Original Papers

Components of predation intensity in the low zone of the New England rocky intertidal region

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Summary. Predation intensity often increases along local gradients of decreasing environmental rigor. Assuming factors such as productivity and heterogeneity do not change along such gradients, potential factors responsible for this pattern include: (1) increased effectiveness per individual predator, (2) increased numbers of individual predators, (3) increased numbers of predator species of the same general morphological attributes, and (4) increased numbers of predator species of different general morphological attributes. I term these factors the components of predation intensity.

In relatively protected low rocky intertidal regions of northern New England, community structure depends in part on the foraging activities of up to six species (three general types) of predators (Lubchenco and Menge 1978). These include three species of crab, two species of seastars, and one thaidid gastropod. This predator guild prevents mussel and barnacle populations from outcompeting *Chondrus crispus*. This red alga dominates space when predators are present, but is outcompeted by mussels when predators are excluded.

Prey consumption rates (mg per predator individual per hr or mg g^{-1} hr^{-1}) in field experiments indicate that the rank from most to least effective predator type is crabs, seastars, and the gastropod. Statistically significant variations occur between predator types (largest differences), species of a given type, and individuals of a species (smallest differences). Estimates of the relative contribution of each species to total predation intensity in the low zone at several sites indicate that each predator species is a major predator at one or more sites. Thus, if one predator species in this guild becomes scarce, the other predators may increase their effects and reduce variation in the total predation intensity exerted by the guild. Comparisons with other systems suggest that increased diversity of types of foraging characteristics in predatory guilds is an important component of increased predation intensity along gradients of decreased environmental rigor.

Introduction

Predation (including herbivores and carnivores) can have a great effect on the behavior, ecology and evolution of organisms. Indeed, Connell (1975) suggests that predation is the single most important biotic factor affecting natural communities. Predators assume an important role in a de-

veloping body of theory attempting to explain local, regional and global patterns of community organization (e.g., Connell 1975, 1978; Menge 1982a; Menge and Sutherland 1976; Menge and Lubchenco 1981; Lubchenco 1978; Lubchenco and Menge 1978; Lubchenco and Gaines 1981; Gaines and Lubchenco 1982; Paine 1974, 1977, 1980; Caswell 1978; Huston 1979; Russ 1980; Vance 1978). Competition between organisms of low trophic status occurs only when they escape consumers by growing too large to be eaten, or by occurring in a spatial or temporal refuge.

Recent attempts to develop and extend this theory have been focused on a more quantitative examination of the intensity of prey consumption by predators (e.g., Menge 1978a, b; Menge and Lubchenco 1981). Typically ecologists determine the effects of consumers by examining the response of a system in the absence of these organisms. However, predation intensity varies between extremes of no effect vs. a normal effect. To gain a clear understanding of the causes of patterns of community structure such as species diversity, a sharper and more quantitative focus on the components of predation intensity is needed. There are at least four such components. These include variation in (1) predator effectiveness (individual level), (2) predator density (species level), (3) number of species of similar morphologies (e.g., snails) and (4) number of consumer types of different morphologies; (e.g., snails, seastars and crabs represent the three different types). In the mid intertidal region of the New England rocky intertidal region I investigated components (1) and (2) (Menge 1978a, b). In the mid zone, the predation intensity exerted by a single species (*Thais lapillus*, a gastropod) is evidently a complex function of its density and behavioral and phenotypic variations in feeding rates of individuals which occur in response to environmental variability. Here, I extend this analysis to include components (3) and (4) in an effort to understand variations in predation intensity observed in the more trophically complex low rocky intertidal region of New England.

Methods

Experiments and observations were made in the low intertidal at five sites from 1972–1976. Ranging from wave-exposed to wave-protected, these sites include East Point, Nahant, Massachusetts; Chamberlain, Maine; Little Brewster Cove, Little Brewster Island, Boston Harbor, Massachusetts; Grindstone Neck, Winter Harbor, Maine; and Canoe Beach Cove, Nahant, Massachusetts (see Menge

1976, 1979 for locations and detailed descriptions of these sites).

The predator guild

The low zone harbors up to six species and three types of predator. These include three crabs (*Carcinus maenas, Cancer borealis,* and *C. irroratus*), two seastars (*Asterias forbesi* and *A. vulgaris*) and one gastropod species (*Thais lapillus*). Crabs consume shelled prey such as barnacles and mussels by crushing or shearing the prey and removing tissue with their claws and mouthparts (Elner 1978; Kitching, Sloan and Ebling 1959). Seastars consume prey both extra- and intra-orally (e.g., Hyman 1955; Sloan 1980) and may eat many prey simultaneously (e.g., Paine 1969b, 1971, 1974; Mauzey et al. 1968; Menge 1972). *Thais* consumes prey singly. They usually bore a hole at least partly through the shell and consume prey tissue by rasping with their radula (e.g., Hyman 1967).

Predator activity in New England is highly seasonal. Observations reported earlier (Menge 1978a, 1979) indicate that *Thais* and *Asterias* spp. are characterized by high levels of movement and feeding in the intertidal region from May to early October each year. From late October to April, *Asterias* spp. retreat to subtidal regions and *Thais* retreat to crevices in the intertidal region. Active seasons are somewhat longer in Massachusetts than in Maine (B. Menge, personal observations). Seasonal activity of crabs is less well known but my field observations indicate that the active season of crabs parallels those of *Thais* and seastars.

Density of predators and mussels in the low intertidal was estimated at each of four sites (Chamberlain, Little Brewster Cove, Grindstone Neck, Canoe Beach Cove) from transects of ten, 0.25 m² quadrats taken each two to three months from 1972–1976 (Lubchenco and Menge 1978; Menge 1976). Size frequency distributions were estimated from samples of predators taken at each site. Shell length (*Thais*), radius (seastars) or carapace width (crabs) were the dimensions measured. Predator biomass (g wet weight/ 0.25 m²) was calculated using these data together with regressions of size vs. total wet weight for each species. Samples for these regressions were collected at Canoe Beach Cove (*Thais, Asterias forbesi, Cancer borealis, Carcinus maenas*) or East Point (*Thais, Cancer irroratus*). *Thais* were sampled at both sites because phenotypic differences in shell morphology and thickness exist between sites exposed to (e.g., East Point), and protected from (e.g., Canoe Beach Cove) waves (Menge 1978b).

Estimates of mussel recruitment were obtained from 10 × 10 cm squares of shag carpet first glued to 10 × 10 cm squares of 13 mm thick plywood and then screwed to the substratum (Menge 1978b). These were placed in high- and low-mid zones under or away from the canopy at each study site. They were replaced monthly. No consistent canopy effects occurred (B.A. Menge unpublished data).

Estimation of predation intensity

The effect of predators was determined by establishing replicated predator exclusion experiments in the low intertidal at the four sites listed above from 1973–1975 (Menge 1976, 1978b; Lubchenco and Menge 1978). Each replicate consisted of three 10 × 10 cm quadrats: a caged exclosure, a shade control (roof) and an uncaged control. These were installed in March (Massachusetts) or April (Maine) before the annual recruitment of barnacles and mussels and before predators became active. Experimental quadrats were censused at monthly intervals.

An index of predation intensity was estimated by calculating the percent difference in prey abundance between predator exclusion and control in each replicate for 1973 (all sites except Canoe Beach Cove) and 1974 (all sites except Chamberlain). This method of estimating predation intensity assumes that all prey mortality not due to predators is similar between sites, approximately true at least in summer when abiotic and nonpredation mortality is lowest.

