Predation Intensity in a Rocky Intertidal Community

Relation between Predator Foraging Activity and Environmental Harshness

Bruce A. Menge

Department of Zoology, Oregon State University, Corvallis, OR 97331, USA

Summary. Knowledge of predation intensity and how and why it varies among communities appears to be a key to the understanding of community regulation. Along the rocky shores of New England, predation intensity in the mid intertidal zone appears to be low with exposure to severe wave shock, low desiccation stress, and a sparse cover of canopy algae, and high at areas protected from waves, with high desiccation potential and a dense cover of algae. As a result, predators at exposed headlands have no controlling influence on community structure, while at protected sites, they exert a strong and controlling effect on community structure.

Experimental-observational studies of the effects of wave shock and desiccation on survival, foraging range and activity of the primary predator in this community (*Thais lapillus*) indicate that:

(1) wave shock is a continuous and actual source of mortality at exposed sites but is relatively unimportant at protected sites;

(2) mortality rates from desiccation at protected sites are potentially high and greater than at exposed sites; however,

(3) actual desiccation stress is greatly reduced at protected sites by a dense algal canopy;

(4) mortality from desiccation is greater in the higher mid intertidal than in the lower mid intertidal.

Comparisons of activity patterns of *Thais* from April through November (these snails are usually active from May to early October) at an exposed and a protected site suggest snails at the former site restrict their active feeding to crevices while those at the latter site forage throughout the habitat. Field experiments support this hypothesis. Hence, differences in predator effectiveness at exposed and protected communities are probably due in part to the influence of wave shock. Exposed areas receive frequent severe wave shock in all seasons, even summer. Thus, the risk of being swept off the shore for snails foraging away from the shelter of a crevice at such areas is apparently great and exerts a strong selective force on foraging

range. The importance of waves as a selective agent is further reinforced by the fact that crevices are nearly barren of prey, while just a few cm beyond the limits of the crevice, prey occur in great abundance.

In contrast, at protected sites wave shock is never as severe as at exposed sites and is a relatively minor factor among several which might affect the foraging activity of a *Thais*. A major factor which varies among protected sites is the algal canopy. The influence of this factor is considered in a companion paper.

Introduction

That predation is important in regulating patterns of community structure has gained wide acceptance among ecologists (Paine, 1966, 1971, 1974, 1976; Dayton, 1971; Connell, 1975; MacArthur, 1972; Harper, 1969; Sprules, 1972; Dodson, 1970, 1974a, b; Janzen, 1970; Menge 1976a, b; Menge and Sutherland, 1976; Lubchenco, 1978). On both a local and geographical scale, the high diversity observed in communities in relatively benign habitats may in part be a function of the high effectiveness of predators in controlling their prey and preventing resource monopolization by a few species (Paine, 1966, 1974; Connell, 1975; Menge and Sutherland, 1976). At the other end of the scale, the typically low diversity in relatively harsh habitats may be in part a consequence of reduced predator effectiveness in such habitats, permitting a few prey species to dominate community structure and organization (Connell, 1975; Menge and Sutherland, 1976). This hypothesis thus postulates that effectiveness or intensity of predation is a key variable in understanding the regulation of community structure.

Predation intensity can be influenced by both (1) innate characteristics of predators (e.g. functional responses, switching, morphological constraints on feeding rates and types of prey that can be consumed; Holling, 1960; Murdoch, 1969; Murdoch and Oaten, 1975; Oaten and Murdoch, 1975a, b) and (2) the physical and biotic environment. Though some ecologists have devoted attention to innate characteristics of predators (see review in Murdoch and Oaten, 1975), little is known about how predation intensity is affected by variations in the environment. Hence, an important but heretofore neglected problem is to determine how predation intensity varies along gradients of environmental harshness in relation to extrinsic features of the environment (which may directly or indirectly alter predator activity, feeding rates, and prey capture) and intrinsic characteristics of predators.

It is well known that the physical environment may directly affect diversity and other aspects of structure in communities. This may occur through temporal heterogeneity (e.g. various physical disturbances, short-term, seasonal, annual or longer-term variations in the weather; Dayton, 1971; Loucks, 1970; Levin and Paine, 1974; Taylor, 1973; Wiens, 1974b; Osman, 1977) or spatial heterogeneity (e.g. Pianka, 1967; MacArthur and MacArthur, 1961; Kohn, 1967; Kohn and Leviten, 1976; Wiens, 1973, 1974a; Roth, 1976). However the indirect effect of such "extrinsic" factors on community structure through their influence

on biotic interactions, especially predator foraging and predation intensity, is poorly understood. Though certain types of temporal heterogeneity may inhibit predator activity (e.g. some predators in temperate areas are inactive in winter or during storms; Paine, 1966, 1969; Menge, 1972), the effect of this inhibition on predation intensity is not clear because the prey are influenced by the same factors, though maybe not to the same degree. For example, Connell (1971) has suggested that predators are more restricted by certain physical factors than are their prey.

Spatial heterogeneity (both biogenic and physical) can either increase predator effectiveness (by moderating a variable environment and thereby permitting longer periods of activity and by decreasing the predator's conspicuousness) or decrease effectiveness (by impeding prey capture or by providing refugia for prey; e.g. see Ware, 1972; Huffaker, 1958). However, data on these effects are scarce.

