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Ecology, 63(4), 1982, pp. 1180–1184

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

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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 1978*a*, *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, 1978*a*, *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, 1978*a*, *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 zone, which usually includes three tidal levels: high, mid, and low. Further, food found in cunner guts could come from low intertidal or subtidal regions. *Balanus balanoides*, *Mytilus edulis*, and *Littorina* spp. (species names are not given by Edwards et al.) all occur in both the low and subtidal zones. No other cunner prey are identified to species but all (bryozoans, hydrozoans, amphipods, ascidians, polychaetes) are abundant subtidally and most are rare to absent in the mid zone. Ascidians in particular are rarely seen in places available to cunner anywhere in the intertidal region. Moreover, though many prey types were eaten, *Thais* was not. This seems peculiar given its abundance, wide range of body sizes, occurrence throughout the low and mid zones and nonsecretive activity patterns. Finally, it is unlikely that cunners spend much time feeding in the mid zone, since most prey types eaten occur in low and subtidal zones and the actual time available for feeding in the mid zone is relatively limited, compared to lower zones.

Second, Edwards et al. do not provide a detailed exposition of prey sizes eaten and the potential relative impact of *Thais* vs. cunner on their prey. Without an indication of the prey sizes eaten, it is difficult to know how significant their results might be. For example, consumption of 20–60 large (e.g., >10 mm) prey would be more impressive than ingestion of similar numbers of small (e.g., <5 mm) prey.

Further, rough comparisons can be made between predation rates of cunner and *Thais*. For example, assuming an average *Thais* density of 100 individuals/m^2 (range = 9 to 456+/m^2; Menge 1976, 1978*b*) and a feeding rate of one prey per *Thais* per day, then consumption would be 100 prey·m^{-2}·d^{-1}. Edwards et al. (1981) suggest that 60+ prey are eaten per cunner per day. Assuming that each cunner eats 100 prey/d, then there would have to be 1 cunner/m^2 to have a similar effect to that of *Thais*. In my experience these fishes are never this abundant. Densities of 1 cunner/100 m^2 or 1 cunner/1000 m^2 seem more likely, though these figures may also be high. Thus, cunner effects are most likely to be .01 or .001 that of *Thais*. Hence, cunner gut contents data are equivocal and can even be used to support my earlier arguments. Similar points could be made concerning crabs, but in the absence of concrete evidence, additional comment is unnecessary.

Further Considerations of Thais, *Crab and Cunner Effects*

Additional data further weaken the comments of Edwards et al. (1982). First, manual removals of *Thais lapillus* were done on a small (approx. 10 × 5 m), steep-sided, mid- and low zone reef (Little Brewster Reef = LBR) 20 m from my Little Brewster Cove (=LBC) site (Menge 1976, Lubchenco and Menge 1978). Transects confirmed that these sites were similar so we commenced removing *Thais* from LBR in summer 1974. Over the next 2 yr, 10 000 *Thais* were removed. Most of the later removals were juveniles whose growth and survival was enhanced by the sudden absence of adults. A second manipulation was removal of the fucoid canopy from half of the reef in spring 1975. This was done to examine direct (via whiplash; Menge 1976) and indirect (via enhancement of predator activity beneath the canopy; Menge 1978*b*) effects of a fucoid canopy on mussel and barnacle abundance.

By late July to early August 1975, barnacle cover at the *Thais* removal sites was relatively high and increasing, both under the canopy (32.7 ± 24.4%) and without canopy (46.5 ± 14.0%; Table 1). In contrast, barnacle cover at the control site was low (8.9 ± 7.8%) and declining (Table 1). Barnacle abundances in August are significantly different at these three sites (one-way ANOVA on arcsin-transformed data; F = 12.97; df = 2, 26; P < .001). Multiple comparisons (Student-Newman-Keuls test; Sokal and Rohlf 1969) indicate that *Balanus* cover on the control is significantly less than in either experimental treatment (P < .05). The two treatment mean abundances do not differ. Mussel cover was either increasing or not changing at all three sites. These results are similar to those from earlier experiments on vertical walls (e.g., Menge 1976), where mussels often took 2 yr to outcompete barnacles in predator exclusion cages. Since LBR is generally steeper sided than LBC, the slow increase in mussel cover in this experiment is not surprising. Unfortunately, the steep sides of LBR reduce to approximately a metre the vertical distance which a predator needs to crawl to reach these low-mid zone prey. Thus, in August *Asterias* foraged into the lower mid zone and greatly reduced prey cover, effectively terminating the experiment. Note also that canopy absence results in higher prey densities than canopy presence. This supports my earlier results, though the experiment needs repetition on a horizontal bench rather than a near-vertical reef. However, note that the increase in barnacles and appreciable covers (for vertical walls) of mussels occurred despite the accessibility of LBR to cunners (and crabs) at high tide.