Feeding rate experiments

Feeding rates of individuals of each predator were determined in field experiments conducted at two neighboring sites (0.5 km apart) at Nahant, Massachusetts differing in wave exposure; East Point (wave-exposed) and Canoe Beach Cove (wave-protected; see also Menge 1978a, b). Individuals were isolated in stainless steel mesh cages (*Thais* and *Asterias,* 10 × 10 × 5 cm; crabs, 20 × 20 × 5 cm) with a fixed number of prey (mussels) and allowed to feed for variable periods. Controls were cages enclosing prey but not predators. Factors tested included: 1) wave action. Cages were installed at Canoe Beach Cove and East Point. 2) Canopy. Some cages were beneath an algal canopy (*Ascophyllum nodosum* at the protected site, *Fucus distichus* at the exposed site) and some were not. 3) Time. Experiments were conducted in August and September 1975 (*Thais* and *Asterias forbesi*), and June and July 1976 (*Thais* and crabs). 4) Phenotype – for *Thais* only. Some cages included only exposed-phenotype individuals and some only protected-phenotype individuals (Menge 1978a). Data recorded include (1) predator size, (2) prey size, (3) sizes of prey eaten and surviving, (4) size and number of dead prey not killed by predators (when this could be determined), and (5) predator condition.

Mussels were used as prey because they are a major item in predator diets (Menge 1976, 1979; Lubchenco and Menge 1978; Elner 1978) and are easily handled without damage. Mussels were collected at East Point. Those in *Thais* and *Asterias* experiments ranged in size from 0.9 to 1.5 cm (most were 1.2 to 1.4 cm). Those in crab experiments ranged from 1.0 to 2.0 cm (most prey were 1.5–1.9 cm). I used relatively large predators to ensure that they could eat the sizes of mussels provided. Though sizes of predator and prey may affect feeding rates, this was not investigated. Predator size ranges in experiments were *Carcinus maenas* 3.8–6.0 cm carapace width, *Cancer borealis* 2.7–7.0 cm carapace width, *Cancer irroratus* 4.2–7.2 cm carapace width, *Asterias* spp. 1.9–3.7 cm arm length, exposed-phenotype *Thais* 2.0–2.5 cm shell length and protected-phenotype *Thais* 2.0–2.9 cm shell length.

Prey killed by snails could be identified by the characteristic bore hole on the shell. Prey killed by crabs were crushed and usually in fragments. Only prey killed by seastars could not be distinguished from mussels dying from non-predator sources. Though mussel mortality in controls was low (7.5 to 8.9%), all feeding rates were corrected for this mortality. Replicates wherein the predator was dead or moribund when monitored (Table 1) were excluded from analysis. Experiments were terminated when most mussels had

Table 1. Predator mortality during feeding rate experiments. All individuals were active and healthy at initiation of the experiments

Predator species	Experiments	Canopy present		Canopy absent	
		% dead at termination	N	% dead at termination	N
Thais lapillus	1975 (Aug.–Sept.)	1.3	680	5.3	340
Thais lapillus	1976 (June–July)	0	44	2.3	44
Asterias forbesi	1975 (Aug.–Sept.)	0	48	47.8	46
Cancer irroratus	1976 (June–July)	30.8	13	25.0	4
C. borealis	1976 (June–July)	0	24	17.9	39
Carcinus maenas	1976 (June–July)	0	7	0	6

N = number of individuals, summed over all experiments

Table 2. Duration of field experiments estimating feeding rates of five predator species

Species	$\bar{x} \pm 95\%$ CI (h)	N	Range (h)
Thais lapillus	110.1 ± 2.9	216	62 –173.5
Asterias forbesi	97.6 ± 5.6	112	61.5–149.5
Cancer borealis	72.9 ± 11.1	57	25 –152
Cancer irroratus	98.2 ± 16.5	18	35 –152
Carcinus maenas	115.6 ± 11.1	14	99.5–137

N = total number of replicates summed over all experiments for each species

been consumed in cages with the highest predation rates. Experiment duration varied among species (Table 2). Mean duration was 73 to 115 h or ca. 3 to 5 days. The shortest experiments (with *Cancer borealis*) were 25 h, the longest (with *Thais lapillus*) were 173.5 h. Ranges spanned roughly similar times for each species. This variability was deliberate, since I wanted to determine if predator satiation occurred. Some variation was imposed by delays in monitoring due to storms. Experiments were run at the lower edge of the mid (= lower-mid) zone, about 0.3 m above the upper edge of the low zone. This permitted monitoring during both good and poor low tides.

No claim is made that feeding rates in these experiments approximate those occurring under natural conditions. Experimental artifacts include: (1) predator and prey are confined to cages; (2) size ranges of predator and prey do not necessarily correspond to those occurring normally; (3) prey diet is restricted to mussels; (4) experiments were conducted in the lower-mid rather than in the low zone; and (5) cages probably modify canopy, wave, and desiccation effects. However, cage artifacts should be uniform among replicates, and cages and controls differ only in predator presence or absence. Further, the intent was to estimate *relative* individual feeding rates as affected by the various factors tested. Comparisons are made only within the experimental matrix.

Data analysis

Feeding rates were analyzed using the general linear regression model (Neter and Wasserman 1974):

$$Y_i = B_0 + B_1 X_{ii} + B_2 X_{i2} + \dots + B_{p-1} X_{i, p-1} + E_i$$

Y_i is the feeding rate, B_i's are fitted parameters, E_i is the error term and X_{ii}'s are "indicator variables" (0 or 1) representing a particular effect. For example, canopy presence in a particular experiment would be represented by $X = 1$, canopy absence by $X = 0$. The binary code distinguished between canopy effects (present or absent), time (August or September 1975; June and July 1976), snail phenotype (exposed or protected), wave-exposure (exposed or protected) and crabs (*C. borealis*, [= *C. borealis*, 1; *C. irroratus*, 0], *C. irroratus* [= *C. borealis*, 0; *C. irroratus*, 1] and *C. maenas* [= *C. borealis*, 0; *C. irroratus*, 0]). Equations were generated by the REGRESS subsystem in the Statistical Interactive Programming System (SIPS) created by the Statistics Department, Oregon State University. Appropriateness of parametric tests on these data was evaluated by examining distributions of residuals around the regressions. In all cases the data were normal or were normalized by transformations (see Table captions).

Results

Predation intensity in the low zone

As noted earlier, the first and last days of seasonal feeding activity by snails varies somewhat from year to year. Summarizing my personal observations, in Maine, *Thais* and seastars usually commence activity in April and retreat to shelter in October. In Massachusetts, activity begins and ends about one month earlier and later, respectively. I use May 1 to September 30 for Maine and April 1 to October 31 for Massachusetts to restrict feeding periods to months when snails almost always actively feed. Activity of crabs observed while diving suggests that though they may be active all year in the subtidal, and thus may potentially forage in the low zone any month, activity is greatest in summer and least in winter. All these considerations lead to minimum estimates of predator activity time.

In general, abundances of *Thais* and *Asterias* spp. are highest and those of crabs are least (Table 3). Total numerical abundance of predators is least at Canoe Beach Cove (the most protected site) and highest at Grindstone Neck (the second most protected site). Striking differences in relative numerical dominance by predator species exist among the areas. *Thais* is most numerous at Grindstone Neck, *Asterias* spp. dominate at Chamberlain, *A. forbesi* and *Thais* are both abundant at Little Brewster Cove and *A. forbesi* and *Carcinus* co-dominate at Canoe Beach Cove (Table 3).

Predator biomass at each site in 1973 and 1974 was estimated by multiplying the density of each species times its mean individual biomass and summing over all predator species for each year (Table 3). Mean individual biomass was estimated by converting each individual linear dimension in a sample to a biomass estimate (using the regressions in Table 4), and then averaging these biomass values (Table 3).