In research reported earlier (Menge, 1976a, b), I examined the relative importance of competition and predation in controlling community structure at six rocky intertidal areas in northern New England. These areas differed in two major physical characteristics (wave shock and desiccation) and in several biological characteristics (including predator abundance, abundance of mussels (*Mytilus edulis*) and barnacles (*Balanus balanoides*), and canopy cover by fucoid algae; see summary in Table 1). A major implication of the results of this study (i.e. Menge, 1976b), was that predation intensity appeared to vary among the sites. This, and a companion paper (Menge, 1978), report the results of a series of experiments and observations undertaken to determine how extrinsic factors influence the effectiveness of the gastropod *Thais lapillus* in controlling its prey. In this paper, I consider the effect that two physical factors have on the differences in predation intensity observed between exposed and protected areas. Specifically, I examine (1) the effect of wave shock and desiccation on survival of *Thais*, and (2) the influence of wave shock on the foraging activity and range of *Thais*. The companion paper (Menge, 1978) considers the effect of several factors, but especially canopy cover, on feeding rates of this predator in an effort to explain variable predation intensities among protected sites.

Characteristics of the System

Both biological and physical characteristics of the study sites change along a wave exposure gradient. The characteristics of the six sites studied most intensively (Menge, 1976a, b; Lubchenco and Menge, 1978) are summarized in Table 1. Major trends include (1) wave shock is most severe at Pemaquid Point, Maine, and least severe at Canoe Beach Cove, Massachusetts; (2) potential desiccation is subjectively judged to be least at the most exposed areas and greatest at the least exposed areas, (3) the more protected areas have an intermediate-to-dense canopy cover of fucoid algae while the exposed areas have a sparse canopy cover, and (4) predator density varies considerably between areas (Table 1). The biotic factor controlling distribution, abundance and diversity at each area is listed in the last column of Table 1 and was determined

Table 1. Summary of pertinent physical characteristics, community structural patterns, and controlling factors in the mid intertidal zone of six New England rocky intertidal communities

Study site	Physical environment[a]		Ex-posure index[b]	Canopy cover %	Cover of: mussels / barnacles	*Thais* density ($\#/m^2$)	Controlling biotic factor (mid and low intertidal)
	Wave shock	Des-iccation intensity					
Pemaquid Point	Severe, frequent, direct	Low	7.43	0–10 (*Fucus distichus*)	$\sim 90\%$ / $\sim 3\%$	16–80	Interspecific competition
Little Brewster Point	Severe, frequent, direct	Low	2.44	(no data-similar to Pemaquid Point)	(no data-similar to Pemaquid Point)	(no data-similar to Pemaquid Point)	Interspecific competition
Chamber-lain	Often severe, frequent, in-direct (lee of headland)	Inter-mediate	1.58	30–85 (*F. dis-tichus*)	$\sim 70\%$ / $\sim 5\%$	36–152 (max.= 436 if juveniles included)	Predation
Little Brewster Cove	Occasionally severe, indirect (lee of island)	Fairly high	1.20	15–30 (*F. vesicu-losus* and *Ascophyl-lum*	$\sim 20\%$ / $\sim 20\%$	72–156	Predation
Grind-stone Neck	Usually mod-erate, infre-quently severe, indirect (lee of island)	Inter-mediate infre-quently severe	0.56	65–90 (*F. ves-iculosus*)	$\sim 20\%$ / $\sim 5\%$	108–456 (max.= 1056 if juveniles included)	Predation
Canoe Beach Cove	Minor, occas-ionally mod-erate, indirect (protected cove)	Frequently severe	0	85–95 (*Asco-phyllum*)	$\sim 5\%$ / $\sim 5\%$	9–32	Predation

[a]   Based on personal observations, exposure indices, and field experiments on survival of *Thais* under variable desiccation stress. Desiccation stress is probably greatest in summer

[b]   An index based on the loss rate of cages used in experiments. See Menge (1976b) for further explanation

from experiments reported earlier (Menge and Sutherland, 1976; Menge 1976a, b; Lubchenco and Menge, 1978). The main pattern of interest here is that, though predators are present at the most exposed areas, they have no controlling influence on their prey at these areas. Hence it would seem that predation intensity is not a simple function of density; i.e., predator abundance is presumably only one of a complex set of factors which determine predation intensity.

To investigate the relationship between predator density and predation intensity along this wave exposure gradient, experiments on predator survival, feeding rates and foraging range were initiated at three sites located at the Marine
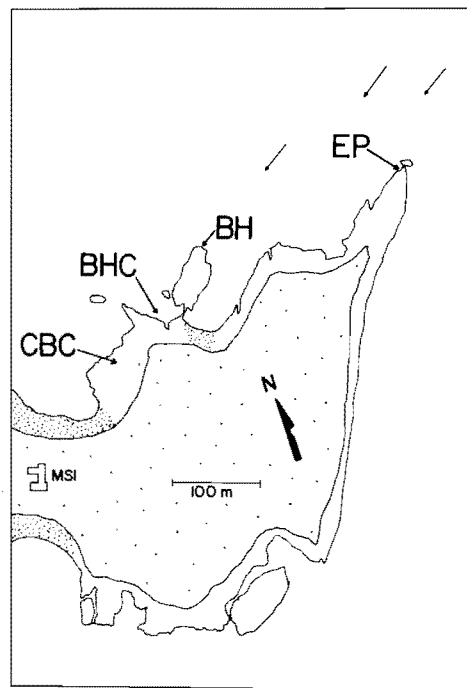
Fig. 1. Sketch of the study areas at Nahant, Massachusetts. *Dense stipple* = gravel/sand beaches; *sparse stipple* = land. *EP* East Point; *BH* Bennett Head; *BHC* Bennett Head Cove; *CBC* Canoe Beach Cove. *MSI* is the Marine Science Institute of Northeastern University. Scale is approximate. *Arrows* indicate wind direction during nor-easters

Science Insitute, Northeastern University, Nahant, Massachusetts. The three Nahant sites were East Point, an exposed headland; Bennett Head Cove, moderately exposed to waves; and Canoe Beach Cove, a protected site (Fig. 1). East Point is similar to Pemaquid Point and Little Brewster Point (Table 1) and is characterized during the summer and autumn by a dense cover (about 90–100%) of barnacles and mussels, little (about 10%) unoccupied primary space, and a very sparse cover (about 5%) of the fucoid alga *Fucus distichus*. Bennett Head Cove is similar to Chamberlain, Little Brewster Cove and Grindstone Neck and has an intermediate cover (about 50%) of barnacles and mussels, much unoccupied primary space (about 50%), and a fairly dense cover (50–75%) of *Fucus vesiculosus* and *F. distichus*. Canoe Beach Cove has a low total cover (about 10%) of barnacles and mussels, much unoccupied primary space (about 90%) and a dense canopy (about 85–95%) of the fucoid *Ascophyllum nodosum*.

