Oecologia (Berl.) 34, 17–35 (1978)

Oecologia

Predation Intensity in a Rocky Intertidal Community

Effect of an Algal Canopy, Wave Action and Desiccation on Predator Feeding Rates

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Summary. The predation intensity exerted by populations of the gastropod *Thais lapillus* at different study areas in the rocky intertidal community of New England is unrelated to predator density. Specifically, very similar intensities are exerted by populations differing in density by at least an order of magnitude. Predation intensity is, in part, a joint function of individual rates of prey consumption and various environmental characteristics. Major factors potentially affecting the individual feeding rates of *Thais* are (1) prey abundance and productivity, (2) other predators, (3) canopy-forming algae, (4) wave shock, (5) desiccation and (6) snail phenotype and/or history. The effects of the first two of these factors seem unimportant. The effects of the latter 4 on prey consumption rates were studied by estimating field feeding rates of snails held in cages with prey in microhabitats which were characterized by one of two alternative states of each factor. For example, microhabitats could be exposed or protected, at higher or lower levels in the mid intertidal, or under a canopy or not. In addition, exposed-phenotype or protected-phenotype snails were used in each experiment.

All of factors (3) to (6) had statistically significant effects except wave shock. The latter would probably also have had a significant effect if the experiments had been performed in the stormier part of the year as well as late summer. The results indicate that sparse populations of *Thais* can exert intense predation pressure on their prey if they are in protected sites covered with a dense canopy (i.e. in cool, moist habitats in calm waters). Areas with sparser canopy (i.e. greater desiccation stress) and more severe wave shock or both apparently reduce average feeding rates of snails. This appears to explain the paradoxical lack of correlation between predation intensity and snail density.

An unexpected result with potentially major implications is the nonlinear response of *Thais* feeding rates to combinations of factors (3) to (6). Four-way analyses of variance on experiments at exposed and protected sites indicate that 7 of 14 1st-order interactions, 2 of 8 2nd-order interactions, and even 1 of 2 3rd-order interactions are statistically significant. These results suggest

0029-8549/78/0034/0017/$03.80

that individual predators cannot be assumed to be identical, and that so-called "higher order" interactions cannot be safely ignored in models of interacting multi-species systems. Hence, it appears that to obtain a thorough understanding of the organization of natural communities, both field and theoretical ecologists alike should begin to grapple with such complexities of nature rather than ignore them.

Introduction

A previous paper (Menge, 1978) began an experimental examination of the influence that characteristics of the physical and biotic environment can have on predation intensity exhibited by a predaceous gastropod (*Thais lapillus*) in the New England rocky intertidial region. The general ecological importance of such a study is considered in detail in that paper. Briefly, surveys of the literature on the effects of predation on community structure suggest these effects can vary widely (e.g. Connell, 1975; Menge and Sutherland, 1976; Lubchenco, 1978). In some cases predation (in the broad sense, including herbivory) clearly has a strong influence on community structure, while in others it does not. A major hypothesis emerging from such studies is that predation intensity, strictly defined as the probability that a prey individual will be killed by a predator, is a function of both physical and biotic characteristics of the environment. Thus a clear understanding of the impact of predators on community structure is dependent on understanding how both predator foraging activity and rate of prey consumption is influenced by several environmental characteristics, including environmental harshness and the biota associated with the predators (Connell, 1975; Menge and Sutherland, 1976; Menge, 1976).

A focus on individual feeding rates and how and why they vary was suggested by the results of an earlier analysis of the organization of the New England rocky intertidal community (Menge, 1976). This study revealed wide variation in predator density between four areas which were relatively protected from the force of high energy waves (Menge, 1976; Fig. 1). The rank of these areas according to increasing predator density is Canoe Beach Cove, Chamberlain, Little Brewster Cove and Grindstone Neck. Paradoxically, predation intensity, here operationally 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 relatively less variable at these areas and unrelated to predator density (Menge, 1976; Fig. 1). The rank of the 4 relatively protected areas according to increased predation intensity is Little Brewster Cove, Chamberlain, Grindstone Neck, and Canoe Beach Cove. Note in particular that the area with the lowest predator density has the highest predation intensity (Fig. 1). This lack of correlation suggests that qualitative variations among individuals of *Thais* are of major importance in determining the effectiveness of this predator population in controlling the abundance of its prey. Below, I consider the influence of (1) prey abundance and productivity, (2) other predators, (3) canopy-forming fucoid algae, (4) wave shock, (5) desiccation (all extrinsic characteristics)

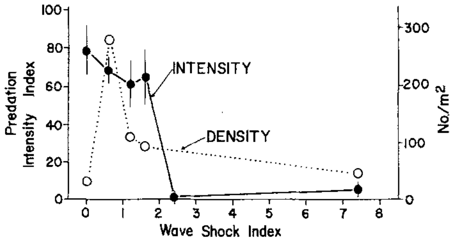

Fig. 1. Comparison between an index of predation intensity (see text for source) and mean density of predators (*Thais lapillus*) at six areas arranged along a wave shock index (based on a cage-loss rate calculated in Menge, 1976). Bars are 95% confidence ranges

and (6) snail phenotype and/or history (an intrinsic characteristic) on the rate of prey consumption of individual *Thais*. The study sites for the experiments and observations reported below are described in earlier papers (Menge, 1976; 1978; Lubchenco and Menge, 1978). All techniques used in the following were relatively simple and straight-forward and are described below where appropriate.

Effect of Prey Abundance and Productivity

Differences in predation intensity could in fact simply reflect differences in prey abundance and/or productivity. However, the available data on prey productivity do not support this hypothesis. Since *Thais* preys almost exclusively on *Balanus* and *Mytilus* (Menge, 1976; Lubchenco and Menge, 1978), prey productivity with respect to *Thais* should be primarily dependent on recruitment densities and growth rates of these two species. My data on these patterns are limited (Table 1, Fig. 2), but they do permit a crude index of intra- and inter-area variation in recruitment of both species and growth in barnacles.