Predation intensity at each site in each year was estimated as the first peak difference in prey abundance between exclosures and controls (e.g., Fig. 1). In these experiments, prey cover usually reached a peak in July, August or September, after which a decline in cover sometimes occurred (Fig. 1). This decline was due to either an invasion of exclosures by small *Thais* and seastars which ate prey and caused a decline in their abundance, or to my thinning

Table 3. Estimation of predator biomass in 1973 and 1974 at each of four study sites. Data are mean values and 95% confidence intervals. Sample sizes as shown in parentheses

Site	Species	Yr	Density (no./0.25 m^2)	Mean linear dimension[a] (cm)	Mean individual biomass (g wet weight)	Biomass per 0.25 m^2	Total predator biomass per 0.25 m^2 1973	Total predator biomass per 0.25 m^2 1974
Chamberlain	Thais lapillus	1973	11.1 ±4.5 (20)	1.4±0.1 (118)	0.6±0.1 (118)	6.7	122.1	282.9
	Thais lapillus	1974	8.3 ±7.7 (10)	1.6±0.1[b] (73)	0.8±0.2[b] (73)	6.6		
	Asterias vulgaris	1973	20.6 ±13.1 (20)	2.3±0.1 (331)	4.0±0.6 (331)	82.0		
	Asterias vulgaris	1974	45.5 ±15.0 (10)	3.2±0.3[c] (113)	5.6±1.0[c] (113)	254.8		
	A. forbesi	1973	7.2 ±4.2 (20)	3.0±0.3 (66)	4.4±1.2 (66)	31.7		
	A. forbesi	1974	3.8 ±3.0 (10)	3.2±0.2[c] (87)	5.2±0.8[c] (87)	19.8		
	Carcinus maenas	1973–75[d]	0.02±0.05 (40)	[e]	[e]	0.02		
	Cancer borealis	1973–75[d]	0.15±0.2 (40)	[e]	[e]	1.7		
Little Brewster Cove	T. lapillus	1973	19.4 ±15.6 (10)	2.3±0.1[f] (104)	1.9±0.2[f] (104)	36.9	63.6	13.9
	T. lapillus	1974	3.2 ±1.7 (10)	2.3±0.1[f] (104)	1.9±0.2[f] (104)	6.1		
	A. vulgaris	1973	2.0 ±2.3 (10)	2.9±0.6[f] (4)	4.7±4.3[f] (4)	9.4		
	A. vulgaris	1974	0.1 ±0.2 (10)	2.9±0.6[f] (4)	4.7±4.3[f] (4)	0.5		
	A. forbesi	1973	6.6 ±5.6 (10)	2.1±0.2[f] (53)	2.4±0.6[f] (53)	15.8		
	A. forbesi	1974	2.4 ±1.6 (10)	2.1±0.2[f] (53)	2.4±0.6[f] (53)	5.8		
	C. maenas	1973–76[d]	1.1 ±1.1 (40)	1.4±0.6 (5)	0.8±1.2 (5)	0.9		
	C. borealis	1973–76[d]	0.05±0.1 (40)	[e]	[e]	0.6		
Grindstone[g] Neck	T. lapillus	1973	74.6 ±34.1 (20)	1.9±0.2 (72)	1.4±0.3 (72)	104.4	188.8	87.2
	T. lapillus	1974	23.5 ±15.6 (10)	2.5±0.7 (144)	2.4±0.2 (144)	56.4		
	A. vulgaris	1973	2.2 ±1.2 (20)	4.8±0.5 (224)	38.2±7.0 (224)	84.0		

[a] Data from July whenever possible, since this represents the approximate midpoint in summer feeding. Further, Thais and Asterias spp. population size structures change over the summer, with increasing number of juveniles occurring from June to September. Dimensions measured were Thais, shell length; Asterias spp., radius or arm length (center of disk to tip of most typical arm); crabs, carapace width

[b] Value is from mid zone data since low zone values were missing. In justifying this substitution I note that samples taken in mid and low zones on other dates were approximately equal

[c] Values from June 1974; no July data were taken

[d] Density values are averaged over several summers due to great mobility and relatively low abundance of these crabs. See text for further comment

[e] Size estimates from Canoe Beach Cove were used in these cases, since crab size structure was not sampled at the other sites

[f] Values from July 1975; no size data were taken in 1973 or 1974

[g] A. forbesi does not occur at this site

Table 3 (continued)

Site	Species	Yr	Density (no./0.25 m^2)	Mean linear dimension[a] (cm)	Mean individual biomass (g wet weight)	Biomass per 0.25 m^2	Total predator biomass per 0.25 m^2	
							1973	1974
Grindstone[g] Neck	A. vulgaris	1974	3.5 ±4.7 (10)	3.4±0.4 (93)	8.7±2.8 (93)	30.4		
	C. maenas	1972–75	0.02±0.04 (53)	[e]	[e]	0.01		
	C. borealis	1972–75	0.04±0.05 (53)	[e]	[e]	0.4		
Canoe Beach Cove	T. lapillus	1974	0.8 ±0.6 (10)	2.3±0.2 (54)	2.1±0.3 (54)	1.7	–	31.4
	A. vulgaris	1974	0.9±1.9 (10)	3.0±0.3 (73)	7.0±1.5 (73)	6.3		
	A. forbesi	1974	4.1 ±3.1 (10)	2.8±0.3 (100)	4.9±1.4 (100)	20.1		
	C. maenas	1974–76	3.1 ±2.1 (30)	1.1±0.1[b] (78)	0.7±0.3[b] (78)	2.2		
	C. borealis	1974–76	0.1 ±0.1 (30)	3.6±0.4 (16)	11.1±2.7 (16)	1.1		

Table 4. Regression equations $(Y = aX^b)$ for four predator species at Canoe Beach Cove and East Point

Predator species	Equation[a]	n	r^2 [b]
Thais lapillus exposed	Wet weight = 0.14 (shell length)$^{3.12}$	50	0.87**
Thais lapillus protected	Wet weight = 0.14 (shell length)$^{3.01}$	46	0.97**
Asterias forbesi	Wet weight = 0.04 (arm length)$^{2.58}$	69	0.92**
Cancer borealis	Wet weight = 0.31 (carapace length)$^{2.61}$	34	0.94**
Carcinus maenas	Wet weight = 0.26 (carapace width)$^{2.92}$	10	0.99**

[a] Wet weights are all in g, lengths or widths are in cm. Thais wet weights are total weight including shell. Crab and asteroid wet weights include the carapace and endoskeleton, respectively. Data are from separate samples of predators from those used in the feeding rate experiments, though all are from the same field population
[b] ** = $P < 0.01$

the prey (mostly mussels by this time; see Menge 1976; Lubchenco and Menge 1978) to prevent prey mortality due to overcrowding.

Predator biomass and predation intensity are significantly inversely correlated (predation intensity = 96.2–0.298 predator biomass; $n = 19$, $r = -0.63$, $P < 0.01$; Fig. 2). A similar result was observed in the mid zone (Menge 1978a, b), where Thais lapillus is the numerically and functionally dominant predator (Menge 1976, 1982b). In this case, I suggested that this pattern was largely due to variations in the predatory effectiveness of individual Thais (Menge 1978a, b, 1982b). In the low zone, the added complication

of different species and types of predator requires an evaluation of the effects of these variables on the relative effectiveness of each.

Feeding rates

Variation due to differences in predator size or predator satiation

Two major sources of uncontrolled variation in the feeding rate experiments are variation in size and satiation of individuals. First, predator sizes were selected to be typical of adult sizes for each species but to vary relatively little around this size. Regression analyses of predator sizes (i.e., X = shell length for Thais, arm length for Asterias and carapace width for the crabs) on feeding rates (Y = mg h^{-1} individual^{-1}) were done for different conditions of wave exposure and canopy (see below for experimental design). In only one of eleven cases were feeding rate and size correlated with a slope significantly > 0 (Cancer borealis in wave protected, canopy covered experiments; rate = $-6.27 + 2.51$ carapace width; $F = 5.41$, d.f. = 1, 21, $P = 0.03$). With this exception, the feeding data may be analyzed without correcting for size differences. This does not mean that feeding rates are constant over all sizes of each predator species. Rather, variations in feeding rate over the sizes of predator used in the experiments are not significant.

