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used by Dueser and Shugart (1979), two are noteworthy here. Dueser and Shugart interpreted unequal species abundances (i.e., sample sizes) as conveying meaningful information about habitat exploitation by the subject populations. Carnes and Slade, on the other hand, are interested only in species comparisons that are independent of abundance. This contrast reflects fundamentally different concepts of the niche, being focused on the environment in the first case and on the organism in the second. Also, Dueser and Shugart computed their niche metrics relative to the weighted origin (grand centroid) of the discriminant space. Carnes and Slade (1982) recommend computing an unweighted estimate of the average of all sampling sites, whether or not these sites were represented in any species sample. It is clear that these two procedures will produce different estimates of the niche pattern statistics if the unweighted origin differs significantly from the weighted origin. Only experience will reveal whether the collection and inclusion of "species absence" data will prove worthwhile and cost effective.

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MOBILE PREDATORS AND THE STRUCTURE OF MARINE INTERTIDAL COMMUNITIES[1]

D. Craig Edwards,[2] David O. Conover,[3] and Frederick Sutter III[3, 4]

Field experiments and quantitative sampling have been very productive in demonstrating the relative importance of physical factors, competition, and predation in structuring various intertidal communities (Connell 1961, 1972, 1975, Paine 1974, Menge 1976, Menge and Sutherland 1976, Peterson 1979a, b, Wiltse 1980). Even the best methods, however, have their concomitant limitations and affect to some extent the phenomena under study. We address a small, but general, methodological problem that may have large consequences for interpretations of how predators alter intertidal communities. Specifically, the effects on community structure of such highly mobile intermittent predators as crabs, fishes, and birds are hard to

demonstrate and easy to overlook or misinterpret, but assuming them to be unimportant may perpetuate oversimplified models of community interactions. We illustrate, using evidence of our own and from the literature, how this problem may apply in a particular well-studied situation, and question the assumption that *Thais lapillus* is the only significant predator of mid-intertidal rocky shores in New England (Menge 1976, 1978b). We also indicate approaches for resolving the problem and implications of such work.

The General Problem

Faunal elements. The advantages of intertidal habitats for quantitative and experimental studies, viz., their direct accessibility at low tide and the predominance of sedentary species, are both offset by (1) their comparative inaccessibility at other times, and (2) the many mobile consumer species that interact with and prey upon their resident biotas on tidally, diurnally, and annually rhythmic schedules. At high tide, for example, various fishes, especially by day, and crustaceans, often by night (Ropes 1969), prey upon the intertidal biota; and fishes (Stephenson and Searles 1960), crabs (Virnstein 1977, Peterson 1979a), and shrimp (Bell and Coull 1978) have been shown in experiments to alter significantly the composition of

rocky intertidal, sandy near-shore, and salt-marsh community assemblages. Peterson (1979a), noting the importance of crab predation on protected European rocky shores, suggested highly mobile predators might have similar effects in comparable North American sites. Likewise at low tide, shore birds and mammals consume intertidal organisms, often at rates far exceeding those of invertebrate predators (Milne and Dunnet 1972, cf. Edwards and Huebner 1977) and at rates that alter benthic diversities (Schneider 1978). Just before migration, some shorebirds nearly double their masses while feeding almost entirely on a single intertidal dominant (Hicklin and Smith 1979). The absence or scarcity of mobile predators during low-tide studies does not show their effects on shore communities to be unimportant.

Methodology. Even in the best field experiments where the abundance of a single predator is manipulated manually with minimal disturbance to the natural community, and especially in natural experiments involving altered abundances of a predator (cf. Connell 1974, 1975), close monitoring is required to ensure that the effects of the manipulated predator are not compensated for through dietary switching of alternative mobile predators. Most field experiments with predators, however, must employ fences or cages whose unintended effects can be varied and appreciable (cf. Virnstein 1978, Dayton and Oliver 1980). Such barriers inadvertently alter physical conditions, the physical structure of the site, larval recruitment, growth and survivorship rates, and the abundances and interaction effects of other species. The use only of predator exclosures and nearby control areas has particular side effects that may apply in the case example below. Prey within enclosures may attract local (as well as mobile) predators to control areas (cf. Menge 1976: Fig. 5), while the physical structure of experimental apparatus may provide cover or obstructions for motile predators. Moreover, with no predator enclosure treatments to show the effects of the manipulated predator, predation from unrecognized mobile sources may be confounded with the intended exclosure-treatment effect. Either assuming unintended treatment effects to be unimportant or treating necessary causes as sufficient ones directs attention away from such potentially significant factors as mobile predators.

