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**Assignment**

**REQUIRED**


**SUPPLEMENTAL**


**Comments**

**ON BENTHIC COMPETITION**

This commentary summarizes of some of the current debates raging about models of competition. The text is excerpted largely from Gardner & Gallagher (ms)

**Gallagher et al. (1990)** provide a brief review of soft-bottom benthic competition studies. Wilson (1990) reviews the roles of competition and predation in the soft-bottom benthos. Earlier reviews include Reise (1985) and Peterson (1979a, 1980).
There are many definitions of competition. One of the simplest is ‘the shared utilization of a resource that is demonstrably in short supply.’ It is often very difficult to determine whether resources are in short supply. Many, if not most studies, have failed to document the resource that is in short supply (including Gallagher et al. 1990).

Other definitions of interspecific competition include: “competition is occurring if the increase in the growth rate in one population leads to the decline in the growth rate of another.” This definition doesn’t apply to intraspecific competition, but in the case of intraspecific competition the pragmatic definition is even simpler: “intraspecific competition occurs if an increasing density of the population leads to a decrease in the per capita growth rate.”

There are two broad categories of competition: exploitative and interference competition. In exploitative, or scramble competition, the effects of competition are caused by the consumption of the shared resource. In interference competition, one individual or group of individuals prevents another individual or group of individuals from gaining access to the resource.

**What resources are limiting to the soft-bottom benthos?**

A variety of different limiting resources have been proposed for the soft-bottom benthos, especially deposit feeders. Food of a particular type is usually the resource that is cited as being in short supply for the soft-bottom benthos. Space has also been cited as a limiting factor. Woodin (1974) argued that tube-building organisms compete with burrowing organisms for access to the surface. An increased abundance of tube-building surface organisms led to a decrease in the abundance of the burrowing orbiniid polychaete Armandia. Hulberg & Oliver (1980) proposed an alternate hypothesis for this pattern. Woodin (1974) had used cages to exclude surface deposit feeders, and Hulberg & Oliver (1980) argued that the cage itself attracted more burrowing individuals.

Habitat may be a key limiting resource for some deep-sea populations. Many ‘passive’ suspension feeders in the deep sea must settle on objects on the sea floor so that their feeding appendages protrude through the approximately 1-cm thick deep-sea diffusive sublayer. Jumars & Gallagher (1982) argued that the scarce supply of these objects, e.g., pieces of wood or skeleton, could set the limit on population abundance for these populations.

On an evolutionary time scale, Thayer argued that many sessile benthic organisms were virtually eliminated by the appearance of burrowing deposit feeders. These bulldozer species, by moving the sediment may have led to the local extinction of a number of sessile deposit and suspension feeding groups. Bulldozing is an example of interference competition.

Food is usually the key resource that animals compete for, but not all food is like. White (1979) argued that it is not the organic content of the food so much that limits populations, but the nitrogen content of the food. Soft-bottom benthic ecological studies have largely confirmed this idea. There are usually high concentrations of organic matter in shallow subtidal and intertidal marine sediments. The nitrogen content of the sediments is often low. The ingestion and growth rate of populations is often poorly correlated with the % organic matter in bulk sediments. It is
more often more closely coupled with the amount of nitrogen or labile organic matter in the sediments (e.g., Tenore 1977). The protein content of sediment is often a good predictor of sediment food quality. Larry Mayer and Pete Jumars have led the way in developing assays for the nutritional quality of marine sediments. There most recent assays for ‘nutritional quality’ involve mimicking the digestive enzymes found in deposit feeder guts to assess the amount of organic matter that can actually be extracted by a deposit feeder.

Tenore has argued that it may not be even the nitrogen content of sediments that limits population growth. He has argued that it may be the amounts of essential fatty acids in sediments that limits the growth of organisms like Capitella.

The clearest examples of competition for scarce resources probably involve benthic diatoms. Benthic diatoms have a high protein content, high nitrogen content (with C:N ratios in roughly Redfield proportions), and essential fatty acid composition ideal for the nutrition of marine worms. The relatively high standing stock of benthic diatoms in shallow marine benthic habitats poses a problem for the hypothesis that diatoms are in short supply. Surface and subsurface deposit feeders in nature are often surrounded by very high standing stocks of benthic diatoms. Moreover, Admiraal et al. (1983) documented that most infaunal populations have ingestion rates incapable of consuming more than 10-20% of the daily production of benthic diatoms. How then can they be limiting? Admiraal et al. (1983) provides the solution: much of the standing stock of benthic diatoms may be unavailable to deposit feeders. Either the cells are too large to be ingested, or they pass through the guts of deposit feeders intact.