Field experiments on the foraging range of *Thais* were done at an exposed site (Pemaquid Point) and at a relatively protected site (Little Brewster Cove).

Potential Effects of Wave Shock and Desiccation on Survival of *Thais*

Wave shock and desiccation are considered by many intertidal workers to be the most significant sources of mortality from physical factors for most intertidal organisms (e.g. Lewis, 1964; Kensler, 1967; Dayton, 1971; Levin and Paine, 1974; Connell, 1961 b, 1970; Glynn, 1968; Menge 1976b; Harger,

1970; Harger and Landenberger, 1971). As Dayton (1971) has pointed out, wave shock and desiccation are probably inversely correlated with each other, since if an area is frequently swept by waves, it is unlikely to experience severe desiccation.

Ideally, to provide a convincing case that *Thais* foraging activity is affected in an important way by waves, one should investigate its tolerance limits to various physical factors including wave shock and desiccation. I have not done this, but do have evidence that both wave shock and desiccation are potentially major sources of mortality for *Thais*. This evidence comes from the fate of snails used in feeding rate experiments (described in more detail in Menge, 1978). In these experiments, groups of *Thais* were held with prey in $10 \times 10 \times 5$ cm cages in several microhabitats (substrata either protected by a canopy, by crevices, or unprotected) at selected sites within their normal range along the vertical tidal gradient and along the wave exposure gradient. The experiments were usually run from 3 to 7 days, and provided data on survival of both *Thais* and the mussels that were provided as prey. The experiments were done from late July to late September, 1975.

The mortality of *Thais* in these experiments and several weather characteristics (Anonymous, 1975) over this time period are plotted in Figure 2. Weather characteristics given include daily records (for Boston) of (1) mean wind velocity and prevailing direction, (2) percent of the time the sun was not obscured by clouds, and (3) maximum and minimum air temperatures (°F). Taken together, these factors can be used as a rough index to indicate both stormy periods when wave shock would be expected to be relatively high and periods of potential heat and desiccation stress. For example, a nor-easter occurred on August 6–8, 1975. This is reflected by a relatively high northeasterly wind (Fig. 2A), low insolation (high cloud cover; Fig. 2B), and a sudden onset of relatively cool temperatures (Fig. 2C). Similarly, a period of extremely warm temperatures occurred from July 30 to August 2 (Fig. 2C).

Mortality of *Thais* (presumably from wave shock or desiccation or both) in these microhabitats in each of four different sites is shown in Figure 2D–G. Crevice microhabitats were not included at protected sites because subjectively it appeared that the main microhabitat variable was presence or absence of a canopy. A *Fucus* and an *Ascophyllum* canopy were examined separately because the cover of the former appeared more patchy over space and time than did the latter (e.g. see Menge, 1976b).

Several interesting patterns emerge from this analysis. First, and most obviously, snails in the higher part of their vertical range seem to face a greater risk of mortality from these physical factors ($\chi^2 = 121.27$, 1 df, $P < 0.005$; compare Fig. 2D and F to E and G). Second, snails at protected sites seem to face a greater risk from desiccation than do those at exposed areas. This is suggested by the high mortality in relatively harsh microhabitats (0 in Fig. 2D and F; 18.9% mortality) compared to more moderate microhabitats (F and A in Fig. 2F and G; 3.6% mortality) at protected areas ($\chi^2 = 129.09$, 1 df, $P < 0.005$) vs. the similar mortalities observed in 0 (4.0%) and C and F (3.6%) microhabitats at exposed areas (Fig. 2D and E; $\chi^2 = 0.21$, 1 df, $P > 0.5$). Third, the risk of
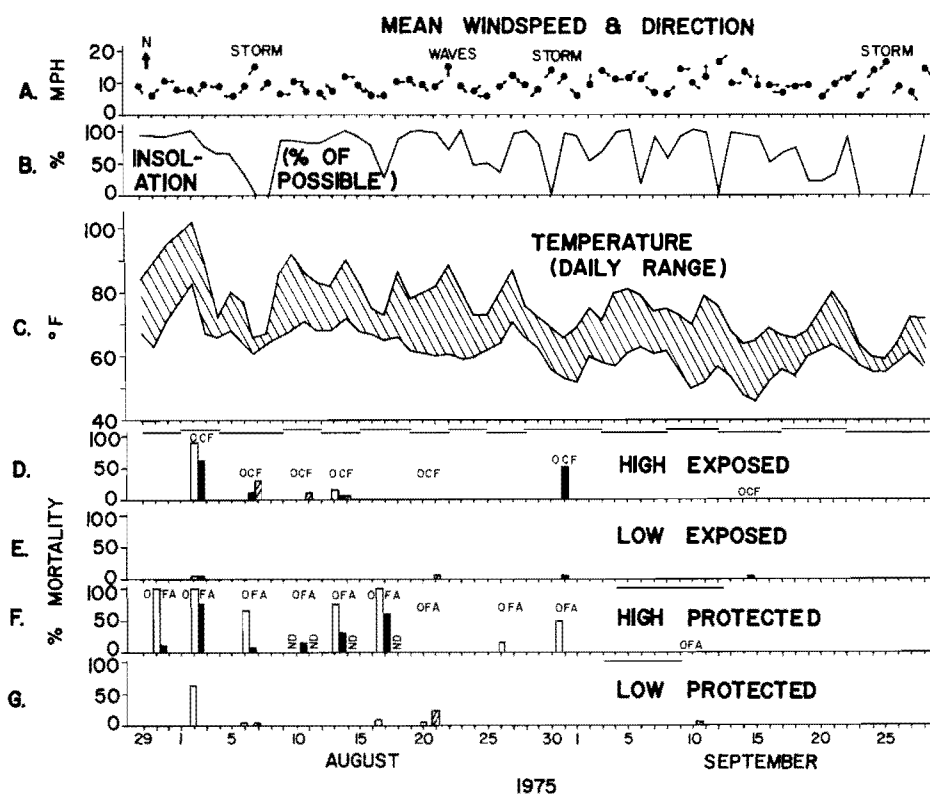
Fig. 2 A–G. Comparison of mortality of *Thais* under different experimental conditions (see text) and contemporary weather patterns. **A** Mean daily direction and velocity of wind. **B** Daily percent of possible sunlight (=#h of sun radiation/#h of daylight). **C** Daily maximum and minimum air temperatures. **D–G** Percent of *Thais* (*n* per bar = 20 snails) dying in each of four sites. Thick horizontal lines above **D–G** indicate time period of each experiment. Code for histograms refers to three microhabitats within each site; *0* no protection, *C* near a crevice, *F* covered by a canopy of *Fucus* spp., *A* covered by a canopy of *Ascophyllum*. If no histogram is shown for a particular experiment, no mortality occurred. *ND* no data available

