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THE PERFORMANCE OF AN INTERTIDAL PREDATOR *THAIS LAPILLUS*, IN RELATION TO STRUCTURAL HETEROGENEITY

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SUMMARY

(1) The influence of substratum heterogeneity on the performance (prey selection, predation rate, protection against high temperatures, desiccation and wave action, growth rates, substratum preference) of the northern Atlantic intertidal predator, *Thais (Nucella) lapillus* L. was examined experimentally in the field.

(2) Dogwhelks had higher growth rates on heterogeneous than on homogeneous surfaces.

(3) Barnacles were of higher quality as prey and varied less in abundance on heterogeneous than on homogeneous substrata.

(4) Dogwhelks were better protected against wave action on heterogeneous than on homogeneous substrata.

(5) Dogwhelks strongly preferred heterogeneous over homogeneous substrata.

(6) Dogwhelk performance was higher on heterogeneous than on homogeneous substrata.

INTRODUCTION

Structural heterogeneity (i.e. the surface topography of biotic and abiotic solid structures) can take many forms: for example, the density of plants in ponds (Gilinski 1984; Main 1987), the topography of intertidal substrata (Kohn & Leviten 1976; Bergeron & Bourget 1986; Bourget 1988) and the number of foliage layers in forests (MacArthur 1965). Structural heterogeneity has previously been referred to as structural complexity, habitat fragmentation, habitat complexity and spatial heterogeneity. The term spatial heterogeneity has also been used to characterize animal and plant distribution patterns (Smith 1972; Holt 1984) and population demographic characteristics (Kern & Bell 1984).

Not all studies of structural heterogeneity have detected a relation between heterogeneity measurements and biological features. For instance, Bell & Coen (1982) found no relationship between biologically induced structural heterogeneity of sand flats and abundance of invertebrates. But increasing heterogeneity has been shown to cause increased species diversity (MacArthur 1965; Pianka 1966; Kohn & Leviten 1976), abundance (Kohn & Leviten 1976; Woodin 1981) and predation efficiency (Brock 1979; Crowder & Cooper 1982).

In the rocky intertidal zone, substratum topography influences diversity (Kohn & Leviten 1976; Spight 1977; Russ 1980; Menge, Lubchenco & Ashkenas 1985), abundance (Emson & Faller-Fritsch 1976; Kohn & Leviten 1976; Bergeron & Bourget 1984, 1986), larval settlement (Russ 1980; Chabot & Bourget 1988; Letourneux & Bourget 1988), size structure of populations (Emson & Faller-Fritsch 1976) and the general persistence and distribution patterns (Hogue & Miller 1981; Menge, Ashkenas & Matson 1983; Bergeron

& Bourget 1986). Further, irregular substrata have been shown to provide refuges from temperature extremes, desiccation (Garrity 1984) and wave action (Menge 1978a). Hence, it is likely that this factor will affect the performance of intertidal organisms. Here, 'performance' represents the overall success of an organism exploiting a given environment over a set period of time shorter than a generation time. For most organisms, performance is determined mainly by the energy balance, which integrates costs and benefits to the organism. The growth rate generally reflects this energy balance adequately (Bayne 1976; Palmer 1983). The measure of performance should be determined in relation to the influence of a particular phenotypic trait or habitat feature on the individual.

Thus, our use of performance differs from that of previous workers who used it to indicate the rate at which an activity is carried out (e.g. locomotor performance, metabolic performance (Webb 1986); crawling performance, flight performance, foraging performance (Arnold 1986)), and who thus indirectly associated performance level with rate of metabolic energy consumption.

An assumption in our approach is that individuals optimize their behaviour in the face of such factors as previous experience, the ability to perceive their overall situation when making a decision, and 'knowledge' of alternative strategies and of the limits imposed by the habitat. All these factors constitute major sources of variability in the performance of individuals.

This study examines the influence of structural heterogeneity on the performance of a common northern Atlantic intertidal predator, *Thais* (*Nucella*) *lapillus* L. Our main objectives were to test the hypothesis that the performance of dogwhelks is increased by substratum heterogeneity and, if so, to elucidate the mechanisms involved by examining (a) prey selection by *Thais* in relation to prey value and abundance, (b) predation rates, and (c) protection against high temperatures, desiccation, and wave action.