**Exploitative competition for diatoms**

Gallagher et al. (1990) describe the interactions between juvenile polychaetes and members of the permanent meiofauna: oligochaetes. Gallagher’s evidence for competition was indirect; he had no direct evidence that diatom abundance affected the population growth of either oligochaetes or the juvenile stages of Hobsonia florida. Hentschel & Jumars (1994) provide this key link. They added DCMU to patches of the Skagit flats intertidal and demonstrated clear effects on the population growth of both oligochaetes and juvenile Hobsonia florida. Hentschel (1998) used stable carbon isotopes to document that it is probably only the juvenile stage of Hobsonia florida that derive most of its energetic needs from benthic diatoms. Larger Hobsonia florida may act as more of deposit feeder, obtaining its energy from a variety of organic carbon sources.

Admiraal et al. (1983) document that a small subset of the benthic diatom standing stock may be the key limiting resource for meiofauna and macrofauna. Even though diatom grazers consume only 10% of the benthic diatom production, their growth rate can still be limited by the abundance of the subset of the diatom community that they actually eat.

Bianchi & Levinton (1984) showed the microphytobenthos appeared to be the key limiting resource for the snail Hydrobia totteni in laboratory cultures. The abundance of particulate organic matter and bacteria was a poor predictor of Hydrobia growth.
Fenchel (Fenchel & Kofoed 1976, Fenchel 1977) provided one of the key papers in the ecological literature demonstrating character displacement. When populations of two gastropods *Hydrobia ulva* and *H. ventrosa* occurred together (i.e., sympatrically), they fed on different sized particles. When they lived apart (allopatrically), they fed on the same size spectrum. The size of particle ingested by *Hydrobia* is directly related to body size, and populations living sympatrically had different size ranges. The case for competitively driven character displacement was made even stronger by Fenchel & Kofoed (1976), who clearly demonstrated that in the laboratory *H. ventrosa* and *H. ulva* can compete intensely for scarce diatom resources. However, later work by Hylleberg showed that the size disparity observed by Fenchel on mudflats where the populations were sympatric may not have been related to competition at all. Both populations have strong large-scale spatial gradients in size distribution. In those subsets of mudflats where the species coexisted, they were different in size, but this may have been due to other factors (e.g., temperature).

Grant (1981) found another example of character displacement in burrowing amphipods. In sandflats where two species occurred sympatrically, they had disjunct depth distributions. When each species was by itself, the depth distributions were broad.

Character displacement due to competition is difficult to demonstrate. Connell (1980) called arguments that character displacement was caused by competition as ‘the ghost of competition past.’ Williamson (1972) had been even more skeptical of examples of character displacement. He argued by analogy that if character displacement arguments were applied to viewing a yacht raise, the spectators should conclude that yachts sail on parallel tacks because they must have run into each other in the past. There are myriad reasons why organisms may feed on different food resources or inhabit different parts of the habitat. One shouldn’t conclude that such phenotypes were caused by competition in the past. Moreover, as Fenchel & Kofoed (1976) showed, even demonstrating that pairs of species can compete in the laboratory or field is insufficient evidence for concluding that character displacement was due to competition.

**Competitive bottlenecks**

Gardner and Gallagher (ms) provide additional analyses of Gallagher’s oligochaete-juvenile polychaete interaction. Levin & Creed (1989) tested such interactions in the laboratory and found that the meiofauna and macrofauna did not compete. This study did not directly control for the key resource cited by Gallagher et al. (1990): benthic diatoms.

**Modeling Competition**

Schoener (1974a, 1986) and Nunney (1980) proposed two criteria for classifying competition models. Their first criterion separates multilevel models, that explicitly model resources, from single-level models, that do not. The second criterion distinguishes between mechanistic and descriptive models. Mechanistic models include equations or terms necessary to explicitly model the mechanism of competition. The mechanistic models are now often derived from foraging theory (e.g., Schoener 1974b). Descriptive models describe population trajectories or equilibrium solutions but cannot necessarily be derived from mechanistic foundations.
The Lotka-Volterra Competition Model

Vito Volterra’s 1926 competition model is single-level and descriptive. Volterra made the simplifying assumption that the competition coefficients were symmetric, resulting in parallel zero-growth isoclines. A. J. Lotka (1932) derived a more general competition equation, which is the equation now referred to in textbooks as the Lotka-Volterra model. We do not follow Hutchinson (1969) in giving Volterra priority, and instead refer to these equations as the Lotka-Volterra model (and equations).