Barnacle recruitment was estimated by counting the number of recruits settling and surviving in the cleared controls of cage experiments reported in Menge (1976). Settlement of *Balanus* in New England lasts from March to June in Massachusetts and May to June in Maine. Thus there is an annual pulse of barnacles into the intertidal. The data suggest that both intra- and inter-site variation are considerable (Table 1). For example, at Grindstone Neck, recruitment of *Balanus* was high in 1972 and low in both 1973 and 1974. Unquantified observations indicated that settlement was even less at this area in 1975 but relatively dense in 1976. Similar variations occur between sites within a year (Table 1). Hence, barnacle settlement seems variable over both space and time at these New England sites.

Monthly settlement density of mussels was estimated at each site from May to October, 1974, by attaching 10 × 10 cm squares of shag rug glued to marine plywood to the substratum whith stainless steel screws. The rug squares could thus be removed and replaced each month with ease. This technique takes advantage of the fact that mussel pediveligers prefer to settle on filamentous substrata (Bayne, 1964; Paine, 1974). However, I use the density estimates obtained only as an index of settlement. The rug undoubtedly has different water retention characteristics than do filamentous algae and I place no confidence in the absolute settlement densities obtained.

Table 1. Recruitment of barnacles and mussels at five sites in New England

Site	Barnacle settlement density (mid), #/100 cm^2 [a]			Mussel settlement density[b] (mid)	Total[c] prey
	1972	1973	1974	1974	
Pemaquid Point	768±311[d] (5)	–[e]	–	–	–
Chamberlain	–	938± 84 (14)	1115±183 (10)	448±348 (8)	1474
Little Brewster Cove	–	481± 62 (12)	–	341±143 (10)	822
Grindstone Neck	1232±213 (14)	378±123 (28)	439±155 (19)	1015±954 (7)	1698
Canoe Beach Cove	–	–	703±136 (12)	227±137 (10)	930

[a] Barnacle recruitment densities (#/100 cm^2) were counted in photographs of experimental treatments not affected by canopy whiplash (Menge, 1976)

[b] Mussel recruitment estimates are counts of the number of *Mytilus* < 1 mm found on the shag rug settlement plates (see text). 1974 experiments were run from May to October. Density is #/100 cm^2

[c] "Total prey" is mean annual *Balanus* density plus mean monthly mussel settlement

[d] Numbers are mean and 95% confidence interval. N (no. of 10 × 10 cm quadrats) is in parentheses

[e] Dashes mean no data are available

Mean monthly mussel settlement in 1974 was much greater at Grindstone Neck than at the other three areas, but this difference is not significant due to the great variation in these experiments (Table 1). Thus, though the "total prey" recruitment index (mean annual barnacle density plus mean monthly settlement of mussels) suggest settlement is greater at the Maine areas than the Massachusetts areas, there is too much intra-site patchiness in recruitment to permit strong inferences. These data support the observations of Seed (1976) that mussel settlement density is sporadic over space and time. I conclude that there is no good evidence that prey recruitment differs consistently between sites.

Barnacle growth at each site was estimated from photographs of controls in the experiments discussed in Menge (1976). Individual barnacles were selected that grew from spring through September, October, or November without physical contact with other individuals. Usually about 10 such individuals could be found per treatment. Although growth of specific individuals can be followed, as Connell (1961a, b, 1970) has so elegantly documented, I present average growth rates in Figure 2. Unfortunately, the data do not permit an examination of temporal variation at a site, since data at Pemaquid Point were obtained in 1972, those at Chamberlain, Little Brewster Cove, and Grindstone Neck in 1973, and those at Canoe Beach Cove in 1974. However, the data for Little Brewster Cove and Grindstone Neck do suggest that intra-site variation in

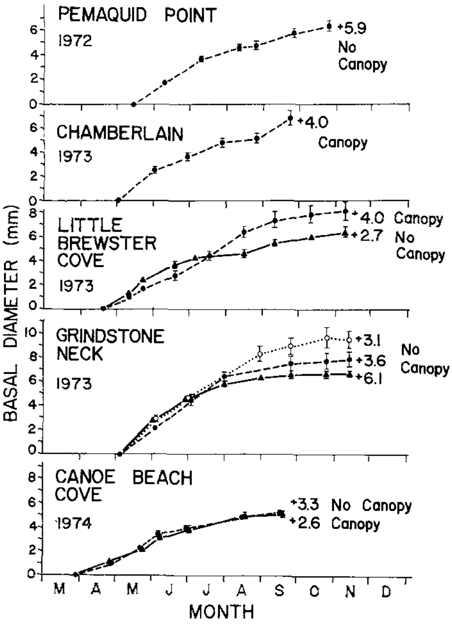

Fig. 2. Growth of *Balanus balanoides* at five areas over one growing season. Data are mean basal diameter ±95% confidence intervals. When interval limit is not visible it does not range beyond the area covered by the symbol for the mean. Tidal height of each cohort ($n = 10$) is given in feet above MLW. "Canopy" means the cohort was overlaid by a cover of *Fucus* spp. or *Ascophyllum nodosum*. Location and description of sites is given in Menge (1976)

growth rates may be equal to, or greater than, between-site variation. For example, growth appears faster at Grindstone Neck at lower tidal levels than at higher ones (Fig. 2). This is presumably related to submergence time or time available for feeding; i.e. barnacles in the low intertidal are submerged longer than those in the mid intertidal and hence can feed longer. Further, the growth curves at Little Brewster Cove suggest that a canopy can have a great effect on growth, since *Balanus* in the higher but canopy-covered treatment grew faster than those in a lower but canopy-free treatment (Fig. 2). However, this is partially countered by the nearly identical growth observed at Canoe Beach Cove in treatments differing in both tidal height and canopy cover.

