.* 32:143-66
 91. Peterson, C. H., Quammen, M. L. 1982. Siphon nipping: its importance to small fishes and its impact on growth of the bivalve *Protothaca staminea* (Conrad). *J. Exp. Mar. Biol. Ecol.* 63:249-68

92. Posey, M. H. 1986. Changes in a benthic community associated with dense beds of a burrowing deposit feeder, *Callinassa californiensis*. *Mar. Ecol. Prog. Ser.* 31:15-22
93. Posey, M. H. 1986. Predation on a burrowing shrimp: distribution and community consequences. *J. Exp. Mar. Biol. Ecol.* 103:143-61
94. Posey, M. H. 1987. Influence of relative mobilities on the composition of benthic communities. *Mar. Ecol. Prog. Ser.* 39:99-104
95. Pyke, G. H., Pulliam, H. R., Charnov, E. L. 1977. Optimal foraging: a selective review of theory and tests. *Q. Rev. Biol.* 52:137-54
96. Quammen, M. L. 1984. Predation by shorebirds, fish, and crabs on invertebrates in intertidal mudflats: an experimental test. *Ecology* 65:529-37
97. Raffaelli, D., Milne, H. 1987. An experimental investigation of the effects of shorebird and fluffish predation on estuarine invertebrates. *Est. Coast. Shelf Sci.* 24:1-13
98. Reise, K. 1977. Predator exclusion experiments in an intertidal mud flat. *Helgo. wiss. Meeresunters.* 30:263-71
99. Reise, K., 1977. Predation pressure and community structure of an intertidal soft-bottom fauna. In *Biology of Benthic Organisms*, ed. F. Keegan, P. O. Ceidigh, P. J. Boaden, pp. 513-19. New York: Pergamon. 495 pp.
100. Reise, K. 1978. Experiments on epibenthic predation in the Wadden Sea. *Helgo. wiss. Meeresunters.* 31:55-101
101. Reise, K. 1983. Biotic enrichment of intertidal sediments by experimental aggregates of the deposit-feeding bivalve *Macoma balthica*. *Mar. Ecol. Prog. Ser.* 12:229-36
102. Rhoads, D. C. 1974. Organism-sediment relations on the muddy sea floor. *Oceanogr. Mar. Biol. Ann. Rev.* 12:263-300
103. Rhoads, D. C., Young, D. K. 1970. The influences of deposit-feeding organisms on sediment stability and community trophic structure. *J. Mar. Res.* 28:150-78
104. Roe, P. 1975. Aspects of life history and of territorial behaviour in young individuals of *Platynereis bicanaliculata* and *Nereis vexillosa* (Annelida, Polychaeta). *Pac. Sci.* 29:341-48
105. Roe, P. 1976. Life history and predator-prey interactions of the nemertean *Paranemertes peregrina* Coe. *Biol. Bull.* 150:80-106
106. Ronan, T. E. Jr., 1975. *Structural and paleoecological aspects of a modern soft-sediment community: an experimental field study*. PhD thesis. Univ. Calif., Davis. 220 pp.
107. Rönn, C., Bonsdorff, E., Nelson, W. G. 1988. Predation as a mechanism of interference within infauna in shallow brackish water soft bottoms: experiments with an infauna predator, *Nereis diversicolor* O. F. Müller. *J. Exp. Mar. Biol. Ecol.* 116:143-57
108. Schneider, D. 1978. Equalisation of prey numbers by migratory shorebirds. *Nature* 271:371-72
109. Schneider, D., Harrington, B. A. 1981. Timing of shorebird migration in relation to prey depletion. *Auk* 98:801-11
110. Schubert, A., Reise, K. 1986. Predatory effects of *Nephtys hombergii* on other polychaetes in tidal sediments. *Mar. Ecol. Prog. Ser.* 34:117-24
111. Summerson, H. C., Peterson, C. H. 1984. Role of predation in organizing benthic communities of a temperate-zone seagrass bed. *Mar. Ecol. Prog. Ser.* 15:63-77
112. Tamaki, A. 1985. Detection of non-interference within a mobile polychaete species. *J. Exp. Mar. Biol. Ecol.* 90:277-87
113. Tamaki, A. 1985. Inhibition of larval recruitment of *Armandia* sp. (Polychaeta: Opheliidae) by established adults of *Pseudopolydora paucibranchiata* (Okuda) (Polychaeta: Spionidae) on an intertidal sand flat. *J. Exp. Mar. Biol. Ecol.* 87:67-82
114. Virnstein, R. W. 1977. The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. *Ecology* 58:1199-17
115. Virnstein, R. W. 1978. See Ref. 125a, pp. 261-73
116. Virnstein, R. W. 1980. Measuring effects of predation on benthic communities in soft sediments. In *Estuarine Perspectives*, ed. M. L. Wiley, pp. 281-290. New York: Academic. 563 pp.
117. Virnstein, R. W., Mikkelsen, P. S., Cairns, K. D., Capone, M. A. 1983. Seagrass beds versus sand bottoms: the trophic importance of their associated benthic invertebrates. *Fla. Scient.* 46:363-81
118. Vlas, J. de. 1979. Annual food intake by plaice and flounder in a tidal flat area in the Dutch Wadden Sea, with special reference to consumption of regenerating parts of macrobenthic prey. *Nether. J. Sea Res.* 13:117-53
119. Watling, L. 1988. Small-scale features of marine sediments and their im-