The Lotka-Volterra model is a six-parameter model. Gallagher et al. (1990) showed that it is possible to fit all six parameters simultaneously with a replicated field experimental data.

\[
\frac{dN_1}{dt} = r_1 N_1 \left( 1 - \frac{N_1 - \alpha_{12} N_2}{K_1} \right)
\]
\[
\frac{dN_2}{dt} = r_2 N_2 \left( 1 - \frac{N_2 - \alpha_{21} N_1}{K_2} \right).
\]

where, \( \alpha = \text{Interspecific competition coefficient.} \)
\( K = \text{Carrying capacity.} \)
\( r = \text{maximum per capita growth rate.} \)

The original Lotka-Volterra competition model has been a foundation of theoretical ecology, and the mechanistic underpinnings of the model have been derived (e.g., Schoener 1974b, Abrams 1980). Gause (1934) was one of the first of many to design competition experiments to apply the equations and based his competitive exclusion principle on them. MacArthur & Levins (1964, 1967) based their theory of the niche on Volterra’s (1928) competition equations.

The Lotka-Volterra competition equations have been criticized as an unrealistic description of Nature. Many ecologists attacked the Lotka-Volterra model’s assumptions, particularly the populations growth follows the logistic equation. That is, the per capita growth rate decreases linearly with population size. Schoener (1973) and Pomerantz et al. (1980) reviewed the literature and found few populations obey the logistic growth model. Most exhibit curvilinear density dependence (e.g., Wilbur 1974, Smith-Gill and Gill 1978). Such curvilinearities would violate one of the assumed linear relationships in the Lotka-Volterra model. The Lotka-Volterra model also assumes that the zero-growth isoclines are linear. Nunney (1980) showed that linear zero-growth isoclines are possible even with non-linear density dependence in single-species growth rates.

Gardner and Gallagher (ms) confirmed this result and provide a descriptive model with linear zero-growth isoclines and non-linear single-species growth rates. Ayala (1969 & 1971) found nonlinear zero-growth isoclines in Drosophila competition experiments and used these data to criticize Gause’s competitive exclusion principle.
The Volterra model assumes that the interspecific competition coefficients ($\alpha_{ij}$) are constant, additive, and are independent of other species abundances (i.e., there are no higher-order interactions). A number of ecologists have attacked these assumptions. Hairston et al. (1968) and Neill (1974) documented higher-order interactions among competing species of laboratory microcrustacean populations. Neill’s (1974) paper is based on the microcrustacean microcosms described more fully in Neill (1975). Neill’s (1974) statistical methods have been criticized by Pomerantz (1981). Pomerantz (1981) argued that the matrices used by Neill (1974) in his regression models were nearly singular (a problem in fitting regression models; after performing a Singular Value Decomposition on a matrix, if the ratio of the largest to the smallest singular value is in the thousands, then the fit of a regression model can not be considered adequate). Vandermeer (1981) could not detect significant higher order interactions in his studies of protozoan competition (Vandermeer 1969), and offered the sage that advice that higher-order interactions undoubtedly occur in nature and in laboratory studies but that they might not be important enough to include in models. Why use complex models if simple ones will do?

Case & Bender (1981) argued that most tests for higher-order interactions are tests of a compound null hypothesis: “The species are competing with constant $\alpha_{ij}$’s and higher order interactions don’t occur.” Worthen and Moore (1991) argue that many higher-order interaction effects are merely examples of indirect effects. An indirect effect is the effect of one species on the interaction between two others. A higher order interaction is the effect of one species on the per capita effects of one species on another (e.g., a change in $\alpha$ in the Lotka Volterra model). Gardner and Gallagher (ms), argue that constant $\alpha_{ij}$’s are a feature of the Lotka-Volterra model but not of any of the other non-linear competition models. As noted first by Nunney (1980), curvilinear zero-growth isoclines preclude constant $\alpha_{ij}$’s.

Gilpin & Ayala (1973) and Ayala et al. (1973) analyzed many descriptive alternatives to the Lotka-Volterra equations and chose one equation (our Eq. 2, below) as being the best alternative to the Lotka-Volterra model. This model included a non-linearity parameter ($\theta$) in modeling intraspecific competition. This Gilpin-Ayala model fit data on competition among Drosophila species better than the Lotka-Volterra model, could model curvilinear zero-growth isoclines, and included the Lotka-Volterra model as a special case. This model or a slight variation of it (the $\Theta$-Ricker model) has been applied by Gilpin et al. (1976), Gilpin et al. (1986), Thomas et al. (1980) and Pomerantz et al. (1980) primarily to laboratory Drosophila populations.