With two exceptions, these data do not support the hypothesis that differences in barnacle growth rates might explain some of the between-site differences in predation intensity. The exceptions are Grindstone Neck, where barnacle size tends to be greater than at the other areas, and Canoe Beach Cove, where barnacle growth slows in September (though it is similar to the other sites earlier in the year; Fig. 2).

As indicated above, no data on mussel growth are available. A review of the literature indicates that growth of *Mytilus edulis* appears in general to be site-specific (Seed, 1976) and ideally should be quantified at each area. However, subjective impressions gained while monitoring experiments at my study sites do not suggest any consistent differences in mussel growth that could account for the differences in predation intensity observed between areas (Menge, 1976; Fig. 1). Growth of young mussels in predator exclusion cages (Menge, 1976) seemed roughly similar between the sites.

In summary, though prey productivities at the study sites may differ, these differences are not strongly associated with the different predation intensities. Thus, the rank of the areas in order of increasing prey productivities is:

Little Brewster Cove, Canoe Beach Cove, Chamberlain, and Grindstone Neck. From Figure 1, the rank of the areas according to increasing predation intensity (operational definition; see above) is:

Chamberlain, Grindstone Neck, Little Brewster Cove, and Canoe Beach Cove. If the areas with the lowest prey productivity had the highest predation intensity, the latter order would have been:

Grindstone Neck, Chamberlain, Canoe Beach Cove, and Little Brewster Cove. I therefore reject the hypothesis that different prey productivities among the areas can explain the different predation intensities.

Effect of Other Predators

The only predator having an important influence on community structure in the mid intertidal zone at all areas seems to be *Thais* (Menge, 1976). Though such barnacle and mussel predators as crabs (*Cancer* spp., *Carcinus maenas*), seastars (*Asterias* spp.) and a nudibranch (*Onchidoris fusca*) occasionally occur in the mid intertidal, they appear to be transient, too small or rare to have much effect, or both of these (Menge, 1976). Hence, predators other than *Thais* probably have a trivial effect on predation intensity in the mid intertidal.

In the low intertidal, all these predators are present and abundant (Lubchenco and Menge, 1978) and probably contribute significantly to measures of predation intensity. However, consideration of this guild of predators and the predation intensity they exert as a group and individually are beyond the scope of this paper and will be considered elsewhere.

In summary, I reject the hypothesis that other predators are responsible for the observed variations in predation intensity in the mid intertidal region.

Effects of a Canopy, Wave Shock, Desiccation, and Snail Phenotype/History

Experimental Design

To obtain an index of how individual predator effectiveness varies in relation to environment features, I performed experiments designed to determine field feeding rates of *Thais* under different physical conditions. The design of these experiments is given in Table 2. The basic experiment involved using stainless steel mesh cages to hold 5 *Thais* (ranging in length from 2.0 to 2.1 cm) and 20 mussels (with one exception) as prey (ranging in length from 1.0 to 1.4 cm) at each site (Table 2). The exception was an experiment lasting 7 days (vs. 3 to 4 days in other experiments) in which 30 mussels were used to avoid food limitation. Mussels were used as prey because they are readily obtainable, can be isolated and moved without damge (unlike barnacles, which cannot

Table 2. Design of experiments on feeding rates of predators in relation to tidal height, exposure to wave shock and desiccation, and spatial heterogeneity[a]

		Exposed area			Protected area		
		No heterogeneity	Crevices	Canopy (*Fucus distichus*)	No heterogeneity	Canopy (*Fucus vesiculosus* and *spiralis*)	Canopy (*Ascophyllum nodosum*)
High mid	*Thais* exposed[b]	2	2	2	2	2	2
	Thais protected[b]	2	2	2	2	2	2
	Control[c]	1	1	1	1	1	1
Low-mid	*Thais* exposed	2	2	2	2	2	2
	Thais protected	2	2	2	2	2	2
	Control	1	1	1	1	1	1

[a] Numbers are number of cages in each treatment
[b] *Thais* collected from areas either exposed to or protected from wave action
[c] The control has no *Thais* present in the cage

be detached without killing them), and are evidently one of the two preferred prey species of *Thais* (Menge, 1976).

Predators and prey were measured and placed in the cage during a low tide. When the experiment was terminated, the total number of prey remaining was counted, the number eaten was noted, and when possible, those eaten were measured. Like many other whelks, *Thais* drills a characteristic hole in the mussel shell. Thus, dead mussels not having a drill hole in a *Thais* cage were assumed to have died from other causes and were not included in calculations of prey consumption rates (the level of such mortality was about 7%). This provided a built-in control to supplement other controls (mussels with no predators) established in these experiments (Table 2). These controls indicate that a low level of mussel mortality (28 to 1468 or 1.9%) is caused by *Thais* outside the cage. Such mortality was considered insignificant and the feeding rates were not corrected for this source of error.

The number of replicates of each treatment is given in Table 2. The two *Thais*-phenotype treatments (i.e. snails collected from exposed and protected habitats) were established to permit detection of differences in feeding behavior or rate between these two distinct phenotypes of *Thais*. *Thais* from exposed habitats are generally smaller and have relatively thinner and less elongate shells than do snails from protected habitats (Moore, 1936; Osborne, 1977; personal observations). The genetic basis of these differences is not clear, though distinct genotypes have been documented in European *Thais lapillus* (Staiger, 1957).

The basic data yielded by these experiments include sizes and numbers of prey eaten during the experimental period. *Mytilus* size was converted to biomass using a linear regression of prey length on prey biomass: ln (*Mytilus* biomass in g) $= -5.2006 + 3.1394$ ln (*Mytilus* length in cm) ($n = 109$, $F = 4248$, $P \ll 0.001$).

