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MEASURING EFFECTS OF PREDATION ON BENTHIC COMMUNITIES IN SOFT SEDIMENTS

Robert W. Virnstein

*Harbor Branch Foundation, Inc.
RR 1, Box 196
Fort Pierce, Florida*

Abstract: Most studies on effects of predation on benthic communities in soft sediments have relied either on correlation and pattern analysis or, more recently, on the use of mesh cages to exclude potential or suspected predators from areas of the bottom. Because such cages usually produce other physical effects besides excluding predators, results from such studies are often difficult to interpret. I propose that a combination of techniques is mandatory. The approaches can be broadly classified as either non-manipulative or manipulative. The non-manipulative approaches include 1) observation; 2) correlation and pattern analysis, such as abundance and distribution of predators and prey; 3) gut content analysis; and 4) analysis of age class structure. None of these methods can demonstrate that predation causes certain effects, but they can show that predation does occur and they should be used to formulate hypotheses which can then be tested with manipulative techniques. Manipulative approaches have the advantage that both controls and replication are possible; they include 1) laboratory studies, 2) microcosm studies, and 3) field studies. Where they are possible and can be done correctly with controls and replication, field studies are preferred because their results relate directly to the natural system. The use of more than one technique is necessary since each single technique tells only a part of the story. No single approach is both controlled enough to be interpreted without question and natural enough to be extrapolated to the field.

Introduction

A central question in ecology has long been, what factors control the distribution and abundances of organisms? For communities in soft sediments, experimental evaluation of the role of predation has been investigated only recently, primarily using cages which can result in many problems (Virnstein 1978). Most prior studies relied primarily on correlation or pattern analysis. In this paper, I argue that a number of additional approaches, used in combination, are a much more powerful tool for measuring the effect of predation than is any single method.

General Approaches

In broad terms, the approach to determining the effects of predation can be either non-manipulative or manipulative. Non-manipulative approaches (inferences based on systematic sampling or observation) include strictly observational studies, gut analysis studies, size class analysis, and correlation, regression, and pattern analysis studies of predator-prey abun-

dances. Such studies may show 1) that a predator does feed on a given prey or 2) that prey abundance decreases when predators are abundant. However, 1) this feeding may have an insignificant effect on the prey, and 2) the predator and prey may both be responding to the same external factor(s), rather than one being causally related to the other.

Manipulative approaches generally consist of altering predator densities in some manner and then testing for a response in the prey populations. Such studies may be easier to do in aquaria in the laboratory, but conditions are not natural. Field studies afford the most natural conditions but little control. This lack of control is both an advantage (Connell 1974, 1975) and disadvantage (Virnstein 1978). With respect to degree of control and naturalness, microcosm studies offer an approach intermediate to field and aquarium studies.

Specific Approaches

I. Non-manipulative Techniques

The first three approaches considered are non-manipulative, and are based on observations or systematic sampling. All should lead to the formulation of testable hypotheses.

Observation

Careful observation could possibly tell how, where, when, and perhaps on what a species is feeding. As such, it can be a powerful tool. Fiber optics and X rays may provide views within the sediments. A dissecting microscope mounted above an aquarium or dish of sediment can show activity and behavior patterns of small predators. Remote cameras in the field may provide important evidence of predator activity. However, for infauna of soft sediments in turbid estuaries, observational capabilities in the field are usually severely limited. Such information is not sufficient to determine the effect on the prey assemblage but could distinguish actual predation from physical disturbance, which other methods cannot do.

Gut Content Analysis

Analysis of the gut contents of suspected predators can confirm that a certain species of prey is actually eaten. However, interpretive caution must be exercised here, because many animals, if ingested whole, may pass live through the gut of a predator. If prey are damaged beyond recognition, serological techniques may be necessary to determine which species of prey have been eaten (Feller et al. 1979) and can provide quantitative data on amounts present. The use of $^{13}\text{C}/^{12}\text{C}$ ratios (Haines and Montague 1979), usually employed in relating trophic structure to primary producers, permits an evaluation of the relative quantitative importance of each prey type in the predator's diet.