**Facilitation**

Gallagher et al. (1983) found facilitation in an intertidal soft-bottom benthic community. An increase in the abundance of tube-building surface deposit feeders often results in an increase in the abundance of other members of the community. Epstein & Gallagher (1992) analyze indirect effects in benthic ciliate communities. By adding different meiofaunal and macrofaunal components to field patches, a typical result is an increase in the abundance of other species.

The general conclusion from these studies is that positive interactions among populations cannot be ignored, and may be as important as competition in structuring the numbers and types of species present in a community.
**Predation**

*Does predation control soft-bottom benthic community structure?*

Does predation control the distribution and abundance of the benthic infauna? At the start of quantitative benthic ecology, the answer would probably have been yes. Petersen (1918) began his quantitative studies of Danish benthic communities to assess the amount of fish food available for the benthos. Just because fish feed on benthic organisms does not mean that they are major sources of benthic infaunal mortality. Blegvad (1928) performed one of the first caging experiments in the soft-bottom benthos, finding that those benthic species consumed by bottom-feeding fish (plaice) increased dramatically beneath the cages. Based on Blegvad’s results, it would appear that epibenthic predators like bottom-feeding fish, crab, and shrimp may control benthic community structure. Unfortunately, there have so few convincing demonstrations of the importance of predation since that John Gray in his 1981 book on benthic ecology that predation was relatively unimportant in controlling community structure.

Thorson (1966) capped off a brilliant career by arguing that soft-bottom benthic community structure was largely determined by three factors: physical factors (substrate and depth), habitat selection, and intense predation on settling larvae. Thorson argued that the major predators of the settling larvae were either meiofaunal-sized predators or deposit feeders. Thorson (1966) didn’t place much emphasis on the role of competition or food resources in controlling the distribution or abundance of the benthic infauna. Presumably, benthic species evolved to identify habitat cues so that they would settle in habitats where suitable food was likely to be present. Mary Watzin (1986) produced some of the nicest results showing that the meiofauna, especially turbellaria, prey on the settling larvae of the benthic macrofauna. There have been few other quantitative studies demonstrating the importance of predation on the recruits of the benthic larvae. It is known that only a small percentage of the larvae that recruit to a given benthic environment reach reproductive age. The sources of mortality for these juvenile stages have not been well documented.

*Methods for determining predator-prey links*

Feller *et al.* (1979) argued that soft-bottom benthic ecologists have a difficult time assessing predation because it is difficult to document predator-prey interactions in mud and sand communities. Table 1 shows some of the methods for identifying predator-prey interactions in the soft-bottom benthos. When the tide is in, predation cannot be directly observed even in intertidal soft-bottom benthic communities. Most benthic organisms are soft-bodied and are unidentifiable in the guts of their predators. Feller *et al.* (1979) introduced the use of serological assays to assess predator-prey links in the soft-bottom benthos. Characteristic prey antigens can be detected in the guts of predators, a trick borrowed from entomology where serology was used to identify the blood meals of ticks and mosquitoes since the 1920s. Boreham and Ohiagu (1978) review the early applications of serology in entomology.
### Table 1. Methods for identifying predator-prey links (From Feller et al. 1979). L: low, M: moderate, H: high, V: variable

<table>
<thead>
<tr>
<th>Method</th>
<th>Likelihood of artefactual predator or prey behavior</th>
<th>Certainty of Specific Identity</th>
<th>Viability of prey at time of capture known</th>
<th>Differential digestion a problem</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Lab</strong></td>
<td>Offering prey in the laboratory</td>
<td>H</td>
<td>H</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td><strong>Field</strong></td>
<td>Predator exclusion or inclusion</td>
<td>H</td>
<td>L</td>
<td>No</td>
<td>Predation difficult to distinguish from experimental artifacts (e.g., caging or tether artifacts)</td>
</tr>
<tr>
<td></td>
<td>Monitoring labeled prey in the field</td>
<td>L</td>
<td>H</td>
<td>No</td>
<td>Yes</td>
</tr>
</tbody>
</table>

Viability and feeding conditions difficult to realistically simulate.