Table 3. Feeding rates in *Thais lapillus* effectiveness experiments[a]

Tidal height[b]	Canopy cover	Month	Snail phenotype[c]		Site[d]		
					Exposed	Protected	
High-mid	Absent	August	Exposed	$\bar{x}$	0.0149	0.00052	
				CI	0.00001–0.058	0–0.0043	
				n	15	16	
			Protected	$\bar{x}$	0.0038	0	
				CI	0–0.024	–	
				n	15	13	
		September	Exposed	$\bar{x}$	0.205	0.27	
				CI	0.08–0.375	0.153–0.412	
				n	9	10	
			Protected	$\bar{x}$	0.125	0.082	
				CI	0.031–0.272	0.036–0.145	
				n	13	13	
	Present[e]	August	Exposed	$\bar{x}$	0.317	0.155	
				CI	0.161–0.508	0.084–0.247	
				n	9	30	
			Protected	$\bar{x}$	0.126	0.008	
				CI	0.035–0.266	0.0004–0.024	
				n	17	28	
		September	Exposed	$\bar{x}$	0.378	0.319	
				CI	0.226–0.553	0.222–0.429	
				n	13	28	
						Fucus	*Ascophyllum*
			Protected	$\bar{x}$	0.178	0.034	0.383
				CI	0.082–0.304	0.001–0.113	0.282–0.495
				n	10	13	12
Low-mid	Absent	August	Exposed	$\bar{x}$	0.051	0.240	
				CI	0.0055–0.139	0.095–0.437	
				n	17	18	
			Protected	$\bar{x}$	0.05	0.131	
				CI	0.008–0.148	0.041–0.265	
				n	18	18	
		September	Exposed	$\bar{x}$	0.410	0.476	
				CI	0.219–0.635	0.344–0.621	
				n	10	16	
			Protected	$\bar{x}$	0.131	0.386	
				CI	0.010–0.365	0.241–0.554	
				n	10	14	
	Present[f]	August	Exposed	$\bar{x}$	0.294	0.508	
				CI	0.216–0.679	0.368–0.66	
				n	16	35	
			Protected	$\bar{x}$	0.606	0.576	
				CI	0.311–0.922	0.402–0.766	
				n	17	36	
		September	Exposed	$\bar{x}$	0.578	0.622	
				CI	0.257–0.794	0.491–0.760	
				n	11	32	
			Protected	$\bar{x}$	0.581	0.524	
				CI	0.393–0.78	0.410–0.636	
				n	13	30	

Feeding Rates of *Thais*

Experiments on *Thais* feeding rates considered the influence of five factors. These were exposure to waves (experiments conducted at exposed vs. protected sites), tidal height (higher and lower portions of the mid intertidal zone), canopy cover (none vs. *Fucus* or *Ascophyllum*), month (August vs. September, 1975), and snail phenotype (snails collected at exposed vs. protected sites) (Table 3). Feeding rates were calculated as mg (dry weight) of *Mytilus* consumed per treatment (5 snails) per h (Table 3). In the Boston area in 1975, August was an unusually warm month. Temperatures were ≧27° C (80° F) on 17 of 31 days and a record maximum of 39° C (102° F) was reached on August 2. September was cooler, the highest recorded temperature being 27.5° C, with temperatures ≧27° C being reached only 3 out of 30 days (Anon., 1975). These between-month differences in temperatures, and the fact that many of the lowest tides occur during mid-day, are the justification for treating August and September as major differences in the experimental design.

Average feeding rates of *Thais* in all possible treatment combinations, are given in Table 3. Analysis of the five-way design of the experiments by analysis of variance (ANOVA) would lead to one 4th-order interaction, five 3rd-order interactions, ten 2nd-order interactions and ten 1st-order interactions. Since interpretation of these interactions would be night-marish, I chose to first analyze the exposed and protected experiments separately with four-way ANOVA (Tables 4 and 5) and then to compare the parallel treatments at exposed and protected sites with one-way ANOVA (Table 8). As will be seen, interpretation of four-way ANOVAs is also complicated, but provided rewarding and potentially important insights.

Several problems were encountered in analyzing these data. First, estimates of feeding rates were sometimes not usable for some experiments because mussels were lost from the cage during the experiment of the entire cage was torn loose. For statistical testing, these missing values were replaced with the "cell" mean (the means in Table 3 are "cell" means) to make cell size uniform at $n = 18$. Second, both Bartlett's test for homogeneity of variances and the F-max test (Sokal and Rohlf, 1969) indicated that the variances were not always equal.

[a] Rates are mg (dry wt) *Mytilus* consumed per h by five *Thais*. Five *Thais* were used per treatment to reduce the influence of inter-individual variation in feeding activity

[b] Heights are the higher and lower reaches of the mid intertidal zone ("high-mid" = +5 to +6 ft or +1.52 to +1.83 m above MLW and "low-mid" = +2 to +2.5 ft or +0.61 to +0.76 m above MLW)

[c] Snails occurring at exposed headlands have distinctly different phenotypes from those in protected sites. See text for further explanation

[d] Exposed site was East Point; protected site was Canoe Beach Cove. Data were transformed with the arcsin transformation for statistical treatment (see Tables 5 and 6). Means and 95% confidence intervals given above are those yielded by back-transforming the transformed means and confidence intervals (Sokal and Rohlf, 1969)

[e] Canopy species is *Fucus distichus*

[f] Canopy species are *Fucus vesiculosus* and *Ascophyllum nodosum*. With one exception (see body of table), rates in experiments under these canopy species were not significantly different ($P > 0.05$, significance determined by examining overlap in confidence intervals)

Table 4. Four-way anova table (fixed model) on the effectiveness experiments done at the exposed site[a]