The number or biomass of prey eaten per unit area per day can be determined from gut analyses if the following are known: the density of predators, percentage of foraging time in the habitat, and the residence time of food in the gut (see Peterson and Bradley 1978). By comparing this figure with prey densities, the percentage of the prey population eaten per day can be calculated. The inverse of this value would be equal to either 1) the time required to replace the prey population (turnover time), assuming adequate recruitment and constant population size, or 2) the length of time to eliminate the prey, assuming no recruitment. For example, if 2% of the prey are eaten per day, then the turnover time must be not more than 50 days in order to maintain the prey population.

Obviously, if a large percentage of the prey is removed in a short time (relative to turnover time), the effect will be significant. Such work has been done for a mesohaline Chesapeake Bay macrobenthic community fed on by spot, *Leiostomus xanthurus* (A. F. Holland, Martin Marietta Labs, Baltimore, MD pers. comm.), and for a continental slope community fed on by the red crab, *Geryon quinquedens*, and other predators (Farlow 1980). Because the benthos of estuaries is so variable, both spatially and temporally (Boesch et al. 1976; Coull and Fleeger 1977), I would stress that predators collected for gut analyses should ideally be collected from the same area (habitat) and during the same time period as the benthic prey population is sampled.

Analysis of Age Class Structure

Assuming that age can be estimated (e.g., from size or from growth rings or other clues) and that growth rates are known, the total mortality rate for a size class within a time interval can be calculated as the difference between the actual numbers at the end of the time interval and the potential numbers in the next size class if there had been 100% survival. If high mortality is found in size classes well below the maximum size and cannot be attributed to other sources, perhaps a large portion of this mortality can be attributed to predation. However, such a method depends on a number of assumptions and recognition of cohorts. By itself, this method has little value, and would require some supporting information on actual rates of predation.

Correlation Analysis

Correlation analyses (and regression, pattern analysis, etc.) are powerful tools that can show statistically significant relationships between predator and prey abundances (Arntz 1980; Livingston 1980). They may imply (but do not and cannot demonstrate) cause for the relationship, since predator and prey may both simply be responding to the same external factor, such as temperature. It is critically important that sampling be on an appropriate time scale, i.e., shorter than the life cycle of the prey; other-

wise, results of predation may be confused with effects of competition or with recruitment events. Lag times may have to be considered.

The functions of non-manipulative and manipulative approaches are complimentary and non-overlapping. Associations and relationships derived from non-manipulative techniques should be used to formulate hypotheses which can then be tested by manipulative techniques. Since the manipulative techniques are dependent on the prior formulation of testable hypotheses, one should not, for example, simply set out a cage without any prior knowledge or hypotheses as to what is happening.

II. Manipulative Techniques

The following three approaches use manipulative as opposed to observational or sampling techniques and represent a progression from most controlled and least natural to least controlled but most natural situations. In all cases, the density of predators is somehow artificially manipulated and then the response of the prey is determined (Table 1). Additionally, the investigator can act as a predator, removing selected animals. Any one of the manipulative approaches can be used in combination with any of the response measurements (see below). A major advantage of manipulative approaches is that a control and replication are possible and are always necessary.

Laboratory Aquarium Studies

Studies in aquaria in the laboratory provide for the tightest control of experimental conditions. In the simplest approach, prey are added to an aquarium and then a predator is added and allowed to feed for some period of time. From such a study, one could determine whether and at

Table 1. A summary of approaches for measuring the effect of predation.

<i>Approaches</i>	<i>Factors Responding</i>
Non-manipulative	
Observation	}
Gut analysis	
Age-class structure	
Correlation analysis	
Manipulative	
Laboratory studies	}
Microcosm studies	
Field studies	
	Density Distribution Reproduction Growth

what maximum rate a given predator could consume prey. However, such a one prey/one predator system is artificial and unnatural, especially for soft-sediment infaunal communities. The results obtained probably cannot be extrapolated to the field. Such studies can be useful for determining predator preferences for certain species or for sex or size of given species. Additionally, observation becomes an available tool.