mortality from desiccation is greatest during the hottest parts of the time period investigated. Thus, more mortality attributable to desiccation occurred in late July and August (10.1%) than in September (1.7%; $\chi^2 = 110.2$, 1 df, $P < 0.005$). Finally, though this is not clearly indicated by Fig. 2, mortality and loss of snails from the more benign microhabitats (crevices and canopy covered) during storms was greater at the exposed sites (15.9%) than at the protected sites (3.0%; $\chi^2 = 18.44$, 1 df, $P < 0.005$). These were the only periods when *Thais* shell fragments were found in cages (as opposed to whole shells with moribund or rotting snails inside).

In summary, it seems clear that both desiccation and wave shock are potentially serious sources of mortality for *Thais*. Hence, one would expect to find that the activities of this snail are patterned to minimize these sources of risk.
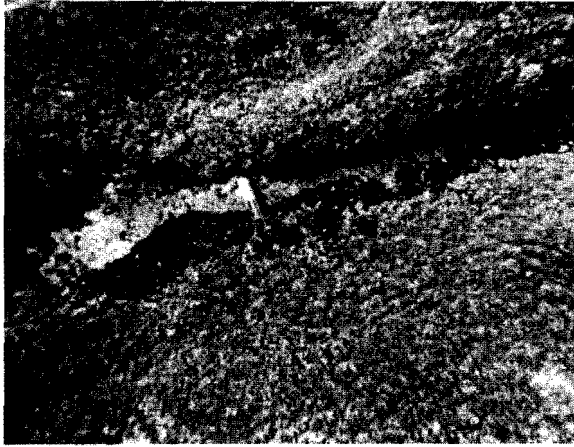
Fig. 3. Photo of the "bare zone" (spanned by the ruler) characteristic of crevices occupied by
Thais (not visible in the photo) at Pemaquid Point. The dark band under the end of the ruler
is *Mytilus*. The remainder of the photo is covered by *Balanus*

Foraging Range of *Thais* in Relation to Wave Shock

Patterns of Abundance of Thais

Several observations suggest that the foraging activity and range of *Thais* are
strongly influenced by wave shock. First, at exposed areas, the only areas which
are consistently free of mussels and barnacles are most of the crevices deeper
than about 10 cm (e.g. Fig. 3). That this "bare zone" of free space is maintained
by *Thais* is supported by the observations that such crevices harbor dense
populations of this snail, and crevices which have no *Thais*, have no free space
and are dominated by *Mytilus*. Thus, patterns of space utilization in crevices
in the mid intertidal at Pemaquid Point are in some ways similar to the entire
mid intertidal zone at more protected areas (e.g., Menge and Sutherland, 1976;
Menge, 1976a, b).

A second observation suggesting that wave shock restricts *Thais* to crevices
at exposed areas but not at protected areas is that these snails remain concen-
trated in crevices at exposed areas during the period of feeding activity (May
to September). At protected areas, *Thais* forage actively over the entire study
site during this period (Table 2). At the exposed area (Pemaquid Point), *Thais*
are always considerably denser (2.2 to 94 times as dense) in and near crevices
(0 m) than they are away from crevices (1–2 m). The absence of snails from
any quadrats in April and the low densities in October and November (Table 2)
probably reflect the facts that the snails retreat so deep into crevices during
winter that they cannot be counted accurately and that waves often inhibit
sampling efforts. In contrast, at the more protected area (Grindstone Neck),
snails are completely inactive during late fall, winter and early spring (October
to early April) but forage actively over the mid and low intertidal in the warmer
months from late April to September or early October (Table 2). Thus, in

Table 2. Seasonal changes in *Thais* density at 0, 1, and 2 m from crevices at an exposed and a protected area during 1975

Study area	Distance from crevice (m)	*Thais* density (# /0.25 m²)							
		April	May	July	August	September	October		November
							adult	juv.[c]	
Pemaquid Point (exposed; canopy cover = 8–27%)[a]	0	0	94	190	90	156	11[b] (3.2)		23
	1	0	1	16	41	28	4.5[b] (2.7)		4
	2	0	2	36	26	13	2.5[b] (1.6)		0
Grindstone Neck (protected; canopy cover = 90–98%)[b]	0	189 (40.3)	8 (1.2)	32 (9.4)	11 (6.6)	16 (3.7)	14 (4)	5 (2.2)	—[d]
	1	55 (33.6)	43 (7.7)	43 (15.2)	29 (9.6)	22 (5.0)	11 (4.4)	7 (3)	—
	2	4 (2.7)	111 (35.7)	17 (12.2)	50 (8.9)	30 (7.2)	8 (3)	11 (3.3)	—
	3	2.5[a]	107 (36.7)	—	—	—	—	—	—