Source of variation	Degrees of freedom	Sums of squares	Mean square	F
Main effects				
Tidal height	1	7,002.14	7,002.14	44.22***
Canopy cover	1	18,334.43	18,334.43	115.79***
Month	1	5,355.68	5,355.68	33.82***
Snail type	1	1,414.70	1,414.70	8.93**
First-order interactions				
Tidal height × Canopy cover	1	1,103.04	1,103.04	6.97**
Tidal height × Month	1	16.61	16.61	0.10
Tidal height × Snail type	1	549.94	549.94	3.47
Canopy cover × Month	1	2,403.52	2,403.52	15.18***
Canopy cover × Snail type	1	78.34	78.34	0.49
Month × Snail type	1	642.53	642.53	4.06*
Second-order interactions				
Tidal height × Canopy cover × Month	1	4.39	4.39	0.03
Tidal height × Canopy cover × Snail type	1	1,323.27	1,323.27	8.36**
Tidal height × Month × Snail type	1	484.51	484.51	3.06
Canopy cover × Month × Snail type	1	130.23	130.23	0.82
Third-order interaction				
Tidal height × Canopy cover × Month × Snail type	1	31.87	31.87	0.20
Error (within subgroups)	272	43,068.39	158.34	
Total	287			

$* = F_{0.05\,(1,\,\infty\,\mathrm{df})} = 3.84$ $** = F_{0.01\,(1,\infty\,\mathrm{df})} = 6.63$ $*** = F_{0.001\,(1,\infty\,\mathrm{df})} = 10.8$

[a] All variances but one are equal. All effects are fixed. Statistics were performed on data transformed with the arcsin transformation (Sokal and Rohlf, 1969)

If the one cell with a mean feeding rate and variance of 0 (Table 3) is ignored, the arcsin transformation solved this problem for protected experiments, but not for the exposed experiments where one experiment (i.e. the exposed, low, canopy-covered, August, protected snail phenotype experiment) still had an unusually high variance after transformation. However, since ANOVA has been found to be relatively robust to violations of its assumptions (e.g. Binder, 1959; Boneau, 1960; Cochran, 1947; Donaldson, 1968), I ignored this problem and proceeded with the ANOVA.

Assuming the above problems have little effect on the analysis, Tables 4 and 5 indicate that all factors (tidal height, canopy cover, month and snail phenotype) have highly significant effects. That is, the feeding rates in Table 3 are strongly influenced by each of the factors. In general, feeding rates in the low-mid intertidal are significantly greater than in the high-mid intertidal, those under a canopy are greater than those not under a canopy, those in September are greater than those in August, and those of exposed-phenotype snails are greater than those of protected-phenotype snails. With one exception

Table 5. Four-way anova table (fixed model) on the effectiveness experiments done at the protected site[a]

Source of variation	Degrees of freedom	Sums of squares	Mean square	F
Main effects				
Tidal height	1	31,036.65	31,036.65	241.25***
Canopy cover	2	9,388.69	4,694.34	36.49***
Month	1	8,000.71	8,000.71	62.19***
Snail type	1	3,077.13	3,077.13	23.92***
First-order interactions				
Tidal height × Canopy cover	2	1,158.62	579.31	4.50*
Tidal height × Month	1	1,930.20	1,930.20	15.00***
Tidal height × Snail type	1	1,331.35	1,331.35	10.35**
Canopy cover × Month	2	1,655.73	827.86	6.44**
Canopy cover × Snail type	2	139.56	69.78	0.54
Month × Snail type	1	31.88	31.88	0.25
Second-order interactions				
Tidal height × Canopy cover × Month	2	1,393.25	696.62	5.41**
Tidal height × Canopy cover × Snail type	2	600.64	300.32	2.33
Tidal height × Month × Snail type	1	115.32	115.32	0.90
Canopy cover × Month × Snail type	2	725.87	362.94	2.82
Third-order interaction				
Tidal height × Canopy cover × Month × Snail type	2	915.61	457.80	3.56*
Error (within subgroups)	408	52,487.82	128.65	
Total	431			

$* = F_{0.05\,(1,\infty)} = 3.84$ $** = F_{0.01\,(1,\infty)} = 6.63$ $*** = F_{0.001\,(1,\infty)} = 10.8$

$* = F_{0.05\,(2,\infty)} = 3.00$ $** = F_{0.01\,(2,\infty)} = 4.61$ $*** = F_{0.001\,(2,\infty)} = 6.91$

[a] Bartlett's test for homogeneity of variance (Sokal and Rohlf, 1969) indicates variances are equal

(Table 3), canopy effects do not depend on the canopy species (though canopy patchiness may be important; see Menge, 1978), since feeding rates under *Ascophyllum* and *Fucus* in protected sites were not statistically different (Table 3). Basically, these results suggest that feeding rates and, presumably, the effectiveness of *Thais* as a predator are strongly influenced by desiccation (an extrinsic factor and a function of tidal height, canopy cover, and month of the active season) and snail phenotype or history (an intrinsic factor). Specifically, feeding rates tend to be greatest in cooler, damper habitats and exposed-phenotype snails feed faster than do protected-phenotype snails.

A result of this analysis of considerable interest is that several higher-order interactions are significant. In experiments at exposed areas, three 1st- and one 2nd-order interaction(s) are significant (Table 4), while at protected areas four 1st-, one 2nd-, and the 3rd-order interactions are significant (Table 5). Interpretation of these requires examination of the appropriate 2-way or 3-way tables.