Second, since predators were in cages from about one to seven days, individuals may have become satiated after a few days. Thus, longer experiments would have lower feeding rates. Regression analyses of duration of experiment (X = h) on feeding rates (Y = mg/h for Thais and Asterias and mg g^{-1} h^{-1} for the crabs) were done for each set of environmental conditions in each design. The only significant regression was for Cancer borealis under a canopy (i.e., ln (Feeding rate in mg g^{-1} h^{-1}) = $-0.76 - 0.0096$ (duration in h); $P = 0.014$, $F = 7.20$, d.f. = 1, 20). Examination
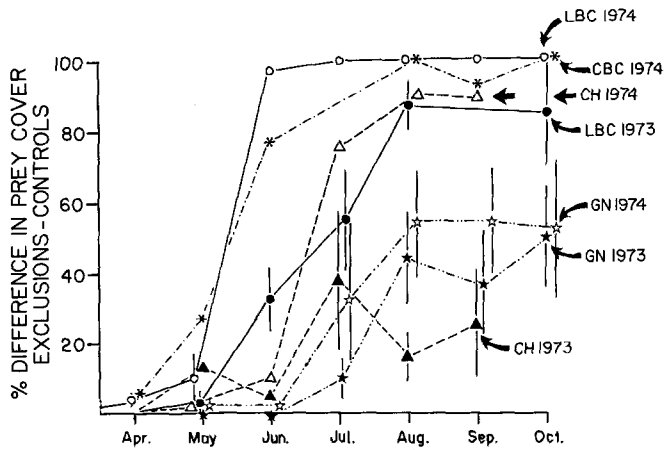
Fig. 1. Percent difference in prey (*Balanus balanoides* and *Mytilus edulis*) cover during the active season (approx. summer) at the four study sites in 1973 and 1974. No data are available at Chamberlain from 1974 or Canoe Beach Cove in 1973. Estimates of predation intensity come from the months when peak or the largest differences occur. CH = Chamberlain, LBC = Little Brewster Cove, GN = Grindstone Neck, CBC = Canoe Beach Cove in this and subsequent figures
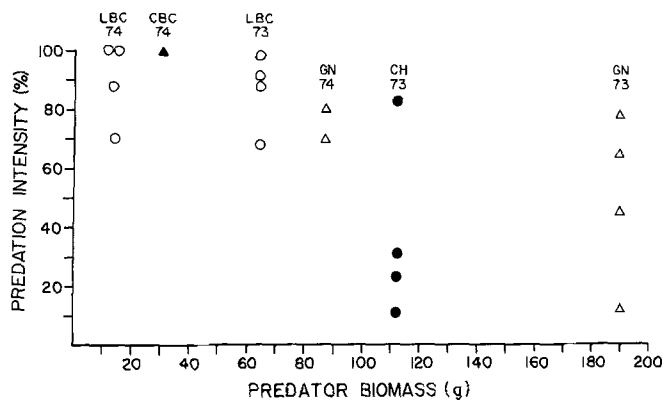

Fig. 2. Relationship between total biomass density of predators (see Table 3) and predation intensity in the low zone at four study sites. The index of predation intensity, i.e., mean percent difference between abundance of prey in control and predator exclusion, is discussed in the text. Each point represents a single replicate

of a scattergram indicated that the significance of this regression was due to high rates measured during 24 h experiments. That is, feeding rates are highest on the first day of the experiment and slow down over time, presumably due to satiation. To remove this bias, I used only crab feeding rates from experiments lasting between 49 and 152 h. Regression analyses on the reduced data set reveal no relationship between feeding rate and experiment duration (e.g., ln (feeding rate in mg g^{-1} h^{-1}) = $-1.58 - 0.0024$ (duration in h); $P = 0.72$, $F = 0.13$, d.f. = 1, 11). This adjustment also makes experimental durations more comparable for each crab species (e.g., Table 2).

In summary, with the exception of *Cancer borealis* data (adjusted as indicated above), no bias in predator feeding rates can be attributed to different sizes of predators used (within species) or variation in experiment duration.

Table 5. ANOVA table for effects of several factors on *Thais lapillus* feeding rates. Data were transformed ($\log_{10}[Y+1]$) before analysis. All sums of squares and mean squares were coded by multiplying by 100. Only significant interactions are included in the table[a]

Source of variation	d.f.	MS	F	r²
Regression	15	0.64	5.36***	0.34
Residual (error)	155	0.12		
Main effects				
Canopy (present vs. absent)	1	0.02	0.16	0.001
Month (June vs. July)	1	1.49	12.57***	0.053
Phenotype	1	0.91	7.67**	0.032
(exposed vs. protected)				
Wave exposure	1	1.25	10.57**	0.045
(exposed vs. protected)				
Significant interactions				
2-way				
Canopy × month	1	0.79	6.67*	0.028
Phenotype × wave exposure	1	1.31	11.03**	0.047
3-Way				
Canopy × month × phenotype	1	0.59	4.98*	0.021
4-way				
Canopy × month × phenotype	1	0.92	7.74**	0.033
× wave exposure				
Total	170	0.16		

[a] * = significant at 5% level, ** = significant at 1% level, *** = significant at 0.1% level

Individual variation in *Thais lapillus*

Analysis of variance on *Thais* feeding rates (mg [dry weight] *Mytilus* consumed h^{-1} per individual predator) indicates that the four-way interaction (i.e., canopy × month × snail phenotype × wave exposure) is significant (Table 5). To sort out the effects of each factor, I plotted cell means for each of 16 possible combinations (Fig. 3). At the wave-exposed site without a canopy, neither snail phenotype fed in June, while in July, exposed phenotypes (= resident) fed faster than protected phenotypes (= non-residents). With a canopy, residents fed at similar rates in both months. Non-residents did not feed in June, and in July, fed at a rate similar to non-residents in the no canopy treatment. The canopy effect at the wave-exposed site was greatest on resident snails, but unexpectedly, resident snails fed faster with no canopy. In summary, at the wave-exposed site non-residents were not affected by a canopy, while feeding of residents was enhanced by a canopy in June and inhibited in July.

At the wave protected site, protected-phenotype (= residents at this site) snails always fed faster than exposed phenotypes (= non-residents; Fig. 3). Hence, with one exception (exposed-phenotype under a canopy at the wave-exposed site), snails always fed faster in their resident habitat. Feeding rates at the wave-protected site were usually lower in June than July, except for the protected-phenotype under a canopy, which fed at similar rates in both months. In contrast to the result at the wave-exposed site, feeding was usually enhanced by the canopy at the protected site except in July for the protected phenotypes. Here feeding rates were similar with and without a canopy. In summary, feeding of non-residents and residents at the protected site
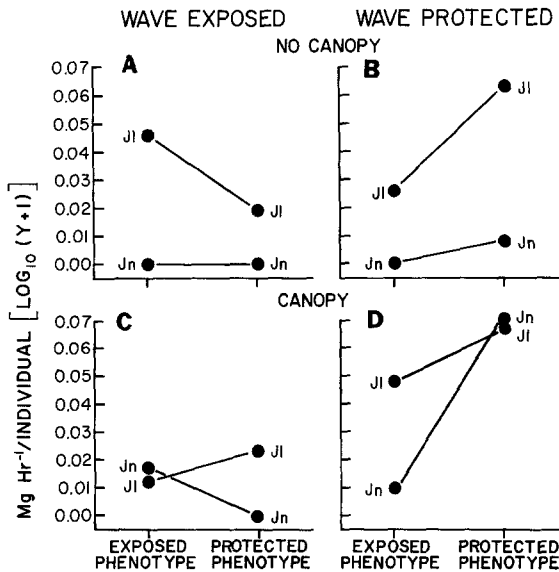
Fig. 3. Analysis of four-way interaction in *Thais* feeding rate experiment. Each point is the cell mean for each of the 16 possible combinations of effects. Jn = June; Jl = July. No canopy = A + B, canopy = C + D. Wave exposed = A + C, wave protected = B + D. Rates are mg (dry weight) *Mytilus* consumed per h by one *Thais*, corrected for mussel mortality in controls and *Thais* mortality in experiments. Canopy alga was *Fucus distichus* at exposed sites and *Ascophyllum nodosum* at protected sites. "Exposed" phenotype snails occur at sites exposed to wave shock. They have relatively thin, short, wide shells. "Protected" phenotype snails occur in protected sites. They have relatively thick, long, narrow shells (see Menge 1978b). The wave-exposed site was East Point, and the wave-protected site was Canoe Beach Cove; both are at Nahant. N's are 8 for all June data, 12 to 14 for July data

was enhanced by a canopy at all times, but the effect was much greater in June than July.