Microcosm Studies

A microcosm, by retaining the whole assemblage of animals along with associated sediment and other physical structures (e.g., seagrass, animal tubes and burrows), is a much more natural system, and results can be extrapolated more validly to the field. The manipulation of predator densities is still quite controllable, but prey densities are more difficult, although not impossible, to manipulate.

Such multispecies assemblages may be set up by placing undisturbed cores of sediment from the field into tanks, or by putting sediment into tanks with running unfiltered seawater and then adding prey and/or allowing recruitment to occur naturally. Microcosm studies may represent the next-best alternative when field studies are too complicated to interpret (Bell and Coull 1978; Virnstein 1978).

Field Studies

Field experimental studies (primarily caging, but other methods may work, depending on the character of the predator) have the advantage of retaining the system in an essentially natural state and letting all factors but the one under control vary naturally in both the control and experimental treatments. Assuming adequate controls are provided, problems of caging studies (see Virnstein 1978) are primarily related to changes in current structure above the sediment (Hulberg and Oliver 1980) and the presence of a physical structure, and their effects on recruitment and attraction of animals. In seagrass beds, for example, exclusion of decapod crustacean predators for any but a very short term seems nearly impossible, due both to recruitment and subsequent fast growth, and to attraction to the cage structure (unpubl. data; R. J. Orth, Virginia Institute of Marine Science; K. L. Heck, Benedict Estuarine Lab, MD; W. G. Nelson, University of Bergen, Norway; and S. A. Woodin, Johns Hopkins University, MD, all pers. comm.). Addition of predators is easier than exclusion, but densities above normal may not reflect normal activities or food selection of predators. This method cannot show that predators are normally important.

If regular seasonal fluctuations of prey occur and one wishes to test whether these are due to predators, the best time to set out a cage would be just before the decline in prey abundance. In this way, if predators are producing the decline, then prey abundance should not decline inside the cage, but would outside the cage. To set out a cage at other times and ex-

pect an increase in prey density inside the cage requires not only that predators be excluded and are important, but also that recruitment of prey occur during the time that the cage is in place.

To separate effects of differential recruitment from predation, reopening (removing) a cage may provide an answer. The abundance of predators at this time is important in determining the results.

What to Measure

Once predation intensity is manipulated, whether in the laboratory, microcosm, or field, the responses of the soft-sediment community can be measured (Table 1). Most commonly, changes in adult population density are measured; this is the most immediate effect of the mortality. If size selection is important, the size-class structure of a prey population can be altered. Changes in the spatial distribution of prey, both horizontally (Vargas 1979; N. K. Mountford, Chesapeake Biological Lab, MD pers. comm.) and vertically, could occur in response to predation. Predators could cause prey to shift to more cryptic or other microhabitats where predation is less effective, such as at the base of rooted plants.

Although I am considering predation here to be the eating of whole animals, non-mortality effects due to the loss of body parts (e.g., siphons, palps, lophophores, etc.), whether by natural or artificial (by the investigator) predation, may also be important. These effects could be measured as changes (presumably decreases) in reproductive output and growth rate (see Peterson 1980) due to the increased energy expenditure necessary to replace lost tissues.

Other indirect effects might be changes in recruitment success due either to decreased reproductive output, or to changes in adult population density. However, such changes are probably not measurable for species with planktonic larvae (this does not include most meiofauna). Although only adult populations are usually censused, effects of predator activity on larval or juvenile recruitment may be even more important. Harder to detect would be changes in prey populations that occur as changes in the timing of events, e.g. seasonal abundance peaks and time of spawning.

Some Examples and Problems of Applicability

Because field methods lack control and laboratory methods lack naturalness, some combination of methods is necessary for a proper balance of control versus naturalness. I doubt that any one method is both controlled enough to be interpreted without question and natural enough to be applicable to the field situation. For example, Nelson (1979; pers. comm.) presents a convincing story that predation by pinfish (*Lagodon rhomboides*) on amphipods in seagrass beds in North Carolina and Florida has a significant effect, but only as a result of a combination of types of evidence. Amphipod abundance decreases soon after pinfish become

abundant and increases again after pinfish leave the area. Pinfish do eat amphipods presented as food items in aquaria and will significantly reduce amphipod numbers in microcosm experiments. Additionally, field-collected pinfish had large numbers of amphipods in their stomachs. In field caging experiments, the results were muddled because pinfish also fed on decapod crustaceans which in turn feed on amphipods.