Table 6. Interpretations of higher-order interactions at the exposed site[a]

	Interaction					Interpretation
A. (1st)	Tidal height ×		Canopy cover		Difference	A canopy has a greater positive effect on feeding in the low area than in the high
			Absent	Present		
		High	11.93	23.97	+12.04	
		Low	17.87	37.75	+19.88	
		Difference	+5.94	+13.78		
B. (1st)	Canopy cover ×		Month		Difference	A lack of canopy in August more severely inhibits feeding than a lack of canopy in September
			August	September		
		Absent	7.70	22.10	+14.32	
		Present	29.43	32.28	+ 2.85	
		Difference	+21.65	+10.18		
C. (1st)		Month ×	Snail phenotype		Difference	Exposed snails eat significantly faster than protected ones in September than they do in August
			Exposed	Protected		
		August	19.29	17.84	− 1.45	
		September	30.90	23.48	− 7.42	
		Difference	+11.61	+ 5.64		
D. (2nd)	Tidal height ×	Snail phenotype ×	Canopy cover		Difference	A canopy cover increases the feeding rate of exposed snails more than protected snails in the high area, but in the low area, a canopy cover increases the feeding rate of protected snails more than it does exposed snails
			Absent	Present		
	High	Exposed	13.90	29.19	+15.29	
		Protected	9.95	18.75	+ 8.80	
		Difference	− 3.95	−10.44		
	Low	Exposed	21.37	35.92	+14.55	
		Protected	14.37	39.58	+25.21	
		Difference	− 7.00	+ 3.66		

[a] The data are cell means of transformed (arcsin transformation) feeding rates. Signs of differences assume that in general feeding rates are higher (1) under a canopy than away from it, (2) in the low than in the high, (3) in September than in August, (4) in protected snails than in exposed snails. All but the last of these a priori assumptions is correct (see Table 3)

Experiments at the Exposed Site. There are three significant 1st-order interactions. First, tidal height and canopy cover interact such that though both a canopy cover and a habitat lower in the intertidal increase feeding rate, the low, canopy-present combination results in a disproportionately greater feeding rate than either factor alone would produce (Table 6). Thus predation intensity is synergistically increased by the interaction of two factors moderating desiccation. Second, month and canopy cover interact such that, though lower feeding rates are generally obtained where canopy was absent, the no canopy-August combination severely reduced the feeding rates (Table 6). In this case the interaction of hot weather (August) combined with desiccatory conditions (no canopy) reduces predation intensity more than would be expected by their separate effects. Third, month and snail phenotype interact such that though rates are usually higher in September than in August and exposed-phenotype snails feed faster than protected-phenotype ones, exposed-phenotype snails accelerate their feeding rates more in September than do protected-phenotype snails (Table 6). Evidently exposed-phenotype snails can either (1) accelerate their feeding rates more when conditions moderate than do protected-phenotype snails, or (2) prolong feeding activity more when conditions become more stressful.

The one significant 2nd-order interaction in exposed experiments is between tidal height, canopy cover, and snail phenotype (Tables 4 and 6). This interaction subsumes the tidal height × canopy cover 1st-order interaction discussed above. Here feeding rates are greater in canopy-covered, low-mid intertidal habitats. However, the canopy increases the feeding rates of exposed-phenotype snails more than those of protected-phenotype snails in the higher area while a canopy in the low area increases rates of protected-phenotype more than exposed-phenotype snails (Table 6). Thus, predation intensity is synergistically increased by the interaction of two factors moderating desiccation intensity and snail phenotype and/or history. The effect of snail phenotype and/or history may be related to the facts that exposed-phenotype snails are infrequently covered by a canopy while protected-phenotype snails are nearly always under or near a canopy and that desiccation is less at exposed than at protected sites. Hence the higher part of the mid intertidal is liable to have less influence on exposed-phenotype than it does on protected-phenotype snails.

Experiments at the Protected Site. At the protected site the 3rd-order, one 2nd-order, and four 1st-order interactions are significant, in addition to all the main effects (Table 5). The significant 3rd-order interaction basically means that the effect of a factor on the feeding rate is dependent on the combination of the other three factors. For example, Table 7 indicates that exposed-phenotype snails always feed faster than protected-phenotype snails except in two specific instances. These are (1) under *Fucus* in August in the low-mid intertidal and (2) under *Ascophyllum* in September in the low-mid intertidal (Table 7F). Many instances of synergism are apparent in the latter table. For example, the difference between feeding rate of protected-phenotype snails in low and high experiments is usually much greater than the difference in the rate of exposed-phenotype snails, except in the August experiments with no canopy. Thus feeding rates of protected-phenotype snails are inhibited more in high experiments than would be expected by considerations of each factor separately. Note that there is less variation in mean feeding rates in low than in high experiments (Table 7F, standard deviations among the means are 6.64 and 10.47, respectively).

The 2nd-order interaction (Table 7E; tidal height × canopy cover × month) suggests that in the high-mid intertidal the *Fucus* canopy does not have as great an effect on feeding rates in September as it does in August. Further, in August the lack of a canopy seems more inhibitory in the high-mid intertidal than in the low-mid intertidal.

Table 7. Interpretations of higher-order interactions at the protected site. Method of interpretation is the same as in Table 6, but differences in rates are not shown to minimize confusion[a]

Interaction	Tidal height ×	Canopy cover			Interpretation
		Absent	*Fucus*	*Asco*	
A. (1st)	High	9.09	11.46	20.89	A canopy has a great effect on feeding; but in the low, canopy spp. seems relatively unimportant, while in the high *Ascophyllum* has a greater effect than *Fucus*
	Low	24.12	33.02	35.16	

Interaction	Tidal height ×	Month		Interpretation
		August	September	
B. (1st)	High	7.40	20.23	Conditions in the high intertidal have a much more inhibitory effect on feeding in August than they do in September
	Low	28.58	32.96	

Interaction	Tidal height ×	Snail type		Interpretation
		Exposed	Protected	
C. (1st)	High	18.24	9.39	Occurrence in the low intertidal has a relatively greater effect on the feeding rates of protected snails than exposed ones
	Low	31.68	29.85	

Interaction	Month ×	Canopy cover			Interpretation
		Absent	*Fucus*	*Asco*	
D. (1st)	August	9.59	19.77	24.60	The importance of a canopy cover to the maintenance of a high feeding rate is relatively greater in August than September, when the absence of a canopy has a relatively small effect on feeding rates
	September	23.62	24.71	31.45	

