Importance of predatory infauna in marine soft-bottom communities: reply to Wilson

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ABSTRACT: Wilson (1986) has criticized the application of a 3-level interactive model, epibenthic predators – predatory infauna – other infauna, to marine soft-bottom communities. His model, though inexact, shows that preferential predation on predatory infauna by epibenthic predators is a requirement of the 3-level model. His reanalysis of the caging studies used to test the 3-level model, however, is unacceptable as it analyzes only 32 % of the original data set and ignores predation by omnivores which is known to be important in structuring some soft-bottom communities. Despite its shortcomings, Wilson's reanalysis still supports a 3-level model. Experiments have demonstrated that many soft-bottom communities are more, not less, complex than the 3-level model indicates. Strict application of a 2-level model risks missing important interactions among the infauna.

INTRODUCTION

I have suggested that predatory infauna be considered separately from non-predatory infauna when predicting the outcome of interactions in marine soft-bottom communities and have proposed a 3-level interactive model for these communities (Ambrose 1984a). I initially tested this model by comparing the ratio of the abundance of predatory infauna to non-predatory infauna in the presence and absence of epibenthic predators and found that the ratio increased as predicted following the removal of epibenthic predators. Wilson (1986) demonstrates that preferential predation on predatory infauna by epibenthic predators is a requirement of the 3-level model, but finds no support for such predation in the literature. Wilson also reanalyzes the data set I used to test my model using a different definition of predatory infauna and finds no significant difference in the ratio of predatory infauna to non-predatory infauna between caged and uncaged areas. Consequently, he argues for a less complex 2-level model with fishes, crabs, and birds as predators and all infauna as prey. Wilson is correct that preferential predation is a requirement of the 3-level

model, but he ignores evidence of preferential predation. His reanalysis is unacceptable for reasons which I will outline below and therefore not an adequate test of the 3-level model. In fact, a 3-level model is required if the numerical responses of predatory and non-predatory infauna following the exclusion of epibenthic predators are to be explained.

Since publishing my model, more evidence on the role of predatory infauna in structuring soft-bottom communities has become available (Kent & Day 1983, Commito & Ambrose 1985a, Commito & Schrader 1985, Schubert & Reise 1986). This evidence and my own research (Ambrose 1984b,c, d, 1986) has led me to modify my original 3-level model, but in favor of more complexity, not less. I will address Wilson's points in the order they appear in his paper and then discuss the evidence which I think supports the existence of multi-level interactions in soft-bottom communities.

MECHANISM OF PROPOSED INTERACTIONS

By modeling the effects of preferential and non-preferential predation on the ratio of predatory infauna to non-predatory infauna, Wilson (1986) shows that the 3-level model depends on preferential predation. Wilson's model, however, is inexact because it does not use a continuous function to analyze changes in the

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ratio of predatory to non-predatory infauna. Calculus, not simple arithmetic, is required if changes in the abundance of predatory and non-predatory infauna are to be exactly modeled. Wilson uses simulations to avoid an integral model, but they are actually unnecessary to demonstrate that preferential predation is a requirement of the 3-level model. When epibenthic predators prey non-preferentially their predation will not affect the ratio of predatory to non-predatory infauna because they are consuming prey only in proportion to the prey's relative abundances. No change in the ratio will occur then when epibenthic predators are removed. The only process affecting the ratio when epibenthic predation is non-preferential is predation by predatory infauna on non-predatory infauna, and that process occurs in the presence and absence of epibenthic predation.

EVIDENCE OF PREFERENTIAL PREDATION BY EPIBENTHIC PREDATORS

Despite Wilson's (1986) claim, predatory infauna are often preyed upon preferentially by epibenthic predators, though the data that can be used to assess preferential predation are limited. In my earlier paper, I argue that predatory infauna may be more susceptible to epibenthic predation than non-predatory infauna because they are more active on the sediment surface. Wilson correctly points out that some predatory infauna are always found beneath the sediment surface and as a result of experimental evidence I modified the model to apply to surface-active predatory infauna (Ambrose 1984b, Commito & Ambrose 1985b). More information is needed, however, to correctly identify surface-active predatory infauna. Many of the most ubiquitous predatory infauna are active on or just beneath the sediment surface (e. g. nereids, phyllodocids, phoxocephalids, tanaids, corophiids, some nemerteans; see Commitio & Ambrose 1985a for review). Deep-living predatory infauna might also be preferred prey for epibenthic predators though more data are needed to test this possibility. Many of the deep-living predatory infauna are large as adults (e. g. nephtids, glycerids, and nemerteans) and are therefore likely to be preferred simply because epibenthic predators are more likely to encounter them when searching the sediment than smaller non-predatory infauna.