Recovery of labeled prey usually low.
<table>
<thead>
<tr>
<th>Method</th>
<th>Likelihood of artefactual predator or prey behavior</th>
<th>Certainty of Specific Identity</th>
<th>Viability of prey at time of capture known</th>
<th>Differential digestion a problem</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>Direct field observations</td>
<td>V</td>
<td>V</td>
<td>Yes</td>
<td>No</td>
<td>Difficult in soft substrates</td>
</tr>
<tr>
<td>Monitoring of predator &amp; prey abundances</td>
<td>L</td>
<td>L</td>
<td>No</td>
<td>No</td>
<td>Causation uncertain</td>
</tr>
<tr>
<td>Visual analysis of gut contents</td>
<td>L</td>
<td>V to H</td>
<td>No</td>
<td>Yes</td>
<td>Highly dependent on observer expertise</td>
</tr>
<tr>
<td>Serological analysis</td>
<td>L</td>
<td>L to H</td>
<td>No</td>
<td>Yes</td>
<td>Cross reactions are a major problem as is consumption of “non-living” food. Only source food webs can be determined</td>
</tr>
<tr>
<td>δ¹⁵N &amp; δ¹³C analysis of predator tissues</td>
<td>L</td>
<td>L</td>
<td>Yes</td>
<td>Yes</td>
<td>Specificity of prey highly uncertain. Sensitivity for small samples is a problem.</td>
</tr>
<tr>
<td>Measuring bioaccumulation of specific chemicals</td>
<td>L</td>
<td>V</td>
<td>No</td>
<td>Yes</td>
<td>Bioaccumulation &amp; transfer efficiencies must be known or assumed</td>
</tr>
</tbody>
</table>

**Virmstein (1980)** reviews how field experiments can be used to document the effects of predation in the soft-bottom benthos. There are four basic methods for experimentally
demonstrating the effects of predation (Table 1). Predators can be added or removed, and these manipulations can be one-shot affairs (pulse experiments) or manipulated over long time periods (Press experiments). The terms Press and Pulse experiments were introduced by Case and Bender.

Table 1. Methods for demonstrating the effects of predation on community structure. In a pulse experiment, predators are manipulated for a short time only. In a press experiment, the abundances are manipulated for long periods of time. In some experiments, labeled Both, predator removal is followed by addition of predators to the same plot. It may be statistically impossible to detect the effects of a short-term removal of predators (a few days) on benthic infaunal populations (indicated with a $\varnothing$).

<table>
<thead>
<tr>
<th>Predator abundance</th>
<th>Enhanced</th>
<th>Reduced</th>
<th>Both</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Pulse</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gallagher <em>et al.</em> (1990)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Epstein &amp; Gallagher (1992)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Press</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reise (1977, 1978, 1979)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kneib &amp; Striven (1982)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Martin <em>et al.</em> (1990)</td>
<td>Young &amp; Young (1977)</td>
<td>Young <em>et al.</em> (1976)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Davey &amp; Geroge (1986)</td>
<td>Virnstein (1977)</td>
<td></td>
</tr>
</tbody>
</table>

Conclusions on predation effects

There are relatively few general conclusions to be reached about the effects of predation on benthic communities. Reviews of the role of predation include: Virnstein (1979), Peterson (1979b), Ambrose (1984), Reise (1985), and Wilson (1986, 1990). Epibenthic predators — such as plaice, flounder, and crab — can exert strong effects on selected benthic prey species. These effects may not translate into strong effects on diversity of the benthic community for several reasons:

- The rate of predation by epibenthic predators, especially on settling larvae, is low compared to the larval recruitment rates.
- Benthic predators may only browse on prey, feeding on feeding appendages (siphons and tentacles) and rear ends. Woodin (1982, 1984) documents browsing and its long-term effects on individual growth. Such predation would exert only small effects at the community level.
- Indirect effects: The prey of epibenthic predators may themselves be predators, producing no net change, or even a reduction of “overall” predation intensity as epibenthic predation increases.
Competitive exclusion is less likely in the soft-bottom benthos than in the rocky intertidal. In the rocky intertidal, crushing and overgrowth can lead to the elimination of competitively inferior species. As noted by Peterson (1979), such interactions are rare in the soft-bottom benthos.

References

**GRAZING, PRIMARILY ON BENTHIC DIATOMS**

“Grazers are usually lumped into the larger category of deposit feeders, or occasionally as ‘selective surface deposit feeders’. Sometimes they are called herbivores. However, many benthic species are either facultative or even obligate predators of the microphytobenthos. Grazers in the Fauchald-Jumars scheme might be termed microphagous surface-feeding herbivores.”