Interaction	Tidal height	× Month ×	Canopy cover			Interpretation
			Absent	*Fucus*	*Asco*	
E. (2nd)	High	August	0.49	8.77	12.94	The effect of canopy cover depends both on month and tidal height. The lack of a canopy has a much more severe effect on feeding rates (1) in August than in September and (2) in the high than in the low. Sites without a canopy in the high-mid intertidal in August are extremely harsh
		September	17.70	14.15	28.84	
	Low	August	18.69	30.78	36.27	
		September	29.54	35.27	34.06	

Interaction	Tidal height	× Month	× Snail type ×	Canopy cover			Interpretation
				Absent	*Fucus*	*Asco*	
F. (3rd)	High	August	Exposed	0.98	15.76	19.46	The effect of any one factor is dependent on the combination of the other three. See text for an example
			Protected	0	1.77	6.41	
		September	Exposed	22.98	20.30	29.95	
			Protected	12.43	8.00	27.73	
	Low	August	Exposed	21.61	27.67	36.83	
			Protected	15.77	33.89	35.70	
		September	Exposed	31.24	38.83	33.91	
			Protected	27.84	31.71	34.21	

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[a] Data are cell means of transformed feeding rates

Table 8. Table of one-way anovas comparing feeding rates of *Thais* in exposed experiments to those in protected experiments (statistics done on data transformed with the arcsin transformation)

Tidal height	Canopy cover	Month	Snail phenotype	*F*[a]	d.f.	Conclusion
High	Absent	August	Exposed	2.84	1,29	No difference
			Protected	1.77	1,26	,,
		September	Exposed	0.28	1,17	,,
			Protected	0.41	1,24	,,
	Present	August	Exposed	2.87	1,37	,,
			Protected	12.75***	1,43	$E>P$
		September	Exposed	0.36	1,39	No difference
			Protected *Fucus*[b]	6.23*	1,21	$E>P$
			Protected *Asco.*[b]	5.35*	1,20	$E<P$
Low	Absent	August	Exposed	5.73*	1,33	$E<P$
			Protected	1.52	1,34	No difference
		September	Exposed	0.43	1,24	,,
			Protected	5.19*	1,22	$E<P$
	Present	August	Exposed	0.56	1,49	No difference
			Protected	0.29	1,52	,,
		September	Exposed	0.17	1,41	,,
			Protected	0.22	1,41	,,

[a] ***=significant at $P<0.001$; **=significant at $P<0.01$; *=significant at $P<0.05$

[b] Rates under a *Fucus* and an *Ascophyllum* canopy are done separately because they are significantly different (see Table 3)

As indicated in Table 7A–D, the four significant 1st-order interactions are more comprehensible. However, these interpretations, and those in Table 7E, are essentially academic, since they are subsumed by the 3rd-order interaction. Yet they are important in that they are all highly significant, while the 3rd-order interaction is not overwhelmingly significant. At the very least, this increases confidence in the ecological meaning of these statistical interactions. Hence, to know how fast a *Thais* of a given phenotype can eat its prey, we need to know up to three, and maybe four characteristics of the environment in which the snail occurs.

The general point these synergisms (and occasional interference interactions, in the statistical meaning of the term) seem to make is that in combination, certain features of the physical environment can produce non-linear responses in predator feeding rates. Further, snail phenotype and/or history is also an important part of the formula, since the feeding rates of the two snail phenotypes are significantly different and do not respond in the same way to the different combinations of the physical environment. The ecological significance of these results will be discussed after considering the effect of wave action on these experimental feeding rates.

Effect of Wave Action

The hypothesis that the feeding rates for each combination of factors at the exposed and protected areas were not different was tested by one-way ANOVA (Table 8). The comparisons suggest that in these experiments, wave shock generally had an unimportant effect on feeding rates, despite the fact that storm-related mortality occurred during the experiments (Menge, 1978). This result is not really unexpected, however, because the experiments were done in August and September, which are generally relatively calm months. Results of other experiments (Menge, 1978) suggest that if these experiments had been run later in autumn or in early spring, a greater wave effect would be apparent. A second feature of these experiments contributing to the lack of difference between exposed and protected habitats is the fact that the snails were essentially cloistered with their prey. Thus, search time was presumably drastically reduced and the snails were exposed to relatively little risk when capturing and consuming a prey. In the more natural situation, capture of a prey involves crawling through the habitat in search of prey and thus includes an element of risk of being dislodged if high energy wave action is a relatively frequent occurrence. Field experiments testing this hypothesis are reported elsewhere (Menge, 1978).

Discussion

The above experiments indicate that individual feeding rates of *Thais* are greatly influenced by several factors. In general, feeding rates are greater in the lower intertidal, under a canopy, and in cooler months of the warmer part of the year than in the higher intertidal, away from the cover of a canopy, and in warm months of the warmer part of the year. These variations in individual feeding rates suggest that populations of snails in different habitats or patches can exert different predation intensities on the prey in these patches or habitats. For example, at the protected sites the impact of 100 snails on their prey in the higher reaches of the intertidal will be less than that of 100 snails in the lower portions of the intertidal. Further, 100 snails would exert less predation pressure on mussels and barnacles occupying an area with a sparse canopy than they would on an area with a dense canopy (compare rates in Table 3). This would seem to go far in explaining why effective predation intensity at protected areas is relatively insensitive to predator density (Fig. 1). For example, 100 snails under a dense canopy might have the same effect as 500 snails under a sparse canopy. Add to this the effect of wave shock on activity and differences in temperature regime and the explanation of how 31 *Thais*/m^2 at Canoe Beach Cove can have a similar effect to that exerted by about 300/m^2 (and at times $>1000/\text{m}^2$; Menge, 1976, p. 388) at Grindstone Neck seems evident: predation intensity is strongly dependent on how individual feeding rates are affected by the environment.