[a] *Thais* density is the average no. in two quadrats

[b] *Thais* density is the average of four quadrats. ± standard error is given in parentheses

[c] Density given as the number per 0.04 m² due to the great abundance of juvenile *Thais*

[d] Dash means no data available

April at Grindstone Neck, *Thais* were concentrated in crevices and scarce elsewhere. In May, these snails had left or were leaving the crevices (they actually leave in conspicuous "waves" when they are abundant as at Grindstone Neck) and remained scattered over the study site until September, when the adult snails retreated to crevices.

Interestingly, juvenile snails (those born during the summer) remain widely dispersed longer than do adults (Table 2), probably for several reasons. First, they are small (0.2–0.5 cm) and probably cannot move as fast. Second, their smallness probably increases the effective density of acceptable crevices or other types of shelter, since a crevice that is too small for a large snail may be large enough for a small snail. Third, adult *Thais* are size-selective predators (Connell, 1961a; Menge, unpublished data) and have virtually eliminated most large prey by September (Menge 1976b, unpublished data). However, since they pass up the small prey (e.g. barnacles ≤ 3 mm diameter, mussels ≤ 5 mm long), prey availability for juvenile *Thais* is still probably relatively great in early to mid autumn, and these snails evidently delay retreating to shelter somewhat longer than do the adult snails (Table 2). Of course, this apparent delay in returning to shelter may also be an adaptation to permit juveniles to grow as large as possible before overwintering.

Table 3. *Thais* density in relation to shelter from crevices. Data taken May through September 1975 (except for Little Brewster Cove which is May through October)[a]

Study area	Distance from crevice (m)	Algal canopy		% Cover[b]
		Absent (#*Thais*/ 0.25 m^2)	Present (#*Thais*/ 0.25 m^2)	
Pemaquid Point (exposed)	0	80.2 ± 9.9 (19)	132.4 ± 16.6 (8)	8.5 ± 1.6 (6)
	1	1.3 ± 0.7 (13)	21.6 ± 5.9 (8)	27.2 ± 2.7 (8)
	2	3.0 ± 3.0 (2)	19.2 ± 5.9 (8)	25.6 ± 5.7 (8)
	3	1.0 (1)	ND[c]	ND
Little Brewster Cove (relatively protected)	0	27.9 ± 8.8 (13)	8.1 ± 2.5 (10)	24.5 ± 6.0 (4)
	1	14.5 ± 9.8 (13)	5.0 ± 2.0 (10)	37.0 ± 14.7 (4)
	2	11.6 ± 5.6 (13)	3.0 ± 1.0 (10)	42.8 ± 3.1 (4)
Grindstone Neck (relatively protected)	0	ND	16.8 ± 3.6 (16)	98.0 ± 0.9 (4)
	1	ND	34.2 ± 5.1 (16)	96.0 ± 3.7 (4)
	2	ND	51.8 ± 12.8 (16)	90.5 ± 4.3 (4)
	3	ND	107.2 ± 36.7 (4)	ND

[a] Data are means ± one standard error. Numbers in parentheses are the number of quadrats sampled

[b] Canopy is *Fucus distichus* at Pemaquid Point, is a mixture of *Fucus vesiculosus* and *Ascophyllum nodosum* at Little Brewster Cove, is *F. vesiculosus* at Grindstone Neck

[c] ND = no data are available

The dispersion pattern of *Thais* also seems influenced by a cover of canopy-forming algae. Table 3 contrasts *Thais* densities (averaged over the warm months) at different study areas in the presence and absence of a canopy. At the exposed area (Pemaquid Point), *Thais* are 27 to 60 times denser in crevices than away from crevices when no canopy is present but are only about seven times denser in crevices when canopy cover (*Fucus distichus*; see Table 1) is about 25%. In contrast, at one protected area (Little Brewster Cove) average snail density in crevices is only 2 to 2.5 times greater than away from crevices, both with and without a canopy (cover ranges from 25 to 43%). Here *Thais* are less dense under a canopy than in the open (Table 2). This may indirectly reflect the "whiplash" effect fucoid algae have on barnacle abundance. A canopy

inhibits recruitment of barnacles by dislodging newly settled barnacle cyprids from the surface (Menge, 1976b; Dayton, 1971; Hatton, 1938; Southward, 1956; Lewis, 1964). This would reduce the abundance of prey for *Thais* under a canopy, but not in patches of space lacking a canopy. Hence, in such patches the resulting resource concentration (barnacles and mussels) evidently attracts the predatory *Thais*.

Finally, at another protected site with a dense snail population and a dense canopy (Grindstone Neck), *Thais* are actually densest away from crevices (Table 3). This suggests crevices at protected areas carry no attractions for *Thais* in the form of food or shelter during the warm months of the year.

Effect of Thais Predation at Varying Distances from Crevices

Though the above data strongly suggest that *Thais* rarely leave crevices at exposed areas, they do not preclude the possibility that these snails may leave a crevice, eat a barnacle or mussel, and return within a tide cycle. However, feeding rates given in Menge (1978) suggest this is unlikely. The most rapid average feeding rate obtained in these experiments was 13 h for an individual *Thais* to consume an individual mussel. This suggests that in general, a *Thais* would be unable to complete a feeding bout within one period of tidal submergence (about 6 h), and hence undetected "dashes" for prey by *Thais* at exposed areas are unlikely. A more likely hypothesis is that though densities of *Thais* are low away from crevices, the few that do leave crevices have a relatively greater per individual effect on prey abundance.