Another means of testing *Thais* effects (suggested by Edwards et al. to be necessary), enclosing them in cages, was done by J. Lubchenco (Lubchenco 1978, 1980, Lubchenco and Menge 1978). In every case (N = 123), results in predator enclosures were similar to those in controls and roofs. Prey were kept low in cover and fucoid algae increased in cover.

A problem with predator enclosures which Edwards et al. ignore is that such experiments may (1) artificially heighten predator density, (2) interfere with cy-

TABLE 1. Effect of the removal of *Thais lapillus* and the fucoid canopy on abundance (percent cover) of *Balanus balanoides* and *Mytilus edulis*, March–August 1975. Data are $\bar{x}$ and 95% confidence interval. Number of quadrats is given in parentheses.

	Percent cover					
			Experimental (Little Brewster Reef)			
	Control (Little Brewster Cove)		Fucoids removed		Fucoids intact	
Date	*B. balanoides*	*M. edulis*	*B. balanoides*	*M. edulis*	*B. balanoides*	*M. edulis*
March 1975	no data	no data	3.8 ± 8.8 (6)	12.2 ± 12.5 (6)	1.0 ± 1.7 (5)	6.6 ± 5.4 (5)
May 1975	17.1 ± 11.9 (10)	4.0 ± 4.2 (10)	25.4 ± 5.8 (7)	10.1 ± 5.2 (7)	9.0 ± 15.3 (5)	6.2 ± 7.5 (5)
Late July, early August 1975	8.9 ± 7.8 (10)	10.8 ± 12.0 (10)	46.5 ± 14.0 (13)	19.9 ± 11.1 (13)	32.7 ± 24.4 (6)	4.8 ± 4.9 (6)

clic foraging ambits, and (3) alter predator feeding activity. Enclosure densities are 1 *Thais*/100 cm^2 or 25 *Thais*/0.25 m^2, while natural densities at midzone protected sites ranged from ($\bar{x}$ and 95% confidence interval) 8 ± 6 to 115 ± 58 *Thais*/0.25 m^2 (Menge 1976). Thus, 25 *Thais*/0.25 m^2 is a realistic manipulation with regard to potential density artifacts. Effects of enclosure on foraging ambit and behavior are unclear, though experiments by Connell (1961) and Menge (1978*b*) suggest that they are small. These results support my suggestion that *Thais* is the most important midzone predator at the sites I studied in New England. *Thais* appears capable of controlling mussels and barnacles in the mid zones at densities of at least 25 *Thais*/0.25 m^2 and above.

Finally, in my earlier experiments, roofs would have acted as cunner exclusions. If crabs are not important predators in the mid zone (see Menge 1976), and roofs do not attract unusual numbers of *Thais* (in five of six experiments at four protected sites the difference between *Thais* numbers under roofs and in controls in the mid zone is not significant; $P > .25$), then prey abundance differences between roofs (cunners absent) and controls (cunners present) should occur if cunners are important predators. Such differences never occurred in the mid zone (Menge 1976). Further, the reasoning behind Edwards et al.'s assertion that the snapshot in Menge (1976: Fig. 5) is proof that *Thais* forage preferentially under roofs is faulty. Using this reasoning, later photography would have suggested that *Thais avoid* roofs and *seek out* controls. I have often seen *Thais* encounter controls before roofs.

A Suggested Experimental Design

To test the importance of fishes and other predators, I would carry out experiments as in Table 2. Their performance over 2–3 yr should test the hypothesis that mobile consumers have significant effects on community structure in the New England mid rocky intertidal.

Of these experiments, manual removals (e.g., of *Thais* or *Asterias*) are easiest to control. However, *Thais* and *Asterias* removals would require constant attention since populations of these species tend to rebound fast via enhanced reproduction or rapid reinvasion following removals.

Other manipulations (Table 2) require some artificial device with side effects which must be controlled. Moreover, manipulation of fast-moving consumers often requires considerable ingenuity and creativity. For example, attempts to evaluate the separate role of birds has led to at least two clever designs (e.g., a cage permeable to all predators but birds, C. Marsh, *personal communication*, and a cage that floats at high tide, M. Quammen, *personal communication*). Combined, such designs should exclude shorebirds at protected sites in New England.