Finally, wave exposure usually reduced feeding rates, though in two instances exposed-phenotype feeding rates were lower at the wave-protected site (Fig. 3). Note that protected-phenotype snails generally feed fastest, particularly under a canopy at the wave protected site (Fig. 3). Furthermore, the convergence of these rates suggests that this may be a maximal feeding rate for *Thais* in this habitat. Thus, individual feeding rates are variable, but vary in different ways depending in part on the specific set of environmental conditions.

There are some interesting differences between these experiments, done June and July 1976 and those done August and September 1975 (Menge 1978b). In 1975, exposed-phenotypes always fed faster than protected-phenotypes (Menge 1978b). In 1976, each phenotype usually fed faster in its native habitat (Fig. 3). Such differences suggest that exposed and protected phenotypes have distinct foraging strategies. For example, differences between the 1975 and 1976 experiments could be explained if protected-phenotypes normally feed more early in the season but are strongly inhibited in any season by wave shock. Exposed-phenotypes may be less affected by waves and reach a feeding peak later in the season. Protected-phenotypes feed faster, particularly in canopy covered areas in July (Fig. 3).

In contrast to 1975, where no differences in mean *Thais* feeding rates occurred at exposed vs protected areas, mean

Table 6. ANOVA table for effects of canopy and month on feeding rate of *Asterias forbesi*. Data were transformed ($\log_{10}[Y+1]$) before analysis. The interaction was not significant

Source of variation	d.f.	MS	F	r^2
Regression	3	0.032	6.22**	0.18
Residual (error)	85	0.005		
Main effects				
Canopy (present or absent)	1	0.046	8.89**	0.086
Month (August or September)	1	0.005	0.97	0.009
Total	88	0.006		

** = significant at 1% level

Table 7. Feeding rates of individual *Asterias forbesi* in low-mid zone field experiments, August–September 1975 at Canoe Beach Cove. Data are mean and 95% confidence interval. N is in parentheses

Canopy cover	Month	Feeding rate mg (dry wt) *Mytilus*/h/seastar
None	August	0.31 ± 0.14 (16)
	September	0.27 ± 0.11 (16)
Present	August	0.51 ± 0.10 (32)
	September	0.44 ± 0.04 (24)

All data were corrected for mussel mortality from sources other than *A. forbesi* in the experiments

Table 8. ANOVA table for effects of canopy on feeding rates ($\text{mg g}^{-1} \text{ h}^{-1}$) of three crab species. Data were transformed ($\ln[Y+1]$) before analysis. The interaction was not significant

Sources of variation	d.f.	MS	F^a	r^2
Regression	5	0.10	8.07***	0.472
Residual (error)	45	0.01		
Main effects				
Canopy (present vs. absent)	1	0.004	0.32	0.004
Crab species (*C. borealis, C. irroratus, C. maenas*)	2	0.11	8.62***	0.202
Total	50	0.02		

a *** = $P < 0.001$

feeding rates at exposed and protected areas in the 1976 experiments are significantly different (Table 5). Feeding rates at protected areas (overall $\bar{x} = 0.10$ mg h^{-1}, $n = 87$) are more than twice those at exposed areas (overall $\bar{x} = 0.04$ mg h^{-1}, $n = 86$). This difference may be explained by the relative severity of wave shock at exposed sites through at least June, while in late summer (i.e., August–September), seas tend to be calm (B. Menge, personal observations). Thus, the 1976 experiments were done in June and July, when a relatively large differential in wave action exists between months, while the 1975 experiments were done in August and September, when the differential is less. This may explain why the exposed vs. protected difference in feeding rates was observed in 1976 but not 1975.

Table 9. Feeding rates of individual crabs in low–mid zone field experiments. June–August, 1976 at East Point and Canoe Beach Cove. Entries are $\bar{x}$ and 95% confidence interval with n in parentheses. Experiments at wave-exposed sites were done only with *Carcinus*

Crab species	Feeding rate			
	No canopy		Canopy	
	(mg/h)	(mg g^{-1} h^{-1})	(mg/h)	(mg g^{-1} h^{-1})
Cancer irroratus	2.5±5.7 (3)	0.1 ±0.5 (3)	3.7±2.7 (13)	0.07±0.05 (13)
Cancer borealis (all)[a]	2.0±1.6 (22)	0.1 ±0.1 (22)	5.5±1.9 (24)	0.3 ±0.1 (24)
(adjusted)[b]	1.7±1.0 (10)	0.1 ±0.1 (10)	3.2±1.4 (13)	0.2 ±0.1 (13)
Carcinus maenas (wave protected)	7.2±1.6 (6)	0.4 ±0.1 (6)	7.9±3.0 (7)	0.3 ±0.1 (7)
Carcinus maenas (wave exposed)	1.9±3.8 (4)	0.04±0.06 (4)	3.3 (2)	0.06 (2)

[a] Includes experiments lasting 24 h (see text for further explanation)
[b] Excludes 24 h experiments

Table 10. ANOVA table on effects of canopy and wave shock on feeding rates of *Carcinus maenas*. Data were transformed ($\log_{10}$ $[Y+1]$) before analysis. The interaction was not significant

Source of variation	d.f.	MS	F	r^2
Regression	3	0.40	6.71**	0.573
Residual (error)	15	0.06		
Main effects				
Canopy (present or absent)	1	0.002	0.04	0.001
Wave exposure (exposed or protected)	1	0.73	12.27**	0.349
Total	18			

** = significant at 1% level

Individual variation in *Asterias forbesi*

Analysis of variance indicates that canopy cover has a strong effect on *A. forbesi* feeding rate (Table 6). However, no difference in rates related to month occurred, nor was the interaction significant. Thus, feeding rates of *A. forbesi* under a canopy are about twice those in the open (Table 7). This difference is probably due to the inhibitory effect of desiccation on activity and feeding of asteroids not covered by the canopy during diurnal low tides.

Individual and interspecific variation in three crab species

Analysis of variance shows that there are differences between crab species feeding rates but the canopy has no effect (Table 8). In general, *Carcinus* feeds faster than the *Cancer* species (Table 9). Though this test indicates canopy has no effect on feeding, absence of a canopy has a strong affect on survival of *C. borealis* (Table 1). *C. irroratus* seems highly susceptible to intertidal exposure regardless of conditions while *Carcinus* is unaffected by aerial exposure (Table 1) or canopy (Table 9).

C. maenas was the only crab whose feeding rate was investigated at the wave-exposed site. Rates at exposed sites with or without a canopy were lower than comparable rates at the protected area (Table 9). Feeding rates of *Carcinus* seem little affected by canopy cover but are evidently strongly inhibited by wave shock (Tables 9 and 10). Thus *C. maenas* feeding rates are greatest at less variable wave-protected sites and lowest at more variable wave-exposed sites.

These data indicate that like snails and seastars, individual crab feeding activity is also variable, at least for *Carcinus* (Table 10). Feeding activity of *C. borealis* is probably indirectly affected by canopy cover through its affect on survival of this crab (Table 1). These data also reveal significant interspecific differences in feeding rates at the protected site (Tables 8 and 9) with *Carcinus maenas* being the fastest consumer of mussels among these species.

The best fit general linear regression models for *Thais, Asterias forbesi* and the crabs are given in the Appendix. Each is highly significant ($P \ll 0.001$) and includes only significant main effects and interactions.