To test the effect of *Thais* at varying distances from crevices, I performed predator exclusion experiments at three distances from crevices at Pemaquid Point and Little Brewster Cove. Similar experiments were done at Grindstone Neck but barnacles failed to settle in 1975 at this area. Since mussel settlement and growth is partly dependent on a barnacle substratum (Menge, 1976b), mussels were not abundant either. Because of these problems, the Grindstone Neck experiments gave no results worth reporting.

The experiments were established at 0 m (actually technical difficulties allowed placement of cages no closer than about 10 cm of a crevice), 1 m, and (in most cases), 2 m distance from a crevice. The sites were selected so that no useful shelters were available nearby other than the main crevice. The basic experimental design has been described in detail elsewhere (e.g. Connell, 1961a; Dayton, 1971; Menge, 1976b). It includes a cage of stainless steel mesh to exclude all predators greater than about 2 mm in width, a roof or sideless cage to test for shading, and an unmanipulated control. No significant differences were detected between controls and roofs either in previous experiments in the mid intertidal (i.e. the shading effect of the mesh is not significant; Menge, 1976b) or in the experiments under discussion (analysis of variance on data transformed by the arcsin transformation; $P > 0.05$ for canopy-covered experiments, $P > 0.5$ for experiments not covered by a canopy). Hence, to simplify interpretation, I report results for controls and exclusions but not roofs. To further simplify presentation, I have lumped abundances (percent cover) of
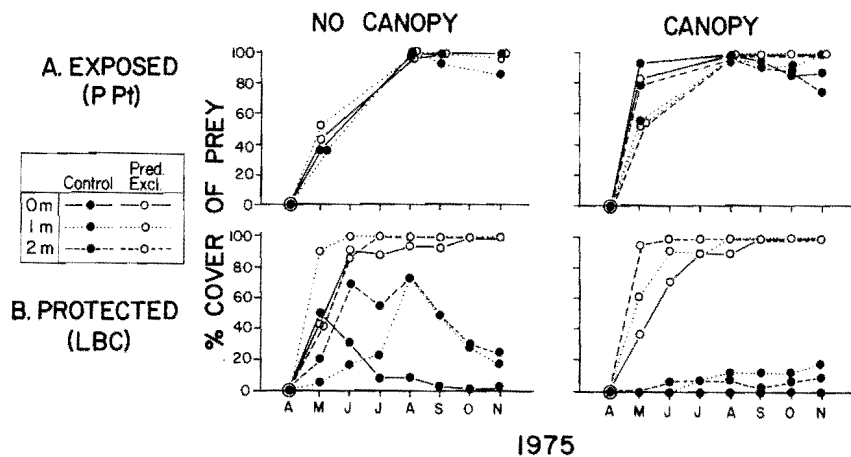
Fig. 4A and B. Effect of *Thais* predation at 0, 1, and 2 m from a crevice at an exposed site (*PPt* Pemaquid Point) and at a protected site (*LBC* Little Brewster Cove) with and without a canopy cover. Prey abundance is total percent cover of mussels and barnacles

Mytilus and *Balanus* together as total prey abundance. This is justified since *Thais* preys almost exclusively on these prey species and so far I have detected no strong differences in preference of *Thais* for either species (Menge, 1976b).

The results of the experiments basically support the notion that the effective foraging range of *Thais* is greatly reduced at exposed as compared to protected areas (Fig. 4). Regardless of whether or not a canopy was present, *Thais* had virtually no effect on prey abundance at Pemaquid Point (Fig. 4A). From mid-summer to November, cover of *Mytilus* and *Balanus* totalled nearly 100% in both controls and exclusions at all distances from the crevices. No significant differences were detected between control and exclusions in experiments with no canopy cover (anova, $P > 0.25$, df$= 1,6$) or those with canopy cover (anova, $P > 0.1$, df$= 1,4$).

In contrast, at the relatively protected Little Brewster Cove, results in controls and exclusions were very different (Fig. 4B). Where no canopy cover occurred, prey cover in controls was initially somewhat similar to that in exclusions. By June, prey abundance in controls was less than in exclusions. By November, when the experiments were terminated, percent cover of prey in all three exclusions was 100%, while in controls it ranged from 0 to 27% (Fig. 4B). The exclusion cage results at areas with a canopy cover present were nearly identical. In controls, prey cover was never as great as in experiments with no canopy, and final cover ranged from 0 to 19%. Differences between controls and exclusions in experiments both with and without a canopy are significant at $P < 0.001$ (anova, df$= 1,4$ in both cases).

These results support the hypothesis that the foraging range of *Thais* is drastically inhibited at wave-swept areas, probably because a snail experiences a great risk of being dislodged by high energy waves if it leaves the relative shelter of a surface irregularity like a crevice. That wave shock is relatively great at exposed areas even in the summer is supported both by the high

exposure index for such areas (Menge, 1976b; Table 1) and by the fact that even during summertime, exposed areas often cannot be sampled because of severe wave action. The lack of data for June and July 1975 at Pemaquid Point is a consequence of this sort of inaccessibility.

Judging by the width of the "bare" zone around crevices at Pemaquid Point (Fig. 3), the severity of this inhibition is considerable. These observations and the lack of any measurable effect of *Thais* in even the 0 m experiments thus seems to resolve one of the paradoxes listed earlier. The lack of influence of relatively dense populations of *Thais* on community structure in communities at exposed headlands (Menge, 1976b) is evidently a consequence of the severe restriction of the foraging range of this snail by the presumed high probability of being dislodged by waves.