Admiraal, W. L. A. Bouwman, L. Hoeckstra, and K. Romeyn. 1983. Qualitative and quantitative interactions between microphytobenthos and herbivorous meiofauna on a brackish intertidal mudflat. Int. Rev. ges. Hydrobiol. 68: 175-192. [This is one of the best general discussions of the quantitative importance of diatoms to grazers (large) and grazers to microphytobenthic production (relatively modest).] {4}


Asmus, H. and R. Asmus. 1985. The importance of grazing food chain for energy flow and production in three intertidal sand bottom communities of the northern Wadden Sea. Helg. wiss. 39: 273-301. [The primary and secondary production of 3 areas (Nereis-Corophium belt, seagrass bed, and Arenicola flat) is measured by oxygen flux and change in specific biomass, respectively. The grazer food-chain on benthic diatoms (dominated by Hydrobia ulvae) is the key carbon source for all three areas.]


Gould, D. G. and E. D. Gallagher. 1990. Field measurement of specific growth rate, biomass and primary production of benthic diatoms of Savin Hill Cove, Boston. Limnol. Oceanogr. 35: 1757-1770. [Diane estimated the specific growth rate of benthic diatoms and calculated the grazing rates required to account for the huge crash of the spring mudflat diatom bloom.


Marsh, A. G. and K. R. Tenore. 1990. The role of nutrition in regulating the population dynamics of opportunistic surface deposit feeders in a mesohaline community. Limnol. Oceanogr. 35: 710-724. [Essential dietary components in food could play a role in the seasonal succession.]


**References:**


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Marsh, A. G. and K. R. Tenore. 1990. The role of nutrition in regulating the population dynamics of opportunistic surface deposit feeders in a mesohaline community. Limnol. Oceanogr. 35: 710-724. [Essential dietary components in food could play a role in the seasonal succession.]

Montagna, P. A. 1984. In situ measurement of meiobenthic grazing rates on sediment bacteria and edaphic diatoms. Marine Ecology Progress Series 18: 119-130. [“C-labeled glucose and bicarbonate are used to label bacteria and diatoms in field incubations. Diatom grazing is important and dominated by small polychaetes, but grazing on bacteria is also important. Grazing rates may be sufficient to control diatom and bacterial standing stocks.”]


Montagna, P. A., B. C. Coull, T. L. Herring, and B. W. Dudley. 1983. The relationship between abundances of meiofauna and their suspected microbial food (diatoms and bacteria). Est. Coast. Shelf Science 17: 381-394. [“Regression analyses show a positive correlation between meiofaunal abundance and diatom standing stock (but not bacterial standing stock). At the gross taxonomic level, total meiofauna do not respond to changes in the food level, even when time lags are considered. Other factors may control meiofaunal abundance (e.g., predation).”]


Pace, M. C. and K. R. Carman. 1996. Interspecific differences among meiobenthic copepods in the use of microalgal food resources. Mar. Ecol. Prog. Ser. 143: 77-86. [“Pelagic and benthic microalgae labeled and fed to 2 harpacticoid species. Both feed on both food types but at different rates.”]


Rieper, M. 1985. Some lower food web organisms in the nutrition of marine harpacticoid copepods: an experimental study. Helg. wiss. 39: 357-366. [“Rieper studies an odd mix of harpacticoids and food sources. Little evidence is provided that the food sources are appropriate for the copepods in the field. Growth on bacteria, 2 ciliate species and Skeletonema costatum are compared.”]

Smith, D. R. G. Hughes and E. J. Cox. 1996. Predation of epipelagic diatoms by the amphipod Corophium volutator and the polychaete Nereis diversicolor. Mar. Ecol. Prog. Ser. 145: 53-61. [“Experimental removal of Corophium using an insecticide produced enhanced diatom densities. Corophium eats 2150 to 3767 cells per day N. diversicolor eats 5476 to 12184 cells per day (nice sig. figs!) n.b. benthic diatoms can reach 5 x 10^6 cells per cm². These feeding rates seem too low to cause much of an effect.”]