As another example of the importance of predators on macrofauna and vice versa, Holland et al. (1980) and Virnstein (1977) found that infaunal densities of macrobenthos in Chesapeake Bay decrease and stay depressed while spot (*Leiostomus xanthurus*) are abundant and that spot do feed on the infauna in the areas studied. Based on daily food rations (calculated from growth rates and efficiency estimates) and density of spot (Holland pers. comm.), the amount of infauna consumed by spot accounts for 95% of the seasonal decline in infaunal biomass. I have shown that infaunal densities increase inside cages where spot are excluded and decrease in cages where spot are included (Virnstein 1979). The most abundant species in spot stomachs were the same species that showed large density increases inside cages. Taken together, the above evidence strongly suggests that predation by spot does have a significant effect on infaunal abundance. I must stress, however, that any single line of evidence by itself is weak.

The presumption in much of the above discussion has been that the predators on the infauna are animals that are much larger than most infauna and that are motile and epibenthic, such as fishes, portunid crabs, gastropods, and starfishes. Recent work by Reise (1977) in the Wadden Sea and by Nelson and Virnstein (unpub. data) in seagrass beds in the Indian River, Florida, has demonstrated the importance of predation by small decapod crustaceans, including penaid and palaemonid shrimps. Holland (pers. comm.) and J. A. Commito (University of Maine, Machias, ME pers. comm.) both found that species of the polychaete *Nereis* could significantly reduce densities of some infauna. Holland worked with *N. succinea* in microcosms; Commito worked with *N. virens* in containers of sediment in the field. No doubt there are also numerous other infaunal animals that are themselves predators on other infauna, e.g. glycerid polychaetes, nemerteans, and turbellarians. Polychaetes from numerous families have a rather formidable jaw apparatus, and although many of these species are found to have mainly sediment or detritus in their guts, there seems little reason to doubt that they could supplement their diet with an occasional animal. High rates of biological activity at the sediment-water interface (Rhoads 1974; Black 1980) must make it difficult (Woodin 1976), or even unlikely, that a newly settled larva can pass through this barrier without being eaten or killed by burial, etc. Indeed, this initial settlement and establishment in the sediment may be the most critical stage of recruitment.

Although all the above statements apply to and are based on studies of macrofauna, I see no reason that any of the statements and procedures

could not also be applied to the meiofauna—the latter are just smaller and their predators are smaller. However, meiofauna are not easily manipulated, sediment parameters are critical, and they have different life history patterns and reproductive rates (Coull and Bell 1979). Numerous species of fish, including spot and gobies (Buzas and Carle 1979) have been collected with meiofauna in their guts. Bell and Coull (1978, 1980) have shown that predation by palaemonid shrimp has a significant regulatory effect on the density and population dynamics of meiofauna in the high marsh where macroinfaunal density was extremely low (Bell 1980).

Many macrobenthic deposit feeders that feed by selectively or non-selectively eating sediments undoubtedly ingest large numbers of meiofauna. Where high densities of macrofaunal surface deposit feeders occur, the entire upper few centimeters of sediment might be reworked (i.e., passed through an animal's gut) every few months (Rhoads 1974; Black 1980). Since the life cycles of many meiofauna are on this order of time, the meiofauna could be heavily cropped, but the rapid turnover rates and the ability to pass through guts live could still maintain relatively high population densities. From the above recent evidence, it appears likely that the meiofauna act not just as remineralizers (Tenore et al. 1977) and do not represent a dead-end closed food web (Heip and Smol 1975), but rather are intimately linked with the macroinfauna and motile epibenthic predators (see Coull and Bell 1979). The separation of the meiofauna from macrofaunal studies may be not only artificial but also unrealistic and invalid. The evaluation of all such predator-prey interactions is of utmost importance for describing and understanding an ecosystem.

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