Two results seem of particularly keen interest. First, this study demonstrates that individual predators cannot be considered equivalent. In some respects, this is quite distressing, as a key assumption in many predator-prey models is that individual predators are identical. My work suggests that this assumption may be violated on at least two counts. First, there are significant intrinsic differences in feeding rates between exposed and protected phenotypes. Second, feeding rates of snails of the same phenotype can differ considerably in response to features of the individual's environment. It would seem that future predator-prey models should be built to include the effects of at least two general classes of variables: the influence of the environment, and individual variation [variation due to differences in phenotype, genotype, or in experience and learning (=history)]. This could be done at the community level by assembling specific and realistic models for predators with different but constant foraging tactics into a larger model which would characterize the predation regime in a particular community. The results in this paper indicate that submodels should be developed to the intraspecific level (i.e. different phenotypes may have different tactics). Such a model would be quite complex and may be unfeasible at present, simply because so little is known about how predation rates are influenced by the factors considered here.

The second result of considerable interest is the discovery that the influence of the various factors on feeding rates is not additive but involves both types of statistical interaction (synergism and interference). That is, two or more factors may interact to produce a higher (or lower) feeding rate than expected. This result was unexpected, and would seem to lend a further cautionary note to both field and theoretical workers alike. Field studies on the effects of predators generally seek a qualitative (i.e. do predators have an effect or not?), rather than a more quantitative result (i.e. how much, and why, does predation pressure vary with density, size, over space and time, etc.?).

Likewise, in their efforts to model the complexities of nature as simply as possible, most theoretical ecologists ignore the so-called "higher-order" interactions in their models, assuming they are of negligible importance. Others have suggested for systems regulated by competitive interactions that in fact such higher-order interactions are quite often important in nature (Wilbur, 1972; Neill, 1974). My study suggests that higher-order interactions may greatly influence the outcome of even simple predator-prey interactions like the one predator-two prey system considered here.

This interaction at least partly involves a sort of mutualism. Thus, the fucoid canopy that so greatly affects the rates of consumption of prey by *Thais*, is itself dependent on the predatory effects of *Thais*. By removing mussels, *Thais* removes organisms that can outcompete fucoid algae (Menge, 1975, 1976; Menge and Lubchenco, in preparation). Experiments performed at several areas indicate that in the absence of *Thais, Mytilus* pulls *Fucus* into the matrix of the mussel bed, eventually either smothering it or tearing it loose when the mussels are washed off the shore during storms. Similar but unquantified observations have been made of *Ascophyllum* being smothered by mussels.

Presumably, then, in the prolonged absence of predators, areas covered with *Fucus* and *Ascophyllum* would develop into areas covered with mussels. Hence, the fucoid canopy appears dependent on removal of *Mytilus* by *Thais*. Lubchenco and I (in preparation) have found evidence of other higher-order interactions in the New England rocky intertidal. Similar sorts of complex interactions undoubtedly exist in other communities; their importance to the understanding of community structure would seem sufficiently great to be deserving of intensive ecological concern.

A final result of interest is the discovery that exposed-phenotype snails have an intrinsically greater rate of prey consumption under nearly all circumstances than do protected-phenotype snails (Table 3). This makes sense when viewed as an adaptation to life in a habitat where high vagility is disadvantageous (see Menge, 1978). Thus, at exposed areas a great advantage presumably accrues to those individuals who can consume a prey rapidly once one has been located. This would serve two functions. First, it would lessen the time a snail would be subjected to the greater risk associated with leaving a safe shelter to seek prey. Second, it would enable a snail to attack *additional* prey individuals sooner, if conditions permitted continued foraging. The tradeoff to this adaptation is not clear, but may involve the thinner shell, smaller mean sizes, and perhaps other, as yet unknown, characteristics of exposed phenotypes of *Thais* such as speed, strength, etc.

In addition to their slower feeding rates, protected phenotypes of *Thais* have thick shells and reach larger mean individual lengths (see above). It is unclear whether a slower feeding rate is of direct adaptive significance or is a necessary but non-maladaptive side effect of more directly advantageous adaptations like the shell characteristics mentioned above. For example, a thick shell may be necessary at protected sites because crabs occasionally occur in such habitats, and are potentially important predators on *Thais* (e.g. see Connell, 1970; Vermeij, 1976; Osborne, 1977). Clearly, *Thais* is ripe material for a detailed study of the life history consequences of occupying habitats with radically different selective pressures.

In conclusion, I believe this study has provided added insight into a key mechanism of community regulation. Major results are first, that a predator's impact on its community is clearly dependent on both intrinsic characteristics of each predator and biotic and physical characteristics of its environment. Second, the non-linear effect of these various factors on prey consumption rates suggests that the complexities of natural ecosystems, though often ignored in the hopes that they are unimportant, are actually of considerable importance. This result further suggests that a thorough understanding of the organization of natural communities may well depend on coming to grips with complex processes such as those considered in this and other papers (e.g. Wilbur, 1972; Neill, 1974; Menge, 1978), rather than ignoring them.

Acknowledgements. I extend thanks to Jane Lubchenco for her constructive comments, encouragement and support. John Wiens provided a thoughtful and thorough reading of the paper and offered many useful comments. Steve Garrity helped with all phases of the work; this assistance is most appreciated. Carol Hibbard assisted ably in much of the field work. Tom Marx gave statistical advice and pointed out several references on violations of assumptions in parametric statistics. Nathan Riser, Director of the Marine Science Institute, Northeastern University, Nahant, Massachusetts, provided laboratory space and protected field sites. The work was supported by NSF grants no. GA 35617 and DES72-01578 A01. Publication costs were defrayed by NSF grant no. OCE76-22251. This is contribution no. 49 from the Marine Science Institute, Northeastern University, Nahant, Mass.

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Received August 8, 1977