A Rocky Shore Example

The interrelated problems of overlooked faunal elements and unintended treatment effects may be illustrated by one aspect of Menge's (1976) study of the causes of structure in the rocky intertidal communities of New England. He concluded, based on quantitative sampling and field experiments using predator-exclusion cages, that predators primarily determine space

utilization and species richness in mid-intertidal areas protected from wave action. This predation effect was attributed to a single species of predatory gastropod, *Thais lapillus*. Field observations suggested *Thais* was the only important predator on the major space-utilizing animals of the mid-intertidal zone, *Mytilus edulis* and *Balanus balanoides* (Menge 1976); and the alternative hypothesis that "other predators are responsible for the observed variations in predation intensity in the mid intertidal region" was specifically rejected (Menge 1978b). Yet a serious problem for the *Thais* predation hypothesis remains: "Paradoxically, predation intensity, . . . defined as the mean difference between percent cover of prey in exclusion cages (where prey experience no predator-caused mortality and percent cover of prey in controls (where prey are exposed to predators), was . . . unrelated to predator density" (Menge 1978b). In fact the site with the lowest density of *Thais* had the highest predation intensity (Menge 1978b: Fig. 1).

Menge's explanation of his paradox does not seem adequate. He first gave indirect evidence that wave shock and desiccation reduce the survival and foraging effectiveness of *Thais* (Menge 1978a) and demonstrated experimentally that tidal level, presence of an algal canopy, month, and snail phenotype and/or history significantly affected the feeding rates of caged *Thais* (Menge 1978b). He then concluded that ". . . the explanation of how 31 *Thais* / m² at Canoe Beach Cove can have a similar effect to that exerted by about 300/m (and at times >1000/m²; Menge 1976, p. 338) a Grindstone Neck seems evident: predation intensity is strongly dependent on how individual feeding rates are affected by the environment" (Menge 1978b). The problems with this "explanation" are: (1) the truth of the final assertion does not logically entail what is to be explained, (2) none of the factors shown to affect feeding rates significantly is shown to differ sufficiently between the sites in question, and (3) these sites which differed most in their densities of *Thais*, are actually shown to be most similar in such pertinent physical and community characteristics as wave shock and percent algal cover (Menge 1976, 1978a: Table 1 Several factors affecting feeding rates were considered to operate by moderating high summer temperature and desiccation stress, so "feeding rates tend to be greatest in cooler, damper habitats" (Menge 1978b On this basis, environmental factors at Menge's high *Thais* density site to the north (44°23'N latitude on the cool and foggy Gulf of Maine) might even be expected to favor greater feeding rates than those at the low density site (42°25'N latitude in Massachusetts Bay thus heightening rather than resolving the paradox.

The apparent paradox, the lack of correlation between predation intensity and predator density, ma

be an artifact of assuming that *Thais* is the only important predator affecting sheltered mid-intertidal rocky shore communities in New England. Crabs (*Cancer* and *Carcinus*) could account for much of the paradox, because they are more numerous at sheltered sites and eat both *Thais* and its prey (Ebling et al. 1964, Kitching and Ebling 1967, and Hughes and Elner 1979). Menge (1976) discounted the predatory importance of crabs owing to their scarcity and small sizes in quadrat samples; but such results may reflect the availability of cover at low tide, not the numbers and sizes of crabs present at high tide. Low-tide samples cannot measure the abundances of mobile, high-tide predators. Another abundant and ubiquitous predator of New England rocky shores, the cunner *Tautogolabrus adspersus,* was not mentioned by Menge, even though the dominant food items of this labrid fish regularly include *Mytilus, Balanus,* or both (Chao 1973, Olla et al. 1975, Shumway and Stickney 1975). Chao (1973) also noted that cunner might affect the vertical distribution of mussels (*Mytilus* and *Modiolus*) at East Point, Nahant, Massachusetts (one of Menge's study sites).