MATERIALS AND METHODS

Study site and organisms

The study was carried out from June 1985 to November 1986 at Ste-Anne-des-Monts (Fig. 1), on the north shore of the Gaspé Peninsula, Quebec, Canada. Here, many large boulders (measuring approximately 2 × 3 m) are present near low water level. Most boulders are granite or conglomerate rock and the surface texture is homogeneous (smooth) or heterogeneous (rough), respectively. The width and depth of surface depressions of rough surfaces of boulders were of the same size-scale (2–3 cm) as the adult body size of the organisms under study. The high tide (mean tidal amplitude = 2.5 m) slightly covered all but the largest boulders, which remained emersed even at high water of spring tides (HWST). Sessile intertidal invertebrates formed distinct zones on most of the boulders. Thus, on these boulders, various prey types and substratum type were within a short distance of, and therefore easily accessible to, *Thais*. Ice covers the shore from late November to April (El-Sabh 1979), and there can be severe ice scouring of exposed surfaces during periods of ice breakup (Bergeron & Bourget 1984; Bourget, Archambault & Bergeron 1985).

The relationship between the dogwhelk *Thais lapillus*, and one of its preferred prey, the barnacle *Semibalanus balanoides* (L.), was studied. At the study site, whelks spent winter (October to early May) clustered near the base of boulders. Some dogwhelks began to forage in mid-May, but foraging became common only early in June, after 2–3 weeks of reproduction. Barnacle larvae settle early in June. *Thais* were first observed preying on the

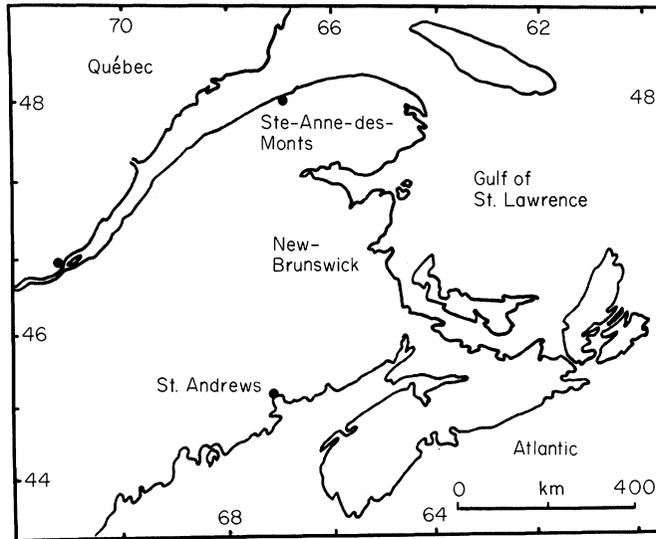


FIG. 1. Map of the estuary and gulf of St. Lawrence (Québec, Canada), showing the study site at Ste-Anne-des-Monts.

barnacle recruits early in July, when they attained a maximum diameter of 3–5 mm. These newly recruited barnacles will hereafter be referred to as juveniles, whereas barnacles 1 year old or more will be identified as adults.

In May 1985, before *Thais* had started to disperse from the winter aggregation sites, a few complete aggregations of individuals were collected to determine the most common sizes. Based on this modal sample, 2.0–2.2 cm (immature) and 2.8–3.0 cm (adult) dogwhelks were chosen for experimentation. Only dogwhelks located on vertical faces of boulders above low water level were used. This ensured that selected animals were acclimatized to such conditions. For similar reasons, individuals (i) located high up on the boulders, (ii) present on surfaces where barnacles were clearly more abundant than mussels, and (iii) found on open surfaces rather than under algae were preferred.

The individuals were tagged and measured. All were placed in a 35 × 60 cm enclosure built on a slightly irregular rock surface bearing barnacles. All dogwhelks spent at least 2 days (most spent 1 week) in this enclosure prior to experimentation.