Comparative feeding rates: differences between types of predators

This predator guild includes three distinct types of predator; snails, seastars and crabs. Each is distinct in shape, locomotion, activity, feeding method and size. Table 11 shows average sizes and feeding rates of animals used in feeding experiments. Since their morphologies vary, wet weight (g) is probably a better index of relative size than some linear dimension. Estimated wet weights were obtained from linear dimensions using the regression equations shown in Table 4. *Thais lapillus* used in the experiments were small (1.7 to 2.1 g), *Asterias forbesi* were intermediate (4.1 g) and crabs are large (18–49 g; Table 11). Correspondingly, feeding rate estimates obtained in field experiments at the protected site indicate that feeding rates ranked by predator type, from slowest to fastest, is snails

Table 11. Comparison between sizes and feeding rates (in mg h^{-1} predator^{-1}) of the three types of predators at the protected site

Predator species	Month		Mean size		Feeding rate (mg/h/predator)	
			Length or width (cm)	Wet weight (g)[a]	No canopy	Canopy
Gastropod						
Thais lapillus	August	$\bar{X}$	–[b]	–	0.05	0.12
(1975; 5 per cage)		CI	–	–	0.03–0.07	0.10–0.14
		n	–	–	36	71
	September	$\bar{X}$	–	–	0.09	0.12
		CI	–	–	0.07–0.11	0.10–0.14
		n	–	–	30	62
Thais lapillus	June	$\bar{X}$	2.4	2.1 (exp)	0.01	0.11
(1976; 1 per cage)		CI	2.28–2.44	1.9 (prot)	0–0.03	0.043–0.173
		n	32		16	16
	July	$\bar{X}$	2.3	1.8 (exp)	0.12	0.15
		CI	2.21–2.33	1.7 (prot)	0.06–0.19	0.10–0.20
		n	56		28	28
Asteroid						
Asterias forbesi	August and	$\bar{X}$	2.8	4.1	0.3	0.5
(1975)	September	CI	2.62–2.98	3.4–4.9	0.2–0.4	0.4–0.6
		n	104	104	32	48
Brachyurans						
Cancer irroratus	June–August	$\bar{X}$	6.4	48.8	5.9[c]	3.4[c]
		CI	4.8–8.0	6.7–90.9		
		n	5	4	3	13
Cancer borealis	June–August	$\bar{X}$	4.7	17.8	2.0[c]	3.7[c]
		CI	4.4–5.0	15.1–20.5		
		n	36	35	10	13
Carcinus maenas	June–August	$\bar{X}$	4.8	24.7	8.6[c]	7.7[c]
		CI	4.4–5.2	19.2–31.2		
		n	14	14	6	7

[a] Wet weights for snails and starfish estimated using equations in Table 4
[b] Dash means no data available
[c] Estimated by multiplying the feeding rates ($\text{mg g}^{-1} \text{h}^{-1}$) in Table 9 by the mean crab weights in column 2 of this table

(0.05 to 0.15 mg h^{-1} predator^{-1}), seastars (0.2 to 0.44 mg h^{-1} predator^{-1}) and crabs (0.98 to 7.9 mg h^{-1} predator^{-1}). In units more easily visualized (no. consumed/day), snails consume 0.2 to 0.3, asteroids consume 0.6 to 1.2 and crabs consume 1.2 to 7.8 mussels per day (Table 12). These data suggest that on a per individual basis, crabs are most, seastars are second most and snails are least effective as predators. Crabs feed at rates 5 to 36 times those of seastars, and seastars feed at rates 2 to 20 times those of snails.

These differences may be a function of at least two differences between predators; size and innate characteristics of each type or species of predator. Assuming that each type of predator is equally affected by enclosures, feeding rates expressed on a per unit of biomass of predator basis should reveal whether or not crabs and seastars are inherently better predators than seastars and snails respectively. Table 13 presents feeding rates estimated on a per gram (wet weight) of predator basis. One-way analysis of variance on canopy rates (or, with *C. irroratus* and *Carcinus*, all rates at the protected site) indicates that there are significant differences among the means ($F = 15.27$; d.f. $= 4$, 86; $P < 0.001$). An SNK test (Sokal and Rohlf 1969) indicates that most feeding rates are different. Exceptions are that

there is no difference between rates of *C. irroratus* and *Thais* or *C. borealis* and *Asterias* (Table 13). Hence, on a per unit weight basis, feeding rates at the protected site in this predator guild exhibit significant differences between species (e.g., crab species) and types (e.g., snails, seastars and crabs).

The predator impact index

Since predator biomass does not correlate positively to predation intensity (Fig. 2), I calculated more direct estimates of predator affect (Table 14). These were derived by multiplying number of prey eaten/day (Table 12), days active/yr (153 in Maine, 198 in Massachusetts; Table 14) and predator density (Table 3). Within species variation was incorporated by using minimum and maximum feeding rates (Table 12) and density (Table 3) of each species, where available. Table 14 indicates that the impact of each species varies among sites. At Chamberlain, *Asterias* spp. appears largely responsible for the predation effect estimated in Fig. 2. At Little Brewster Cove, *Carcinus* and *Asterias* spp. have the greatest effect but *Thais* may be important at higher densities and feeding rates. At Grindstone Neck, *Thais* is most important and at Canoe Beach Cove, *Carcinus* is

Table 12. Numbers of mussels per predator per hour and day for the three types of predators in experiments at the protected site[a]

Predator species		Feeding rate			
		No canopy		Canopy	
		No./h	No./day	No./h	No./day
Gastropod					
Thais lapillus	$\bar{X}$	0.008	0.19	0.013	0.31
(1975, 5/cage)	95% CI	±0.002	–	±0.002	–
	n	66	–	67	–
Thais lapillus	$\bar{X}$	0.007	0.16	0.009	0.22
(1976, 1/cage, July)	95% CI	±0.004	–	±0.003	–
	n	28	–	28	–
Asteroid					
Asterias forbesi	$\bar{X}$	0.03	0.63	0.05	1.25
	95% CI	±0.01	–	±0.01	–
	n	56	–	56	–
Crabs					
Cancer irroratus	$\bar{X}$	0.09	2.09	0.08	2.02
	95% CI	±0.19	–	±0.06	–
	n	3	–	15	–
Cancer borealis	$\bar{X}$	0.06	1.32	0.08	1.99
	95% CI	±0.02	–	±0.04	–
	n	10	–	17	–
Carcinus maenas	$\bar{X}$	0.25	5.92	0.32	7.78
	95% CI	±0.06	–	±0.20	–
	n	6	–	7	–

[a] Canopy species is *Ascophyllum nodosum*. Data for *C. borealis* corrected for size and experiment duration (see text)

Table 13. A. Feeding rates of the three types of predators per gram of predator wet weight at the protected site. Predator wet weights for snails and seastars estimated from regressions in Table 11. Weights for crabs were measured directly. Data in (A) are $\bar{x}$ and 95% CI, n in parenthesis. *Thais* are protected-phenotype individuals

Predator species		Feeding rate (mg g^{-1} (wet weight) h^{-1})	
		No canopy	Canopy
Gastropod	*T. lapillus* – June	0.01 ± 0.02 (8)	0.08 ± 0.05 (8)
	T. lapillus – July	0.012 ± 0.11 (13)	0.08 ± 0.04 (13)
Asteroid	*Asterias forbesi*	0.06 ± 0.02 (20)	0.16 ± 0.04 (28)
Brachyurans	*Cancer irroratus*	0.12 ± 0.52 (3)	0.07 ± 0.05 (13)
	Cancer borealis	0.11 ± 0.07 (10)	0.21 ± 0.09 (13)
	Carcinus maenas	0.35 ± 0.07 (6)	0.31 ± 0.09 (7)

B. Results of Student-Newman-Keuls (SNK) *a posteriori* test for multiple comparisons among mean predator feeding rates with unequal sample sizes

Species rank	Mean feeding rate ($\bar{x}$)	Standard deviation (S)	Sample size (n)	Rank and species				
				1 *Cancer irroratus*	2 *Thais lapillus*	3 *Asterias forbesi*	4 *Cancer borealis*	5 *Carcinus maenas*
1	0.08	0.10	16	–				
2	0.09	0.06	21	0.01^{ns}	–			
3	0.16	0.10	28	0.08*	0.07**	–		
4	0.21	0.15	13	0.13**	0.12**	0.05^{ns}	–	
5	0.33	0.09	13	0.25**	0.24**	0.17**	0.12**	–

Data in matrix are differences between row and column means. NS = not significant; * = $0.01 < P < 0.05$, ** = $P < 0.01$. All are canopy feeding rates except for *C. irroratus* and *C. maenas* which are summed over canopy and no canopy rates