From May to August 1978, we further investigated the feeding of cunner in the intertidal zone at Hodgkin's Cove, Cape Ann, Massachusetts (42°40′N latitude), a site lying between Menge's study areas. The rocky shores of Hodgkin's Cove are protected to semi-protected from wave action, extensively covered with the algae *Fucus* and *Ascophyllum,* and subject to a tidal range of 2.65 m (mean) to 3.08 m (spring). Using SCUBA underwater and glass-bottom boxes at the surface, we often observed 20–40 cunner feeding in ≈10 m wide sections of the rocky intertidal zone where algal canopies and rocky crevices provided shelter. Cunner are often very abundant. Olla et al. (1975) repeatedly observed that ≥50 cunner were attracted to a clump of *Mytilus edulis* within 1–2 min after feeding began. Our catch rate for two anglers, who kept moving along shore to avoid fish clumping around baits, was >20 cunner/h. Unaided surface observations underestimate abundances, because cunner keep close to algal cover and rocky crevices where their dark reddish coloration provides camouflage (see also Dew 1976).

To quantify the feeding of *Tautogolabrus,* we caught 92 fish from the perimeter of Hodgkin's cove following daylight high tides on five dates (Table 1), using lines with either lures or *Littorina* tissues as bait. Having already confirmed the assumption that cunner, which are quiescent at night (Olla et al. 1975, Dew 1976), would contain no food at daybreak (16 of 17 fish taken 0.5 h before sunrise had empty digestive tracts), we were usually sampling the feeding of cunner during a single morning high tide. All organisms occurring in the 82 (of 92) digestive tracts containing food were enumerated (Table 1). Our sample fish had fed primarily on *Mytilus edulis* and *Balanus balanoides*: 61–91% of cunner on any date contained *Mytilus* and 53–100% contained *Balanus*. These percent occurrences much exceeded those for other foods: *Littorina* spp. (17–47%), bryozoans (13–43%), hydrozoans (13–30%), amphipods (7–67%), ascidians (0–11%), polychaetes (0–27%), and several rarer foods. Mean numbers of *Mytilus* per cunner increased from 5.6 to 55.1 from May to August, while mean numbers of *Balanus* decreased from 42.3 in May to 4–6 in June–August; mean numbers of both (*Mytilus* + *Balanus*) ranged from 20 to 60 ($\bar{x}$ = 42). (Cf. Olla et al. 1975: in New York *Mytilus* was important in the cunner's diet only in May–June, whereas it was the major dietary item of another labrid, the tautog *Tautoga onitis,* from May to October.) Our findings confirmed previous reports on cunner predation on *Mytilus* and *Balanus*. Our sample fish, unlike others', were taken only in the rocky intertidal zone; accordingly, our results show more intertidal feeding and a great dominance of *Mytilus* and *Balanus* in the diet. Cunner taken <2.5 h after early-morning high tides contained the largest numbers of *Mytilus* + *Balanus* ($\bar{x}$ = 48–60).

Owing to the lack of adequate field data on the prevailing densities and feeding rates of cunner and other

TABLE 1. Mean number ($\bar{x}$ ± SE) and percent occurrence (%) of *Mytilus edulis* and *Balanus balanoides* in the digestive tracts of 82 cunner from Hodgkin's Cove, Massachusetts, during May to August, 1978. Under time of sampling, ( ) = number of hours after high tide.