Structural heterogeneity and the components of performance

Prey value, abundance and selection by the predator

In order to assess barnacle selection by *Thais*, predation experiments were carried out in twenty enclosure/exclosure cages. Each was built of 1 cm galvanized steel mesh and comprised two adjacent 30 × 30 cm compartments. One compartment was a whelk enclosure and the other an exclosure which served to estimate the natural mortality of barnacles. These paired compartments were fastened to moderately exposed boulders, ten on heterogeneous surfaces and ten on uniform surfaces. For each substratum, two enclosures contained immature dogwhelks and eight contained adult dogwhelks. Ten dogwhelks were placed in most enclosures on 25 July 1985, and subsequently, a census of dead barnacles was carried out every 5 days for 30 days. The barnacles were well spaced so that the empty shells could be removed after each inspection without damaging the

remaining individuals. Based on predation rates described in the literature (Connell 1961; Dunkin & Hughes 1984), we estimated that three of the ten predation enclosures on uniform substrata did not contain sufficient prey abundances, so we reduced the number of *Thais* to three, five and seven, respectively. Consumption of barnacles by *Thais* was found to be considerably lower than predicted by these estimates. Thus, prey were abundant throughout the experiments.

The persistence time of ninety-nine empty juvenile barnacle shells was determined by daily inspections to test whether a 5-day observation interval was adequate. These barnacles were from various types of substratum and conditions of sun and wave exposure. They were numbered, measured to the nearest 0.05 mm and killed with a needle. Empty adult barnacle shells outside predation enclosures remained attached to the substratum several weeks to several months after death, therefore their persistence time was not studied.

To estimate the value of prey for the predator, thirty-two adult and thirty-two juvenile barnacles from each enclosure were randomly selected and measured (shell length along the rostro-carinal axis, and opercular diameter) at the start of the experiment. Prey size preferences by the dogwhelks were used as one index for determining prey value to the predator. Another method of assessing prey value to the predator was to determine their yield index. This index consisted of the energy benefit/cost ratio involved in attacking and consuming a prey. In the dogwhelk-barnacle interaction, the 'cost' element had previously been shown to increase with barnacle opercular diameter (Dunkin & Hughes 1984) and with barnacle volume (Carefoot 1977). Total dry weight (including shell) was used to assess costs. Total dry weight is probably a better indicator of costs than size since it is more directly related to factors determining consumption costs, i.e. barnacle shell thickness and amount of flesh. Handling time, which is also used by some as an indicator of costs related to consuming a prey (e.g. in the flesh mass/handling time ratio), is subject to several factors independent of the prey, such as ambient temperature, level of disturbance due to currents, light or other organisms, and the predators' health and level of hunger, and therefore does not appear to be as good an indicator as total dry weight. Dry flesh weight of prey was also measured as it is probably a good indicator of benefits to the predator. The yield index (dry flesh weight/total dry weight) was used as an indicator of the overall value of a barnacle to *Thais*. Total dry weight and dry weight of flesh were obtained from barnacles randomly located on boulders of each substratum type.

Natural barnacle abundances were determined from fifty (10 × 10 cm) quadrats placed randomly on the vertical surfaces (twenty-four on smooth surfaces and twenty-six on rough surfaces) of fourteen boulders.

Since barnacle natural mortality was low and not related to size, measurements of all dead barnacles in enclosures were used to determine prey selection.

Predation rates

To assess predation rates of dogwhelks on each type of substratum, cumulative numbers of dead *Semibalanus* over the 30-day period were obtained for each predation enclosure. Consumed dry flesh weight was also estimated to measure the rate of predation. The flesh content of barnacles was estimated by regressing dry flesh weight against (shell diameter × opercular diameter) for fifty juvenile and fifty adult barnacles; this combination of shell measurements correlated best with dry flesh weight. Counts and total dry weight of flesh of dead barnacles in enclosures were both corrected for natural mortality prior to determining predation rates.

Protection against high temperatures

To determine the relative protection offered by each type of substratum against high temperatures, body temperature of dogwhelks on both substratum types was measured at low tide under sunny conditions on the 6 August 1985 with a YSI Tele-Thermometer (model 42SC) equipped with a 22-gauge hypodermic probe (YSI model 514). All dogwhelks were on vertical boulder surfaces exposed to direct sunshine and were within a 20-cm vertical distance of the 2.0 m tidal level.

