BENTHIC POPULATION PROCESSES: COMPETITION PREDATION SOFT-BOTTOM BENTHOS

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Assignment

Required

Gallagher, E. D., G. B. Gardner and P. A. Jumars 1990. Competition among the pioneers in soft bottom benthic succession: field experiments and analysis of the Gilpin-Ayala competition model. Oecologia *83*: 427-442.

Whitlatch, R. B. 1980. Patterns of resource utilization an coexistence in marine intertidal deposit-feeding communities. J. Mar. Res. *38*: 743-765.

Supplemental

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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.

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1 - \alpha_{12} N_2}{K_1}\right).$$
$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2 - \alpha_{21} N_1}{K_2}\right). \qquad (1)$$
$$\begin{aligned} where,\ \alpha &= Interspecific\ competition\ coefficient. \\ K &= Carrying\ capacity. \\ r &= maximum\ per\ capita\ growth\ rate. \end{aligned}$$

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)** ompetition 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 (α_{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 α_{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 α in the Lotka Volterra model). Gardner and Gallagher (ms), argue that constant α_{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 α_{ij}'s.

Gilpin & Ayala (1973) and **Ayala *et al.* (1973)** analyzed many descriptive alternatives to the Lotka-Volterra equations and chose one equation (our Equ. 2, below) as being the best alternative to the Lotka-Volterra model. This model included a non-linearity parameter (θ) 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 Θ-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

Method			Likelihood of artefactual predator or prey behavior	Certainty of Specific Identity	Viability of prey at time of capture known	Differential digestion a problem	Comments
Experimental	*Lab*	Offering prey in the laboratory	H	H	Yes	No	Viability and feeding conditions difficult to realistically simulate
	Field	Predator exclusion or inclusion	H	L	No	No	Predation difficult to distinguish from experimental artifacts (*e.g.*, caging or tether artifacts)
		Monitoring labeled prey in the field	L	H	No	Yes	Recovery of labeled prey usually low.

Table 1. Methods for identifying predator-prey links (From **Feller *et al.* 1979**). L: low, M: moderate, H: high, V: variable

Method		Likelihood of artefactual predator or prey behavior	Certainty of Specific Identity	Viability of prey at time of capture known	Differential digestion a problem	Comments
Observational	Direct field observations	V	V	Yes	No	Difficult in soft substrates
	Monitoring of predator & prey abundances	L	L	No	No	Causation uncertain
	Visual analysis of gut contents	L	V to H	No	Yes	Highly dependent on observer expertise
	Serological analysis	L	L to H	No	Yes	Cross reactions are a major problem as is consumption of "non-living" food. Only source food webs can be determined
	$\delta^{15}N$ & $\delta^{13}C$ analysis of predator tissues	L	L	Yes	Yes	Specificity of prey highly uncertain. Sensitivity for small samples is a problem.
	Measuring bioaccumulation of specific chemicals	L	V	No	Yes	Bioaccumulation & transfer efficiencies must be known or assumed.

Virnstein (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 ∅)

	Predator abundance		
	Enhanced	**Reduced**	**Both**
Pulse	**Gallagher *et al.* (1990)** **Epstein & Gallagher (1992)**	∅	
Press	Reise (1977, 1978, 1979) **Kneib & Striven (1982)** Gee *et al.* (1985) Martin *et al.* (1990)	**Blegvad (1928)** **Paine (1966)** **Young & Young (1977)** **Young *et al.* (1976)** **Buzas (1978)** **Berge (1980)** Davey & Geroge (1986)	**Virnstein (1977)**

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."

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On Competition

Evidence for in benthic systems

Soft Bottom Benthos

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Character displacement and Resource Partitioning

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Competitive exclusion (or the lack of it)

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On Modeling Competition

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Soft-bottom Predation

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 systematics, 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.

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