The best but least practical way to manipulate cunners is to close off small embayments with nets and then spear or poison cunner out of one set of experimental replicates, leaving the other unmanipulated as controls. This would be expensive, subject to destruction by even mild storms, and time intensive. More feasible would be to alter a design used in experiments in Panama (Menge and Lubchenco 1981). Here, fishes were excluded using large mesh (0.25-m^2) roofs. Incorporation of a hinged, counterweighted fliptop with floats attached to the counterweights (i.e., opens during low, closes during high tide) allows birds access to the substratum.

Exclusion of crabs alone seems unfeasible at present. However, comparison of results in treatments 5 and 6 (Table 2), which differ only in whether or not crabs are present, should suggest these effects.

All additional treatments (Table 2) are either controls for experimental artifacts (e.g., shading, interfer-

TABLE 2. Experimental design to determine relative effects of five predator types in New England rocky shore communities. + and − indicate presence or absence, respectively, of the indicated predator.

Treatment	Predator					Tests
	Thais lapillus	*Asterias* spp.	Crabs	*Tautogolabrus adspersus*	Shorebirds	
1 Marked quadrat	+	+	+	+	+	Control
2 Manual removal of *Thais*	−	+	+	+	+	*Thais* effect
3 Mesh cage—include *Thais*	+	−	−	−	−	Effects of predators other than *Thais*
4 Manual removal of *Asterias*	+	−	+	+	+	*Asterias* effect
5 Mesh roof, edges 2 cm from substratum, flip top at low tide	+	+	−	−	+	Crab and cunner effect
6 Mesh roof, edges 5 cm from substratum, flip top at low tide	+	+	+	−	+	Cunner effect
7 Coarse mesh roof, edges 5 cm from substratum, flip top at low tide	+	+	+	−	+	Cunner effect; control for mesh shading effect
8 Net mouth of small cove, remove cunner with rotenone or speargun	+	+	+	−	+	Cunner effect
9 Net mouth of small cove, leave cunner	+	+	+	+	+	Control for net effect
10 High (≈50 cm) mesh roof	+	+	+	+	+	Control for mesh shading
11 Marsh dome-Quammen flip top at high tide	+	+	+	+	−	Shorebird effect
12 Marsh dome-unstrung	+	+	+	+	+	Control for dome effect
13 Mesh cage, two or three sides, flip top low tide	+	+	+	−	+	Control for cage wall effect
14 Mesh fence, two or three sides	+	+	+	+	+	Control for cage wall effect

ence with water flow) or are multiple predator exclusions.

Discussion

I again suggest that *Thais* is the most important midzone predator at my New England sites. I also emphasize a point made earlier (Menge 1976, Lubchenco and Menge 1978). Neither *Thais* in the mid zone nor a more diverse predator guild in the low zone are completely and consistently effective in controlling prey. Prey escape the control of these predators even at Canoe Beach Cove. Large (>10-m^2) mats of escaped mussels may persist for months in both mid and low zones in the face of populations of *Thais, Asterias,* crabs, cunners, birds, and mammals. I attribute these "coexistence" escapes (see Menge 1982) to (1) the relative inefficiency of the invertebrate predators; (2) variations in their effectiveness due to relatively great environmental variation; and, despite the claims of Edwards et al. (1982), (3) the minor importance of vertebrate consumers.

Finally, I emphasize that observations (e.g., of cunners with mussels and barnacles in their guts, of snapshots of the leading edge of a large aggregation of *Thais* under a roof, around a cage but, not yet at least, in a control) rarely, if ever, allow interpretation of system dynamics. Observations are absolutely essential throughout a study to allow proper interpretation. However, *as an ideal,* nothing can replace a *properly* controlled and performed field experiment (or set of experiments) in testing hypotheses in ecology. I therefore suggest that rather than resorting to philosophy or observation when flaws in experimental design or technique are suspected, ecologists instead seek creative improvements and increased carefulness in experimental design.

I urge Edwards et al. to test the hypothesis that cunners have a significant impact on barnacle and mussel populations in the mid zone of the New England rocky intertidal. I would welcome the results of a well-designed study regardless of its outcome. However, I presently consider cunners to have little or no effect on community dynamics in the mid zone. I am less sure about crabs, but in the absence of contrary evidence and in the presence of my own experience and that of others familiar with this system, I currently consider these predators to have a minor impact on sessile prey in the *mid* zone. I thus conclude that the comments of Edwards et al. are without merit and that their data do not permit their conclusions.

Acknowledgments: S. Garrity, C. Hibbard, B. Walker, D. Spero, and P. McKie helped with the field work. E. Bourget and J. Lubchenco provided valuable discussion. I deeply appreciate the support of National Science Foundation grants GA-35617, DES 72-01578 A01, and OCE 80-19020.

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