Protection against desiccation

To assess the relative protection offered by each type of substratum against desiccation, we determined the mortality of dogwhelks placed in ten cages (10 × 10 cm) fastened to denuded boulder surfaces high in the intertidal zone for a 30-day period. Cages were paired (one on each substratum type) and were located at tidal heights varying from 2.0 to 2.5 m. Each enclosed four whelks during a first 30-day period (late July to late August 1985), and five whelks during a second 30-day period (late August to late September 1985). A total of forty-six immature and forty-four adult whelks were used. All cages were oriented so that they received maximum exposure to sunshine and minimum exposure to wave action. The five cages on each substratum type (homogeneous, heterogeneous) were paired with regards to exposure and tidal level.

Protection against wave action

To obtain the dislodgement rates of dogwhelks due to wave action, four pairs of roof-free arenas (30 cm wide × 60 cm high) were built side by side on the vertical face of a large boulder nearly fully exposed to wave action. For each pair, one arena was on irregular substratum (the rock surface) and the other one on smooth substratum (cement). The cement was applied early in July 1986 and the experiment was conducted early in September 1986. The arena walls (8 cm high aluminium walls) were coated with white petroleum jelly to prevent the escape of *Thais*. This coating was inspected at each low tide and renewed when necessary. No effect of the coating on the health of the dogwhelks was detected. Two control arenas, located in highly protected conditions, allowed us to monitor whelk escape rates concurrently (number of whelks leaving the arenas on their own per tidal cycle). Only adult dogwhelks measuring greater than 3.0 cm long were used, since escape rates of smaller individuals were high and thus did not permit such experimentation. Eighteen dogwhelks were placed in a small cage fastened in the centre of every arena. At high tide the whelks left the cages via a small opening on one side and could thereafter move about freely in the arenas. All arenas were inspected at each low tide for 6 days. Missing dogwhelks were replaced. The tidal dislodgement rate was calculated as the number of missing whelks/(original number of whelks – number of whelks remaining in the centre cage), the original number of whelks being eighteen.

An arena at one end of the boulder face received little exposure to wave action due to interference of a nearby boulder. Since the physical constraint studied in this experiment (i.e. wave action) eventually appeared to be considerably reduced in this particular arena, the analysis was carried out with and without the results from this arena.

*Relation between structural heterogeneity and performance**Thais condition indices*

To obtain condition indices, the dogwhelks used for the 30-day predation experiment were kept for a further 30 days in the enclosures. In late September 1985, fifty of these

dogwhelks were randomly selected from both substratum types, and shell length (anterior tip of the siphonal canal to the apex) and dry weight of flesh were determined. Dogwhelk condition indices (C.I.) were thus calculated as follows: C.I. = dry flesh weight (mg)/shell length (cm).

Thais growth rates

Dogwhelk growth rates were determined as the increment in shell length and height (posterior margin of aperture to the outside of the largest whorl, measured perpendicularly to shell length) to the nearest 0.05 mm during a 60-day period (July–September 1985) of confinement in the predation enclosures; shell length showed a slightly stronger correlation with dry weight than did shell height, and was thus used to determine growth rates (see Hughes 1972).

Seasonal growth and erosion patterns of *Thais* at this site were obtained by tagging, measuring and releasing another group of dogwhelks in the intertidal zone on 30 November 1985. Individuals were recovered on 25 April, 5 June, 7 September and 4 December 1986.

Substratum selection by Thais

To assess substratum type preference of *Thais*, three 20 × 20 cm cages (1 cm steel mesh) were fastened to a boulder on which both substratum types were present on each side of a clear vertical boundary. The cages were placed such that each substratum type composed half the enclosed area. Enclosed and surrounding surfaces were stripped of all organisms. Seven dogwhelks were placed in each cage for a period of 7–10 days, after which they were replaced by a new set of whelks. The position of each whelk in relation to surface type was noted daily. This experiment was carried out twice in August and once in late September 1985.

When analysing data, covariates for each ANCOVA test were selected as correlating sufficiently with the dependent variable ($P < 0.10$) and not having high intercorrelation with other covariates.

RESULTS

Structural heterogeneity and the components of performance

Prey value, abundance and selection by the predator

Out of the ninety-nine shells of killed juvenile barnacles, which were inspected daily in order to determine their persistence time on rock surfaces, only one was dislodged within 5 days (Fig. 2). Thus, barnacle shells persisted on the substratum longer than the 5-day interval. Moreover, the correlation between persistence time and shell diameter was weak ($r = -0.18$, $P = 0.06$, $n = 99$). Hence, in the following experiments, any shells dislodged before being censused were not significantly size-biased.