**ON COMPETITION**

**Evidence for in benthic systems**

**Soft Bottom Benthos**


Fenchel T (1975) Factors determining the distribution patterns of mud snails (*Hydrobiidae*). Oecologia 20: 1-17


Fenchel T, Kofoed LH (1976) Evidence for exploitative


Hill C, Elmgren R (1987) Vertical distribution in the sediment in the co-occurring benthic amphipods Pontoporeia affinis and P. femorata. Oikos 49: 221-229 [Argues that depth partitioning per se is not convincing evidence of interspecific competition]


Hylleberg J (1986) Distribution of hydrobiid snails in relation to salinity, with emphasis on shell size and coexistence of the species. Ophelia Suppl 4: 85-100


Kastendiek [Cited in Schoener’s reviews]


Mangum CP (1964) Studies on speciation in maldanid polychaetes of the North American Coast. II. Distribution and competitive interactions of five sympatric species. Limnol. Oceanogr. 9: 12-26


Peterson CH (1983) Interactions between two infaunal bivalves Chione undatella (Sowerby) and Protothaca staminea (Conrad) and two potential enemies, Crepidula onyxa (Sowerby) and Cancer anthonyi (Rathburn). J. exp. mar. Biol. Ecol. 68: 145-158


Peterson CH, Beal BF (1989) Bivalve growth and higher order interactions. Ecology 70: 1390-1404 [The interaction between site and density treatments on Mercenaria mercenaria growth; outlined]


Hard-bottom benthos


Connell JH (1961a) Effects of competition, predation by Thais lapillus, and other factors on natural populations of the barnacle Balanus balanoides. Ecol. Monogr. 31: 61-104


Dayton PK (1975) Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecol. Monogr. 45: 137-159


Menge BA (1972) Competition for food between two intertidal starfish species and its effects on body size and feeding. Ecology 53: 635-644


Sousa WP (1979) Experimental investigations of disturbance and ecological succession in a rocky intertidal community. Ecol. Monogr. 49: 227-254 [Tested Connell and Slatyer’s models: the inhibition model applied. Succession results from some species surviving better and retaining space against superior colonizers which survive less]


Character displacement and Resource Partitioning


Fenchel T (1975) Factors determining the distribution patterns of mud snails (Hydrobiidae) Oecologia 20: 1-17


Hylleberg J (1986) Distribution of hydrobiid snails in relation to salinity, with emphasis on shell size and coexistence of the species. Ophelia Suppl 4: 85-100


Mangum CP (1962) Studies on speciation in maldanid polychaetes of the North American Coast. II. Distribution and competitive interactions of five sympatric species. Limnol. Oceanogr. 9: 12-26


Measuring Interspecific Competition Coefficients (Methods)


Case TJ, Bender EA (1981) Testing for higher order interactions. Amer. Natur. 8: 920-929. [They found higher-order interactions.]


MacArthur, R. H. and R. Levins. 1967. The limiting similarity, convergence and divergence of coexisting species. Amer. Natur. 1: 377-385. [This was once of the first papers which provided an equation for estimating a]


Schoener TW (1985) On the degree of consistency expected when different methods are used to estimate competition coefficients from field data. Oecologia 67: 591-592

Vandermeer JH (1969) The competitive structure of communities: an experimental approach with protozoa. Ecology ; 362-371. [They found higher-order interactions exist but may be unimportant; it depends upon the use to which the model is put]

Vandermeer J (1981) A further note on community models. Amer. Natur. 7: 379-380. [Higher order interactions exist but may be unimportant; it depends upon the use to which the model is put]
Competitive exclusion (or the lack of it)


Connell JH (1985) On testing models of competitive coevolution. Oikos 45: 298-300

Davic RD (1985) In search of the ghost of competition past. Oikos 45: 246-298 [See also Connell 1980]


Wiens JA (1977) On competition and variable environments. Amer. Sci. 65: 590-597


On Modeling Competition


Neill WE (1975) Experimental studies of microcrustacean competition, community composition and efficiency of resource utilization. Ecology 56: 809-826 {7}


Schoener TW (1985) On the degree of consistency expected when different methods are used to estimate competition coefficients from census data. Oecologia 67: 591-592

Schoener TW (1985) Some comments on Connell’s and my reviews of field experiments on interspecific competition. Amer. Natur. 126: 300-301


Wiens JA (1977) On competition and variable environments. Amer. Sci. 65: 590-597


Wilbur H (1972) Competition, predation, and the structure of the Ambystoma-Rana sylvatica community. Ecology 53: 3-21 [Along with Neill (1974), the most often cited refutation of the L-V assumption that there are no higher order interactions in communities. Pomerantz notes that the L-V model is multigenerational and can’t be tested with Wilbur’s data]

Williamson M (1972) The analysis of biological populations. Edward Arnold Publishers. [Includes a strong attack on studies which inferred competition from differences in morphology or spatial distributions - see Connell (1980)] [5]

SOFT-BOTTOM PREDATION

Synecology


Blegvad, H. 1928. Quantitative investigations of the Limfjord 1910-1927 with special reference to plaice food. Rep. Danish Biol. Stat. 34: 33-52. [Contains a description of one of the first and maybe one of the most cited caging experiments. Unfortunately, the entire experiment is described in only a few sentences.]