Discussion

The hypothesis that the observed difference in the effectiveness of *Thais* in controlling prey at exposed and protected sites is due primarily to wave shock (Menge, 1976b) is supported by these experiments. Evidently, the populations of snails at exposed sites have different activity patterns from those at protected sites. Snails at exposed sites seem quite restricted in their foraging range, with most of them remaining in the shelter of crevices throughout the year. This is presumably because severe nor-easters may occur in any season in New England, including summer. For example, three nor-easters occurred during the experiments reported in Figure 2. Moreover, examination of weather records (Anon., 1965–1975) reveals that from 1965 to 1975, 28 storms occurred in autumn, 33 in winter, 31 in spring, and 11 in summer. There are thus fewer storms in summer, but they do occur. Personal observations indicate these can be very violent, and the weather data suggest the temporal occurrence and frequency of such storms is unpredictable.

On the other hand, foraging activity is clearly not restricted to crevices at protected sites (Fig. 4, Table 3). Here, *Thais* range widely over the intertidal from May to late September, and at some sites will even range into the high intertidal (e.g. on vertical walls or under a dense canopy; Menge, 1976b). Presumably, the probability of being washed off in a storm is greatly lessened at protected sites because wave energy is much lower at such sites even during storms and the dense algal canopy probably buffers the force of those few large waves striking protected areas. Why these snails retreat to shelter during the colder half of the year is not yet clear but is probably related to reduced food abundance or availability and the fact that during the severest winter storms, the force of waves washing over even the most protected areas can be considerable.

Though *Thais* at protected sites evidently devote little time and energy to coping with wave shock, it appears that an important potential source of mortality at such areas is desiccation (Fig. 2). However, this source of mortality would seem to be of minor importance as an actual mortality cause. Relatively few snails in cages placed under a canopy died in the experiments reported in Figure 2. The substrata under a canopy are always damp and relatively cool (personal observations), even on extremely hot days. Presumably then, the only occasions

when snails in protected areas would experience desiccation stress are when they happen to feed or become inactive in patches of substratum lacking a canopy. Such patchiness is relatively greater at areas with a *Fucus* canopy than it is at areas with an *Ascophyllum* canopy (e.g., Menge, 1976b; Table 1, column 5). Further, *Fucus* canopies tend to be less dense than *Ascophyllum* canopies because the former alga is usually a much shorter and less robust plant than the latter (personal observations). Taken together, these observations suggest that effective desiccation stress is less at *Ascophyllum*-dominated areas than at *Fucus*-dominated areas. This interpretation may explain why mortality of *Thais* was higher in cages under a *Fucus* canopy than in cages under an *Asophyllum* canopy (Fig. 2).

The differences in activity of *Thais* at exposed and protected areas could be either learned or genetic. Snails at exposed sites are phenotypically different from those at protected sites, having thinner shells and a smaller mean individual size (Moore, 1936; Osborne, 1977). However, though in Europe *Thais lapillus* are highly polymorphic at the chromosome level (Staiger, 1957), and would be amenable to studies of population genetics, the genetic basis of such phenotypic characteristics as behaviour, morphology, etc. is not known.

In conclusion, these results are consistent with the hypothesis that predation intensity is a function of environmental harshness (Connell, 1975; Menge and Sutherland, 1976). In the more harsh environment (exposed sites), *Thais* activity seems greatly restricted by the high probability of being washed off the rocks by severe wave activity through out the year. In more benign environments (protected sites), *Thais* activity seems little affected by waves. Rather, the algal canopy seems to exert an important effect on activity through its role in moderating desiccation and its relative patchiness. Thus one component of predation intensity (foraging activity) is apparently influenced by both wave action and the algal canopy (desiccation potential). The influence of these factors, especially the algal canopy on another component of predation intensity, individual feeding rates, will be considered in a subsequent paper (Menge, 1978).

References

Anonymous: Local climatological data for Boston, Mass. National Oceanic and Atmospheric Administration; Environmental Data Service (1965–1975)

Connell, J.H.: Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. Ecol. Monogr. **31**, 61–104 (1961a)

Connell, J.H.: The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology **42**, 710–723 (1961b)

Connell, J.H.: A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. Ecol. Monogr. **40**, 49–78 (1970)

Connell, J.H.: On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Proc. Advance. Stud. Inst., Dynamics Numbers Pop. **1970**, 298–312 (1971)

Connell, J.H.: Some mechanisms producing structure in natural communities. In: Ecology and evolution of communities (M.L. Cody, J.M. Diamond, eds.), pp. 460–490. Cambridge, Mass.: Harvard Univ. Press 1975

Dayton, P.K.: Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. **41**, 351–389 (1971)

Dayton, P.K.: Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecol. Monogr. **45**, 137–159 (1975)

Dodson, S.I.: Complementary feeding niches sustained by size-selective predation. Limnol. Oceanogr. **15**, 131–137 (1970)

Dodson, S.I.: Adaptive change in plankton morphology in response to size-selective predation: a new hypothesis of cyclomorphosis. Limnol. Oceanogr. **19**, 721–729 (1974a)

Dodson, S.I.: Zooplankton competition and predation: an experimental test of the size-efficiency hypothesis. Ecology **55**, 605–613 (1974b)

Glynn, P.W.: Mass mortalities of echinoids and other reef flat organisms coincident with midday, low water exposures in Puerto Rico. Mar. Biol. **1**, 226–243 (1968)

Harger, J.R.E.: The effect of wave impact on some aspects of the biology of sea mussels. The Veliger **12**, 401–414 (1970)

Harger, J.R.E., Landenberger, D.E.: The effect of storms as a density dependent mortality factor on populations of sea mussels. The Veliger **14**, 195–201 (1971)

Harper, J.L.: The role of predation in vegetational diversity. Brookhaven Symp. Biol. **22**, 48–61 (1969)

Hatton, H.: Essais de bionomie explicative sur quelques especes intercotidales d'algues et d'animaux. Ann. Inst. Monaco **17**, 241–348 (1938)