Table 14. Estimated maximum and minimum number and percent of mussels removed/m² during the active season by each predator species in the low zone at the four protected sites.[a] *Cancer irroratus* is omitted from the table since it is most characteristic of exposed shores

Predators	Area							
	Chamberlain		Little Brewster Cove		Grindstone Neck		Canoe Beach Cove	
	No.	%	No.	%	No.	%	No.	%
Thais lapillus								
maximum	838	7.1	418	6.1	2,373	71.4	105	0.6
maximum	2,103	5.2	4,757	23.6	14,135	83.4	196	0.8
Asterias spp.[b]								
minimum	10,719	91.1	1,247	18.1	848	25.5	2,495	14.5
maximum	37,715	94.0	8,514	42.3	2,678	15.8	4,950	20.3
Cancer borealis								
minimum	121	1.0	52	0.8	32	1.0	105	0.6
maximum	183	0.5	79	0.4	49	0.3	158	0.6
Carcinus maenas								
minimum	91	0.8	5,158	75.0	72	2.2	14,535	84.3
maximum	119	0.3	6,778	33.7	95	0.6	19,101	78.3
Total								
minimum	11,769		6,875		3,325		17,240	
maximum	40,120		20,128		16,957		24,405	

[a] Data used are minimum and maximum feeding rates (Table 12), minimum and maximum predator density where available (Table 3) and active seasons of either 153 (Maine) or 198 days (Massachusetts; see text)

[b] *Asterias forbesi* plus *A. vulgaris* densities. Feeding rate of *A. vulgaris* is assumed to = that of *A. forbesi*

Table 15. Estimates of mussel production and an index of predator impact

Characteristic	Area			
	Chamberlain	Little Brewster Cove	Grindstone Neck	Canoe Beach Cove
1. *Mytilus edulis* density (ave. no./m²)[a]	12,779	5,385	18,110	440
2. *Mytilus edulis* recruitment per mo. (May–October; ave. no./m²)[b]	44,800	34,100	101,500	22,700
3. *Mytilus* abundance index (= 1 + 2)	57,579	39,485	119,610	23,140
4. Total predator impact index[c]	0.204 to 0.697	0.174 to 0.510	0.028 to 0.142	0.745 to 1.055

[a] Average mussel density estimated in summer transects taken in the low zone at each area. If summer and autumn data are used (from Table 2 in Lubchenco and Menge 1978), similar results are obtained

[b] Recruitment data obtained as indicated in text and Menge 1978b

[c] Index = total number mussels eaten (Table 14) divided by mussel abundance index (row 3, this table)

most important. Estimates of species effects can vary considerably. For example, at Little Brewster Cove, the range in estimates of percent mussels removed varies 2.2 × (*Carcinus*) to 3.9 × (*Thais*). Further, at this site, the dominant predator in minimum estimates is *Carcinus* while in maximum estimates *Asterias* spp. is dominant.

Estimates of number of mussels removed (Table 14) range widely when variations in density and feeding rate are incorporated. In one case, minimum and maximum estimates vary by an order of magnitude (e.g., *Thais* at Little Brewster Cove) and other estimates vary 2 to 8 fold (Table 14). Much of this is due to density variations (Table 3) but feeding rates also often differ by as much as 2X (Table 12).

Predation rates (Table 14) were compared with an index of *Mytilus* abundance to derive the index of predator impact. The index of *Mytilus* abundance was taken as the sum of recruitment and density. The index of predator impact = total mussels eaten (Table 14) divided by the *Mytilus* abundance index (Table 15). Note that *Mytilus* abundance varies between sites by 5X. Such variation undoubtedly explains part of the inverse relationship between predation intensity and predator biomass (Fig. 2). That is, predator impact will vary in part with prey production (Table 15). I emphasize again that these data are probably inaccurate estimates of absolute predation rates and *Mytilus* abundance in the field. They indicate only relative differences in predator impact and prey availability among sites.
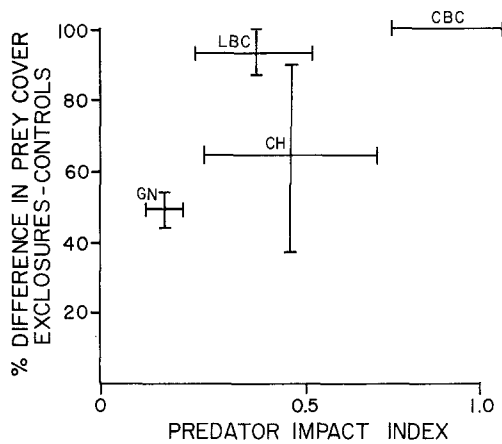
Fig. 4. Relation between the predator impact index (see text) and predation intensity (see caption to Fig. 2). The bars connect maximum and minimum values of the predator impact index and predation intensity at each site

A plot of total predator impact against predation intensity (Fig. 4) indicates that when predator type, number of species of each type, predator density and prey production are considered, predation intensity is positively (though not significantly) related to the index of predator impact (Fig. 4; predation intensity [arcsine transformed] = 51.1 ± 33.7 total impact index; $r = 0.51$; $n = 14$, $P > 0.05$; each combination of maximum and minimum estimates was used in the calculation). This result is encouraging given the derived nature of this index.

The importance of one further factor, interactions among the predator species, cannot be determined from these experiments since feeding rates were calculated using isolated individuals. Some predators prey on others (crabs on seastars and *Thais*, seastars on *Thais*; Lubchenco and Menge 1978; Menge 1979, personal observations), and some may compete (possibly crabs; these seastars do not seem to compete, see Menge 1979). However, the effects of these interactions would have to be elucidated experimentally using either controlled removals of single species, species pairs, etc., or estimating feeding rates of two species together as well as separately. Synergistic interactions could also be important. Finally, availability of alternative prey and differing suites of predator-prey preferences may also affect these interpretations. The importance of these details could only be determined with further work. Despite these potential effects, my experiments suggest that a clear understanding of the relationship between predation intensity and community organization will depend on efforts to evaluate the relative importance of the various components of predation intensity.

Discussion

Predation intensity in the low zone of New England

Previous studies in the mid zone of New England suggested that, as in other communities (e.g., Paine 1966, 1969a, b, 1971, 1974, 1976; Dayton 1971) though other predator species occur in the system, community structure is primarily a function of a single ("keystone") predator species *Thais lapillus* (Menge 1976, 1978b, 1982b). In the low zone, the similar predator effects observed at all wave-protected

sites (Lubchenco and Menge 1978) seem to have a more complex explanation (Table 14). Starfish evidently dominate at Chamberlain, *Thais* at Grindstone Neck, *Carcinus* at Canoe Beach Cove and all three predator types at Little Brewster Cove. Thus, a single but different predator appears most important at each of three sites. At the fourth site, the entire predator guild apparently controls mussel and barnacle abundance. Unlike temperate rocky intertidal communities studied previously, the low zone in New Endland has a guild of predators, each of which may be a "keystone" predator. In this respect this community seems more similar to that on tropical rocky intertidal shores on the Pacific coast of Panama, where occurs a complex assemblage of controlling herbivores and predators (Menge and Lubchenco 1981; Menge et al. unpublished manuscript, Gaines 1982).

Predation intensity in the low zone of New England seems dependent on variation of at least four predator characteristics, here termed the components of predation intensity. These range over four levels of complexity: individuals (e.g., among phenotypes, in different microhabitats), populations (e.g. density, size or age structure), species and types of predator. These factors vary in importance. For example, feeding rates (e.g., Table 12) between predator types range greatly from four (*Thais* vs. *Asterias* spp.) to 25-fold (*Thais* vs. *Carcinus*). Differences between morphologically similar species can be almost as great (e.g., *Carcinus* feeds 3.9 × faster than *C. borealis*). Intraspecific variations among these species (in canopy vs. no-canopy rates) vary less, from 1.3 (*Carcinus*) to 2.0 (*Asterias* spp.). Other factors such as predator size structure, interspecific interactions, prey productivity, and physical differences not correlated with wave shock or desiccation undoubtedly also have effects on predation intensity. Assessment of their respective importances will require additional research.