Very few studies have investigated prey preferences of epibenthic predators. Gut analyses of epibenthic predators cannot be used to support or refute preferred predation on predatory infauna. Knowledge of both prey abundance and predator consumption is required to examine predator preference. Observations on shorebirds and gulls show that these birds often prefer predatory infauna (Goss-Custard 1977, Evans et al. 1979, Curtis et al. 1985, Ambrose 1986). While Wilson's and my interpretation of these studies differ because we disagree on the definition of predatory infauna (see below), Wilson sometimes considers nereids predators. All of the studies show a preference by birds for nereids at least during part of the year.

I am aware of only one study with data which permits an analysis of prey perference by fishes and crabs (Arntz 1979). That study shows that predators prefer a predatory infaunal species although more information on the availability of other infauna is needed to evaluate this result. Virnstein's data (1979) cannot be used to test for predator preferences because it is based on caging studies which are confounded by cage artifacts which favor deposit feeders (Virnstein 1978, Dayton & Oliver 1980, Ambrose 1984a). Nevertheless, more than one predatory infaunal species increased in abundance under cages.

RATIO ANALYSIS

Most of the disagreements between Wilson (1986) and myself stem from our different definitions of predatory infauna. Wilson favors a strict definition and considers predators to be only those species which are known to prey exclusively on adult infauna. Such a definition excludes infauna which are only occasionally predators and therefore ignores a potentially huge source of predation. The main question is 'what are the effects of predation by infauna on the distribution and abundance of other infauna?' The question 'what are the effects of predation by strict predators?' is of less interest and predictive value. It makes no difference to an infaunal prey whether it is consumed by a strict predator or an occasional predator. By refusing to include omnivores in his analysis, Wilson is not testing the same null hypothesis I tested.

Experimental evidence does exist, despite Wilson's claim, which shows that omnivores have an effect on the abundance of other infauna (Reise 1979, Witte & de Wilde 1979, Commito 1982, Ambrose 1984b, c). These studies show significant predation by nereids. Nereids are generally considered to be omnivorous on the basis of gut contents (Fauchald & Jumars 1979, Ambrose 1984b). With the exception of nemerteans and predatory gastropods, it is probably possible to find a reference which indicates that even the strictest predators occasionally engage in non-predatory feeding. For example, glycerids have been shown to be capable of feeding on detritus (Adams & Angelovic 1970).

Wilson also excludes predators on the basis of size, but his definition for adults, all organisms retained on

the mesh size used, is imprecise as it will obviously vary between studies making generalizations impossible. Clearly, the smallest predatory infauna may not prey on the largest adults, but some predators negate the size disadvantage by using toxins to kill large prey (Commito & Ambrose 1985a). Small predators can also kill the juveniles of large prey species. Furthermore, even sublethal predation (e.g. tail nipping) might ultimately affect community structure as it has been shown to affect fecundity, tube building, and defecation (Woodin 1984, Zajac 1985, review by Commito & Ambrose 1985b).

In addition to employing what I consider an inadequate definition of a predator, Wilson also makes several other errors in reanalyzing my ratio data. First, on the basis of convenience only, he excluded 68 % of my data set. The excluded studies (Commito 1976, Lee 1978, Summerson 1980 and most of Young et al. 1976) contain numerous cases where the ratio of predatory infauna to non-predatory infauna increased when epibenthic predators were removed. For example, in Summerson (1980) the ratio was always positive inside grass beds. Furthermore, by restricting the reanalysis to only 18 of the 56 data points that I used, the power of any statistical test applied is severely reduced. Second, he used data from Young & Young (1977) which gives the densities of only the top 10 most abundant species. The entire data set is required if any analysis is to be accurate because predatory infauna are often not the most abundant species. For my analysis, I obtained the complete data from D. Young. Third, he discounted some cases where his analysis showed a greater ratio in caged than uncaged areas because the differences were small (less than 0.015). The hypothesis being tested, however, makes no prediction as to the magnitude of the differences expected.

In Wilson's reanalysis the cage-control statistic is positive in 6 of 8 cases in mud-sand (ties excluded $p <$ 0.145, sign test), in 5 of 7 in grass beds ($p < 0.227$), and in 11 of 15 when data from the 2 habitats are combined ($p < 0.059$). Had all the studies I used been analyzed (not just 32 %) and all species included in the analysis (not just the top 10), results would likely have been more significant despite Wilson's restrictive definition of predatory infauna. The significance level of the sign test when replication is increased by combining seagrass and mud-sand habitats certainly supports the 3-level model.