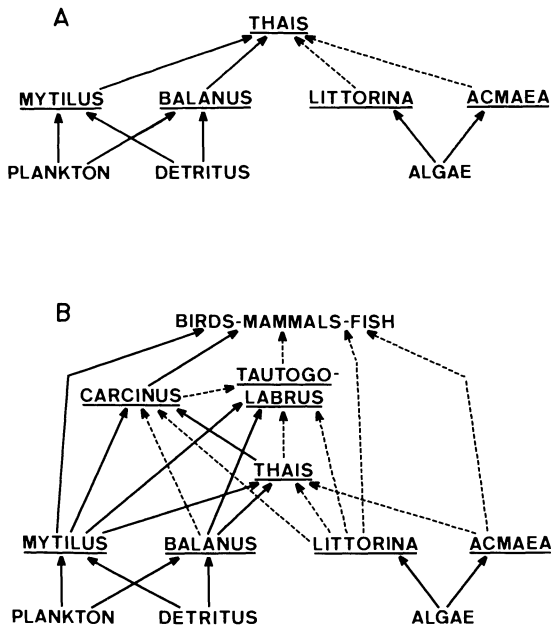| Date	N	Time of sampling	Time of high tide	Mytilus		Balanus	
				%	$\bar{x}$ ± SE	%	$\bar{x}$ ± SE
31 May	21	0930 (1.8)	0741	61.1	5.6 ± 1.5	77.8	42.3 ± 23.3
1 Jun	9	1530 (6.8)	0842	88.9	7.4 ± 2.6	100.0	16.0 ± 4.6
16 Jun	15	1200 (4.2)	0748	80.0	16.0 ± 7.0	53.3	4.2 ± 2.7
7 Aug	22	1630 (3.2)	1321	91.3	39.8 ± 22.8	60.9	6.0 ± 2.0
14 Aug	15	1000 (2.2)	0749	86.7	55.1 ± 31.2	73.0	5.2 ± 1.2
Mean	16.4	. . . (3.6)	. . .	80.4	25.9 ± 8.2	70.3	15.9 ± 5.4

A

B

FIG. 1. Two views of community interactions. A. Menge and Sutherland's (1976) generalized food web for protected rocky intertidal communities in New England treats only the *Thais-Mytilus-Balanus* triad as important in community structuring. Dashed lines = rare or little effect. B. As above, with the addition of highly mobile predators. References in text. Note: these food webs strictly apply only to northern New England (Gulf of Maine); extending them to southern New England would require further additions, e.g., *Tautogolabrus* co-occurs there with another labrid, *Tautoga onitis*; *Carcinus* with another portunid, *Callinectes sapidus*; *Thais* with additional muricids, *Urosalpinx cinerea* and *Eupleura caudata*; etc.

mobile predators in the intertidal zone, we cannot reliably determine the effects of these predators on New England's rocky shore communities. Some comparisons of cunner and *Thais* feeding, however, are relevant. *Thais* spp. eat one or more barnacles per snail per day (Connell 1961, 1970), so the density of *Thais* could directly indicate its predation rate; cunner, however, contain 20–60 *Mytilus* and *Balanus* (plus other prey) per fish per sampling time (Table 1). These values for cunner are less than daily feeding rates or even high-tide daily rates, since ≈40% of the days in May–October have two high tides affording daylight feeding opportunities, and we have observed cunner feeding on both such tides. The annual activity patterns of *Thais* and *Tautogolabrus* are similar, and both eat similar sizes of prey. Given the predatory capabilities of cunner and other fishes, *Carcinus maenas* (Ropes 1969, Elner and Hughes 1978) and other crabs, and predatory birds (Cantin et al. 1974) and mammals, the assumption that *Thais* is the only significant predator

structuring New England's sheltered, mid-intertidal rocky shore communities seems tenuous. It is premature to conclude that highly mobile predators do not significantly affect community compositions here. This case illustrates a problem that may obtain in any intertidal habitat.

Discussion

Our criticisms are easily made and not unknown to others, but obviating them will be difficult. Multiple approaches can fill in the omissions in community studies of either the benthos at low tide or mobile consumers at high tide, and further tests can correct for the complex side effects of field cages. Specifically, where predator exclosures significantly alter community compositions, the meaning of the results depends on two kinds of tests. First, adequate controls must distinguish the effects of the predator(s) under study from (1) the similar ones caused by other biological or physical disturbances, and (2) the effects of the experimental apparatus. Simply duplicating caging tests exactly except for the presence (enclosure) and absence (exclosure) of the predator(s) should indicate the effects of the predator(s) when other conditions, including cage effects, are similar. Cage-mediated effects are then assessed using controls that reduce them stepwise: barriers permeable to larger organisms, portions of cages only, etc., as well as undisturbed areas. Unfortunately, such controls may require much additional effort, and adequate randomly placed replication of treatments and controls throughout a patchy habitat is hard to achieve. Second (or alternatively), the feeding rates of particular predators, singly or in concert, must be shown sufficient to account for the community effects attributed to them. If cage effects are minor, replicated enclosure tests may accomplish this. Otherwise, feeding rates must be found independently. Although very different methods are needed for predators as dissimilar as snails, crabs, fishes, and birds, quantitative field studies of each such predator's abundances, prey-selection, and feeding rates by size/age class could begin to indicate the effects of each on intertidal communities.