Predation intensity and community organization

Dissection of relative contributions of these factors seems important for further development of community organization theory. Community theory holds that species diversity (S = richness or H') is related to predation (and disturbance) intensity in at least one and maybe two ways (see Lubchenco and Gaines 1981 for a recent summary). Most commonly observed is a "hump-shaped" or quadratic curve (i.e., high diversity at intermediate intensities, low diversity at low and high intensities), although an inverse relationship is sometimes found. In both trophically simple and complex communities, predator manipulations can reveal the relationship between diversity and predation intensity. When consumers are excluded one of four diversity responses is observed. First, no change indicates that predators are ineffective (e.g., Menge 1976; Paine 1980). Second, a decline in diversity (e.g., Paine 1966, 1971, 1974; Menge 1976; Russ 1980; Peterson 1979a; McCauley and Briand 1979; Day 1977), indicates that predators normally maintain high diversity. Such declines are usually due to the expression of competitive dominance by one or two species which are normally held in check by the predator. Third, an increase in diversity (e.g., Addicott 1974; Lubchenco 1978; Reise 1977; Peterson 1979b; Day 1977; Virnstein 1977; Woodin 1981) suggests predation is very intense and maintains low diversity. Prey coexisting with predators are predator-resistant, occur in refuges or are highly opportunistic. Fourth,

Appendix

Best fit general linear regression model equations for feeding rates in mg/h of *Thais lapillus* (Tl) *Asterias forbesi* (Af) and in mg g^{-1} h^{-1} for three crab species *Cancer irroratus*, *C. borealis*, and *Carcinus maenas*

Species	Linear regression model	F	d.f.	P	r^2
Thais lapillus	$Y_{Tl} = 0.063 - 0.036X_1 - 0.027X_2 - 0.042\ X_3 + 0.028X_4 + 0.036X_5 - 0.019X_6 + 0.013X_7$ [a]	8.85	7,163	$\ll 0.0001$	0.28
Asterias forbesi	$Y_{Af} = 0.099 + 0.065X_1$ [b]	17.10	1, 87	$\ll 0.0001$	0.16
crabs	$Y_{crabs} = 1.33 - 0.025X_1 - 0.16\,{}^{c}X_2$	19.09	2, 48	$\ll 0.00005$	0.41

[a] X_1 = month (June or July), X_2 = snail phenotype (exposed or protected), X_3 = wave exposure (exposed or protected), X_4 = canopy × month, X_5 = snail phenotype × wave exposure, X_6 = canopy × month × snail phenotype, X_7 = canopy × month × snail phenotype × wave exposure

[b] X_1 = canopy (present or absent)

[c] X_1 = *Cancer irroratus* (present or absent), X_2 = *Cancer borealis* (present or absent); *Carcinus maenas* feeding rate is estimated when X_1 and $X_2 = 0$

diversity may first increase due to successful invasions and increases in abundance by prey and then decrease due to competitive exclusion (e.g., Paine and Vadas 1969; Lubchenco 1978). Thus, predation intensity varies widely in communities differing greatly in complexity.

Clearly, insight on the factors affecting predation intensity must precede a fuller understanding of the role of this factor in maintaining diversity. In particular, why are some trophically complex systems characterized by high diversity at the highest levels of predation intensity (e.g., rocky intertidal communities in the Pacific Northwest; Paine 1980), while others are held at low diversity at the highest levels of predation intensity (e.g., a rocky intertidal community in the Bay of Panama; Menge et al. unpublished data)? What factors limit the intensity of predation that can be reached in a given system? I suggest that different levels of diversity observed within and among communities structured by predation and biotic disturbance represent equilibria. These are set by the interaction between factors enhancing predation intensity (e.g., factors allowing greater densities or sizes, invasion and persistence of more effective predator types, etc.) and factors inhibiting it (e.g. environmental variation or harshness, competition among predators, etc.). For example, in the mid zone of New England, *Thais lapillus* is evidently the only functionally important predator though others are present (Menge 1976, 1978a, b, 1982b; but see Edwards et al. 1982). In the low zone, *Thais* is joined by starfishes and crabs (and possibly fish) as functionally important predators (Lubchenco and Menge 1978, this paper). Why aren't crabs and seastars more important in the mid zone? The experiments in this paper suggest that environmental factors such as wave shock and desiccation have important inhibitory effects on feeding rates (and survival!) of these predators (Tables 1, 6–11). Hence, in this rocky intertidal habitat, predation intensity seems dependent on environmental constraints. Further, predation intensity appears differentially affected by these constraints. As environmental conditions worsen (e.g., desiccation increases with an increase in tidal height), *Cancer borealis* and *Asterias* spp. are probably the first predator species and types to become ineffective predators (Table 1). Further levels of harshness (e.g., increase in wave shock) reduce the effectiveness of *Carcinus* and *Thais* (Tables 5, 10, Fig. 3; Menge 1976, 1978a).

Similar patterns occur in other communities. For example, Menge and Menge (1974) showed that prey inges-

tion rates/g for the seastars *Pisaster ochraceus* and *Leptasterias hexactis* (west coast of North America) differ by nearly an order of magnitude. In the same region, J. Quinn (personal communication) finds that *Thais* spp. feeding rates vary along a gradient of wave exposure. Further, the *Pisaster*-determined lower limit of mussels on these shores (Paine 1974) is lower on more exposed shores than on more protected ones in both Washington (e.g., Dayton 1971) and Oregon (B.A. Menge personal observations). This suggests effectiveness of *Pisaster* predation may decline with increased wave exposure. Also in Oregon, Gaines (1982) finds that qualitative differences in foraging among a guild of taxonomically diverse lower intertidal herbivores leads to important differences in algal species composition and abundance. In England, Seed (1969) found that variations in feeding rates similar to those reported here occurred among *Thais lapillus*, *Asterias rubens* and two crab species. In intertidal (Woodin 1981) and subtidal soft sediment habitats (Virnstein 1977; Van Blaricom 1982), both quantitative and qualitative differences occur between species of controlling predators. Similar examples of major differences among species in a diverse predator guild having important effects on community organization are available in other aquatic habitats (e.g., Lynch 1979; Zaret 1981) and possibly terrestrial ones as well (e.g., Harper 1977).

I conclude that clear understanding of how consumers affect diversity, or more generally community structure, will depend on determining how different components of predation intensity are affected by various environmental constraints. The initial focus should probably be on inter-type differences, though other components should not be ignored.

Predation intensity and community stability

A final implication of these studies concerns the relationship between predation pressure and community stability. Some workers argue that a complex predator guild should help stabilize communities (e.g., Elton 1958; MacArthur 1955; DeAngelis 1975; Menge and Lubchenco 1981). Though theoretical considerations (e.g., May 1974; Pimm 1980) suggest otherwise, some empirical studies (e.g. this paper, Menge and Lubchenco 1981, in preparation) support the earlier view. Thus, if removal or natural reductions of one predator species leads to increases in one or more of the other species in the guild, the overall effect of predation

on the system may not change perceptibly. That is, the removal would probably not be noticed by a naive observer because the community response would be small. This should be particularly true in situations where predators were relatively equivalent in their actual or potential effect. On the other hand, in systems typified by a "keystone" predator, its removal should lead to clear, unmistakable community changes (e.g., Paine 1966, 1980; Pimm 1980). Thus, removals of different predator species and combinations of predator species may be the only means of determining whether or not a single species is the key to the organization of a system. Single species removals leading to either great changes or no changes do not necessarily mean that the single species is a "keystone" (since other single species removals may have the same effect) or that it has no effect (since its effect may be masked by other species in a predator guild), respectively. Although examples of both types of system evidently exist in nature (e.g. Paine 1971, 1974, 1980; Dayton 1971 vs. Menge and Lubchenco 1981, this paper), clear distinguishing characteristics between the two community types are lacking. I suggest that future foci should include identification of these characteristics and study of the dynamics of predation intensity.

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