DISCUSSION

The increase in the proportion of predatory infauna following the exclusion of epibenthic predators, which I demonstrated in my earlier paper (Ambrose 1984a)

and which even Wilson's (1986) restrictive and incomplete reanalysis demonstrates at a less significant level, occurred despite factors favoring increases in abundance of non-predatory infauna under exclusion cages. As I discussed in my earlier paper, cage artifacts, increased sedimentation of fine sediments and organics, and larval trapping will favor an increase in the abundance of non-predatory, deposit feeding, opportunistic species compared to predators. The comparison of the ratio of predatory to non-predatory infauna between caged and uncaged areas is, therefore, a very conservative test for the 3-level model because cage artifacts promote a lower ratio under cages compared to uncaged areas. The fact that the ratio does increase following the exclusion of epibenthic predators is strong support for the 3-level model.

I never proposed that a 3-level interactive model is always valid for all marine soft-bottom communities. The model does not appear to hold for sand communities (Ambrose 1984a), and I suggested that interactions between predatory infauna and their prey may be less important in structuring communities where other forms of control (abiotic disturbance, predation/disturbance) are common (Ambrose 1984b, Commito & Ambrose 1985b). There is excellent evidence, however, that predatory infauna can affect the abundance of other infauna and that predatory infauna are often the preferred prey of epibenthic predators.

The role of predatory infauna in structuring soft-bottom communities is perhaps best understood in intertidal mud communities in Maine, USA. It is in these communities, where predatory infauna have been demonstrated to have their largest effects, that the 3-level model appears to function best. Despite Wilson's assertion, epibenthic predators are important in structuring these communities, though not as important as in some other areas. Phyllodocids (predatory infauna by Wilson's definition) were significantly more abundant under cages compared to uncaged areas after 10 wk of exclusion, and a number of infaunal species, including predators *Nephtys incisa* and large *Nereis virens*, were significantly more abundant in cages than controls after 20 wk of exclusion (Ambrose 1984b). One of the major epibenthic predators in this community, gulls, feed preferentially on large *N. virens* (Ambrose 1986). Wilson's claim that the removal of *N. virens* by gulls is not statistically detectable is irrelevant and erroneous. In the context of the 3-level model the only important point is that *N. virens* are the only infauna preyed upon by gulls. Wilson's interpretation is erroneous because it compares a removal rate incorporating time to variance in *N. virens* density in space. Wilson's criteria for the 3-level model, preferential predation by epibenthic predators on predatory infauna and the ability of predatory infauna to signific-

antly affect the abundance of non-predatory infauna, are clearly met for this community.

The 3-level model may also be valid for other communities. Kent & Day (1983) investigated interactions on an intertidal mudflat in Australia and found that fishes and birds affected the abundance of adult *Ceratonereis pseudoerythaeenis* which in turn affected the recruitment of juvenile *C. pseudoerythaeenis*. Adult nereids probably also affected other infauna but this interaction was not studied. In experiments on tidal flats in the North Sea, Schubert & Reise (1986) found that epibenthic predators significantly reduced the abundance of *Nephtys hombergii*. Predation by *N. hombergii* caused a significant decline in the abundance of several polychaete species. Stomach analysis showed that *N. hombergii* occasionally prey on other predatory infauna indicating considerable trophic complexity in the community.

Though Wilson argues that a 2-level model is the best general description of soft-bottom communities, experimental evidence indicates that even the 3-level model is probably too simple for many communities and that multiple trophic links exist among the infauna. Experiments in the Maine system described above have documented a number of multi-level interactions among the infauna: *Glycera dibranchiata* – *Nereis virens* – other infauna (Ambrose 1984b, c), *Nereis virens* – *Corophium volutator* – other infauna (Commito 1982, Ambrose 1984b), and perhaps *Nereis virens* – *Nephtys incisa* – other infauna (Commito & Shrader 1985). A review of the literature reveals that in 65 % of the cases of well-documented predation by infauna, predators consumed other predators (Commito & Ambrose 1985a).

The increase in the proportion of predatory infauna following the exclusion of epibenthic predators can only be explained using a 3-level model; the conventional 2-level model advocated by Wilson is insufficient. Yet, I do not believe that with our present knowledge it is possible to select a general description of interactions in marine soft-bottom communities. The experimental evidence so far allows the prediction that predatory infauna will be important in several types of habitats (see review by Commito & Ambrose 1985b). A 2-level model is an accurate description of interactions in some soft-bottom communities, but strict application of a 2-level model will miss important interactions in many communities.

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