- portance to the study of deposit-feeding. *Mar. Ecol. Prog. Ser.* 47:135-44
120. Watzin, M. C. 1983. The effects of meiofauna on settling macrofauna: meiofauna may structure macrofaunal communities. *Oecologia* 59:163-66
 121. Watzin, M. C. 1985. Interactions among temporary and permanent meiofauna: observations on the feeding and behavior of selected taxa. *Biol. Bull.* 169:397-416
 122. Watzin, M. C. 1986. Larval settlement into marine soft-sediment systems: interactions with the meiofauna. *J. Exp. Mar. Biol. Ecol.* 98:65-113
 123. Weinberg, J. R. 1984. Interactions between functional groups in soft-substrata: do species differences matter? *J. Exp. Mar. Biol. Ecol.* 80:11-28
 124. Whitlatch, R. B. 1981. Animal-sediment relationships in intertidal marine benthic habitats: some determinants of deposit-feeding species diversity. *J. Exp. Mar. Biol. Ecol.* 53:31-45
 125. Whitlatch, R. B., Zajac, R. N. 1985. Biotic interactions among estuarine infaunal opportunistic species. *Mar. Ecol. Prog. Ser.* 21:299-311
 - 125a. Wiley, M. L., ed. 1978. *Estuarine Interactions*. New York: Academic. 603 pp.
 126. Williams, J. G. 1980. The influence of adults on the settlement of spat of the clam, *Tapes japonica*. *J. Mar. Res.* 38:729-41
 127. Wilson, W. H. Jr. 1979. Community structure and species diversity of the sediment reefs constructed by the maldanid polychaete *Petaloproctus socialis* (Polychaeta: Maldanidae). *J. Mar. Res.* 37:623-41
 128. Wilson, W. H. Jr. 1980. A laboratory investigation of the effect of a terebellid polychaete on the survivorship of nereid polychaete larvae. *J. Exp. Mar. Biol. Ecol.* 46:73-80
 129. Wilson, W. H. Jr., 1981. Sediment-mediated interactions in a densely populated infaunal assemblage: the effects of the polychaete *Abarenicola pacifica*. *J. Mar. Res.* 39:735-48
 130. Wilson, W. H. Jr. 1983. The role of density dependence in a marine infaunal community. *Ecology* 64:295-306
 131. Wilson, W. H. Jr. 1984. An experimental analysis of spatial competition in a dense infaunal community: the importance of relative effects. *Est. Coast. Shelf Sci.* 18:673-84
 132. Wilson, W. H. Jr. 1986. Importance of predatory infauna in marine soft-sediment communities. *Mar. Ecol. Prog. Ser.* 32:35-40
 133. Wilson, W. H. Jr. 1988. Shifting zones in a Bay of Fundy soft-sediment community: patterns and processes. *Ophelia* 29:227-45
 134. Wilson, W. H. Jr. 1989. Predation and the mediation of intraspecific competition in an infaunal community in the Bay of Fundy. *J. Exp. Mar. Biol. Ecol.* 132:221-45
 135. Wiltse, W. I. 1980. Effects of *Polinices duplicatus* (Gastropoda: Naticidae) on infaunal community structure at Barnstable Harbor, Massachusetts, USA. *Mar. Biol.* 56:301-10
 136. Wiltse, W. I., Foreman, K. H., Teal, J. M., Valiela, I. 1984. Effects of predators and food resources on the macrobenthos of salt marsh creeks. *J. Mar. Res.* 42:923-42
 137. Woodin, S. A. 1974. Polychaete abundance patterns in a marine soft-sediment environment: the importance of biological interactions. *Ecol. Monogr.* 44:171-87
 138. Woodin, S. A. 1976. Adult-larval interactions in dense infaunal assemblages: patterns of abundance. *J. Mar. Res.* 34:25-41
 139. Woodin, S. A. 1978. Refuges, disturbance, and community structure: a marine soft-bottom example. *Ecology* 59:274-84
 140. Woodin, S. A. 1981. Disturbance and community structure in a shallow water sand flat. *Ecology* 62:1052-66
 141. Woodin, S. A. 1983. Biotic interactions in Recent marine sedimentary environments. In *Biotic Interactions in Recent and Fossil Benthic Communities*, ed. M. J. S. Tevesz, P. L. McCall, pp. 3-38. New York: Plenum. 336 pp.
 142. Woodin, S. A. 1984. Effects of browsing predators: activity changes in infauna following tissue loss. *Biol. Bull.* 166:558-73
 143. Woodin, S. A. 1985. Effects of defecation by arenicolid polychaete adults on spionid polychaete juveniles in field experiments: selective settlement or differential mortality. *J. Exp. Mar. Biol. Ecol.* 87:119-32
 144. Woodin, S. A., Jackson, J. B. C. 1979. Interphyletic competition among marine benthos. *Am. Zool.* 19:1029-43
 145. Young, D. K., Young, M. W. 1977. See Ref. 30a, pp. 359-81
 146. Young, D. K., Young, M. W. 1978. Regulation of species densities of seagrass-associated macrobenthos: evidence from field experiments in the Indian River estuary, Florida. *J. Mar. Res.* 36:569-93
 147. Young, D. K., Buzas, M. A., Young,

- M. W. 1976. Species densities of macrobenthos associated with seagrass: a field experimental study of predation. *J. Mar. Res.* 34:577-92
148. Zajac, R. N. 1985. The effects of sublethal predation on reproduction in the spionid polychaete *Polydora ligni* Webster. *J. Exp. Mar. Biol. Ecol.* 88:1-19
149. Zajac, R. N., Whitlatch, R. B. 1982a. Responses of estuarine infauna to disturbance. I. Spatial and temporal variation of initial recolonization. *Mar. Ecol. Prog. Ser.* 10:1-14
150. Zajac, R. N., Whitlatch, R. B. 1982b. Responses of estuarine infauna to disturbance. II. Spatial and temporal variation of succession. *Mar. Ecol. Prog. Ser.* 10:15-27