Gray, J. 1981. The Ecology of Marine Benthos. [Predation not that important in the soft-bottom benthos, only affecting bivalve spat]


Redmond, M. S. and K. J. Scott. 1989. Amphipod predation by the infaunal polychaete, Nephtys incisa. Estuaries 12: 205-207. [In these laboratory microcosms, amphipod survival is more closely coupled with Nephtys predation than sediment toxicity]


Segersträle, S. G. 1973. Results of bottom fauna sampling

Segerstråle, S. G. 1978. The negative correlation between the abundances of the amphipod Pontoporeia and the bivalve Macoma in Baltic waters and the factors involved. Ann. zool. Fenn. 15: 143-145. [Explains the long-term inverse cycles of these two species]


Steinberg, P. D. and V. S. Kennedy. 1979. Predation upon Crassostrea virginica (Gmelin) larvae by two invertebrate species common to Chesapeake Bay oyster bars. Veliger 22: 78-84.


Woodin, S. A. 1976. Adult-larval interactions in dense infaunal assemblages: patterns of abundance. J. Mar. Res. 34: 25-41. [Anecdotal evidence is presented that surface deposit feeders and suspension feeders are important predators on larvae, but the evidence is surprisingly weak.]


Young, D. K, M. A. Buzas, and M. W. Young. 1976. Species densities of macrobenthos associated
the seagrass: a field experimental study of predation. J. Mar. Res. 34: 577-592. [This study appeared before Young & Young 1977 appeared, but it was written after. Cages led to increased abundances of predators, making the predator exclusion cages of Young & Young into predator enhancement experiments] {11, 31}

Young, D. K. and M. W. Young. 1977. Community structure of the macrobenthos associated with seagrass of the Indian River estuary, Florida. Pp. 359-383 in B. C. Coull, ed., Ecology of marine benthos. University of South Carolina Press, Columbia. [This paper was written before Young et al. 1976. The caging manipulation did not work, and the authors used the results to criticize Paine's work. They recanted their heresy in Young et al. 1976. The cages may have increased the abundance of small epifaunal predators. The experimental design is too flawed to allow a judgement one way or the other.] {11, 31}

**Auteology of individual soft-bottom predator species:**


Breese, W. P. and F. D. Phibbs. 1972. Ingestion of bivalve molluscan larvae by the polychaete annelid Polydora ligni. Veliger 14: 274. [An anecdotal example of predation, but the picture of a spionid loaded with spat is worth a look.]


HARD-SUBSTRATES (SELECTIVE LISTING):

**Synecology**


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SEROLOGICAL APPLICATIONS
MARINE ECOLOGY

reference list contains serological papers marine ecological literature ( ). papers involve analysis food webs, deal marine invertebrate systems, few (e.g., Ward Perry) serological assays enumerate marine bacteria. minute fraction voluminous immunological literature cited following list. I’ve listed techniques papers extensively own work, few reviews, few classics.

Marine Ecology


**Immunofluorescent assays**


Fliermans & Schmidt’s (1977) soil method applied pelagic nitrifiers


Sunderland, K. D. S. L. Sutton. 1980. serological study


General Techniques Papers


Production Monospecific Antisera Using Precipitin


PRO FOOD WEB theory


Briand, F. J. E. Cohen. 1987. Environmental correlates food chain length. Science 238: 956-960.[Average maximal food chain lengths independent primary productivity environmental variability. However, 3-dimensional habitats (e.g., ocean forest canopy) longer food chain lengths 2-dimensional habitats. Moore et al.’s 1989 commentary]


May, R. M. 1973. Stability complexity model ecosystems. Princeton University Press, Princeton, N. J. [Diverse well-connected model communities necessarily stable. criterion community governed community matrix (c.m.) stable perturbations eigenvalues c.m. negative real parts. May expands Gardner Ashby's earlier Monte-Carlo analysis finds stability s(mC)^0.5<1, s interaction strength m number species.(p. 65).]


Roberts, F. S. 1978. Graph theory applications problems society. SIAM Publications, Philadelphia. [Chapter 5 devoted food webs, niche overlap graphs, toxicity phase space]


**ANTI-FOOD-WEB THEORY**


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