Huffaker, C.B.: Experimental studies on predation: dispersion factors and predator-prey oscillations. Hilgardia **27**, 343–383 (1958)

Janzen, D.H.: Herbivores and the number of tree species in tropical forests. Am. Natur. **104**, 501–528 (1970)

Kensler, C.B.: Desiccation resistance of intertidal crevice species as a factor in their zonation. J. Anim. Ecol. **36**, 391–406 (1967)

Kohn, A.J.: Environmental complexity and species diversity in the gastropod genus *Conus* on Indo-West Pacific reef platforms. Am. Natur. **101**, 251–260 (1967)

Kohn, A.J., Leviten, P.J.: Effect of habitat complexity on population density and species richness in tropical intertidal predatory gastropod assemblages. Oecologia (Berl.) **25**, 199–210 (1976)

Levin, S.A.,Paine, R.T.: Disturbance, patch formation, and community structure. Proc. Nat. Acad. Sci., U.S. **71**, 2744–2747 (1974)

Lewis, J.R.: The ecology of rocky shores, pp. 323. London: English Universities Press 1964

Loucks, O.L.: Evolution of diversity, efficiency, and community stability. Am. Zool. **10**, 17–25 (1970)

Lubchenco, J. (formerly Menge, J. Lubchenco): Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. Am. Natur. **112**, (in press, 1978)

Lubchenco, J., Menge, B.A.: Community development and persistence in a low rocky intertidal zone. Ecol. Monogr. (in press, 1978)

MacArthur, R.H.: Geographical ecology, 269 pp. New York: Harper and Row 1972

MacArthur, R.H., MacArthur, J.W.: On bird species diversity. Ecology **42**, 594–598 (1961)

Menge, B.A.: Foraging strategy of a starfish in relation to actual prey availability and environmental predictability. Ecol. Monogr. **42**, 25–50 (1972)

Menge, B.A.: Ecological implications of patterns of rocky intertidal community structure and behavior along an environmental gradient. In: Ecology of fouling communities (J.D. Costlow, ed.), pp. 155–180. Washington D.C.: Office of Naval Research Printing Office 1976a

Menge, B.A.: Organization of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. Ecol. Monogr. **46**, 355–393 (1976b)

Menge, B.A.: Predation intensity in a rocky intertidal community. Effect of an algal canopy, wave action and desiccation on predator feeding rates. Oecologia (Berl.) **34**, 17–35 (1978)

Menge, B.A., Sutherland, J.P.: Species diversity gradients: synthesis of roles of predation, competition, and temporal heterogeneity. Am. Natur. **110**, 351–369 (1976)

Menge, J.L.: Effect of herbivores on community structure of the New England rocky intertidal region: distribution, abundance and diversity of algae. Ph. D. Thesis, Harvard University, Cambridge, Mass. (1975)

Moore, H.B.: The biology of *Purpura lapillus*. Part 1. Shell variation in relation to the environment. J. Mar. Biol. Assoc. U.K. **21**, 61–89 (1936)

Murdoch, W.W.: Switching in general predators: experiments on predator specificity and stability of prey populations. Ecol. Monogr. **39**, 335–354 (1969)

Murdoch, W.W., Oaten, A.: Predation and population stability. Adv. Ecol. Res. **9**, 1–131 (1975)

Oaten, A., Murdoch, W.W.: Functional response and stability in predator-pray systems. Am. Natur. **109**, 289–298 (1975a)

Oaten, A., Murdoch, W.W.: Switching, functional response, and stability in predator-prey systems. Am. Natur. **109**, 299–318 (1975b)

Osborne, C.: Ecology of shell color polyphenism in *Thais lapillus*. Ph. D. Thesis, Yale University, New Haven, Conn., 337 pp. (1977)

Osman, R.W.: The establishment and development of a marine epifaunal community. Ecol. Monogr. **47**, 37–63 (1977)

Paine, R.T.: Food web complexity and species diversity. Am. Natur. **100**, 65–75 (1966)

Paine, R.T.: The *Pisaster-Tegula* interaction: prey patches, predator food preference and intertidal community structure. Ecology **50**, 950–961 (1969)

Paine, R.T.: A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. Ecology **52**, 1096–1106 (1971)

Paine, R.T.: Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia (Berl.) **15**, 93–120 (1974)

Paine, R.T.: Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. Ecology **57**, 858–873 (1976)

Pianka, E.R.: On lizard species diversity: North American flatland deserts. Ecology **48**, 333–351 (1967)

Roth, R.R.: Spatial heterogeneity and bird species diversity. Ecology **57**, 773–782 (1976)

Southward, A.J.: The population balance between limpets and seaweeds on wave-beaten rocky shores. Rep. Mar. Biol. Sta. Pt. Erin, No. **8**, 20–29 (1956)

Staiger, H.: Genetical and morphological variation in *Purpura lapillus* with respect to local and regional differentiation of population groups. Annee Biol. **33**, 251–258 (1957)

Sprules, W.G.: Effects of size-selective predation and food competition on high altitude zooplankton communities. Ecology **53**, 375–386 (1972)

Taylor, D.L.: Some ecological implications of forest fire control in Yellowstone National Park, Wyoming. Ecology **54**, 1394–1396 (1973)

Ware, D.M.: Predation by rainbow trout (*Salmo gairdneri*): the influence of hunger, prey density, and prey size. J. Fish. Res. Board Canada **29**, 1193–1201 (1972)

Wiens, J.A.: Pattern and process in grassland bird communities. Ecol. Monogr. **43**, 237–270 (1973)

Wiens, J.A.: Habitat heterogeneity and avian community structure in North American grasslands. Am. Midl. Nat. **91**, 195–213 (1974a)

Wiens, J.A.: Climatic instability and the "ecological saturation" of bird communities in North American grasslands. The Condor **76**, 385–400 (1974b)