Resolving the relative community structuring roles of different predators (and how these vary when particular predators' numbers fluctuate) would clarify the full role of predation in particular communities of different types, and hence, the place of predation in a general theory of diversity (cf. Huston 1979). If predation in fact primarily structures the community at issue above, a further issue arises. How does the level of predatory control of community composition vary with changes in the trophic complexity and diversity of communities? Is the primary role of a higher level (secondary) carnivore, the starfish *Pisaster ochra-*

ceus, in the structuring of diverse Pacific rocky shore communities (with primary carnivores, Thais spp., in important subordinate roles) in fact assumed by a lower level (primary) carnivore, Thais lapillus, in the simpler communities of sheltered New England rocky shores (see Menge and Sutherland 1976)? Our information suggests that higher level mobile carnivores, especially crabs and fish, have at least significant subordinate roles in the structuring of the latter communities, and that, pending further tests, an extended food web (Fig. 1) provides a more realistic working model of community interactions there.

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REPLY TO A COMMENT BY EDWARDS, CONOVER, AND SUTTER[1]

Bruce A. Menge[2]

Edwards et al. (1982) argue that cunners (and crabs) are important predators in the mid intertidal zone of New England and thus that *Thais* are relatively less important than I had concluded (Menge 1976). Here I (1) critically examine their argument, (2) present additional evidence supporting my earlier results, and (3) suggest an experimental design that would test their hypothesis.

Re-examination of the Argument of Edwards et al.

The key point made by Edwards et al. is that the cunner, *Tautogolabrus adspersus* (though they mention crabs, they largely ignore these consumers in their paper), may account for the observed disparity between *Thais lapillus* (a predaceous gastropod) density and the presumed effect of these predators (e.g., Menge 1976). My suggested explanation was that predation intensity depends on more than predator density. Specifically, I argued that individual feeding activity is sensitive to micro- and macroenvironmental variation, e.g., canopy cover, wave action, and related physical and biological variables. Thus, *Thais* individuals fed faster at the low-density, most protected site (Canoe Beach Cove = CBC) and slower at a high-density, less protected site (Grindstone Neck = GN;

Menge 1978a, b). As a result, predation intensity was more nearly equal than simple predator density would indicate. However, Edwards et al. argue that the sites varying the most in *Thais* density are the most similar in physical environment. Yet the physical regimes at these two sites are still different (e.g., Menge 1976, 1978a, b). Summarizing, CBC, a more southerly site, has a thicker, more uniform canopy cover in time and space, waves never strike directly, the topography is irregular, and *actual* desiccation and freezing effects are relatively small. At the more northerly GN, canopy cover is thinner and patchier in space and time (though average cover is relatively high), the topography consists of long, smooth benches (which probably enhance wave shear forces rather than breaking them), wave shock is both more direct and more severe, and *actual* desiccation and freezing effects are more severe. Thus, at GN, *Thais* forage for a shorter period of the year, are probably more inhibited in foraging by waves, cold, or heat, have fewer shelters, and are smaller on the average than at CBC (juveniles are by far the most abundant size class at GN). Much of this summary has been published (Menge, 1976, 1978a, b). Whether or not these differences are "sufficient" to explain the variation in *Thais* effect can only be determined with additional research.

A more critical and approachable aspect of the criticisms of Edwards et al. is whether or not cunners are important midzone predators. Reconsideration of their data casts further doubt on this argument. If cunners are important midzone predators, they must (1) feed in the *mid* intertidal zone, and (2) have a significant effect on the prey which occur there. These points are avoided by Edwards et al. First, these authors never mention where in the intertidal zone the fishes feed. Cunners are merely said to feed in the rocky intertidal