Prey type. Neither juvenile or adult barnacle abundances, obtained from the fifty quadrats on vertical surfaces, were found to differ significantly between substratum types (Table 1), mainly because of high intra-group variability. This variability, however, was higher on smooth than on irregular surfaces, as shown by the coefficients of variation.

Prey type selection was studied by comparing the ratio of juvenile to adult prey consumed to the ratio of total surface covered by each prey type. The latter ratio provided an estimate of the likelihood of encounter of juvenile and adult barnacles. If no prey type

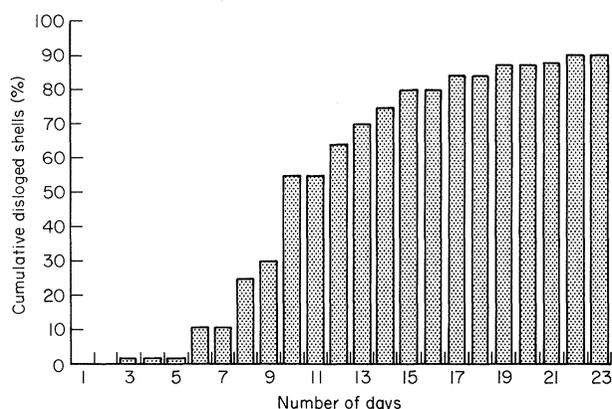


FIG. 2. Time before dislodgement of dead juvenile *Semibalanus balanoides* shells. All killed barnacles were inspected daily for 23 days ($n=99$).

selection occurs, we expect juvenile and adult barnacles to be consumed in proportions equal to their likelihood of encounter, and the ratios of juveniles to adults consumed to be similar to the ratio of their respective abundances (percentage cover). However, both adult and immature dogwhelks preferred juvenile over adult barnacles (Table 2). Furthermore, the yield index (dry flesh weight/total dry weight) of juvenile barnacles was higher than that of adults (Table 1).

Juvenile prey. Juvenile barnacles were generally larger on heterogeneous than on uniform surfaces (Table 3). Yield indices of juvenile prey were also higher on heterogeneous substrata (Table 3).

Prey size selection was first examined by comparing shell diameters of barnacles randomly selected in enclosures at the start of the experiment with the diameters of barnacles consumed during the first 10 days. Average size of barnacles consumed by immature dogwhelks was significantly larger than that of barnacles available to them

TABLE 1. Yield index (dry flesh weight/total dry weight) and numbers of juvenile and adult *Semibalanus balanoides* prey from fifty quadrats. S.D. = standard deviation, C.V. = coefficient of variation

| | \bar{x} | S.D. | C.V. (%) | n | P | Test |
|---------------------|-----------|-------|----------|-----|-------|--------------|
| (i) Yield index | | | | | | |
| Juveniles | 0.145 | 0.080 | 55.2 | 39 | <0.04 | ANOVA |
| Adults | 0.109 | 0.021 | 19.3 | 50 | | |
| (ii) Prey abundance | | | | | | |
| Juveniles Smooth | 68.79 | 93.76 | 136.3 | 24 | 0.24 | Nested ANOVA |
| Juveniles Rough | 122.96 | 88.86 | 72.3 | 26 | | |
| Adults Smooth | 4.17 | 9.66 | 231.9 | 24 | 0.16 | Nested ANOVA |
| Adults Rough | 10.19 | 11.69 | 114.7 | 26 | | |

TABLE 2. Prey type selection by immature and adult *Thais*. Ratio of numbers of juvenile to adult prey consumed compared to ratio of areas covered by each prey type (Student's *t*-test)

| Predators | Prey type ratio | \bar{x} | S.D. | <i>n</i> | <i>t</i> | <i>P</i> |
|-----------------|----------------------------------|-----------|-------|--------------|----------|----------|
| Immature whelks | Juvenile consumed/adult consumed | 70.78 | 46.88 | 4 } 4 } | 4.52 | 0.02 |
| | Area juvenile/area adult | 5.47 | 2.08 | | | |
| Adult whelks | Juvenile consumed/adult consumed | 10.19 | 3.04 | 16 } 16 } | 4.53 | 0.0002 |
| | Area juvenile/area adult | 2.02 | 0.47 | | | |

TABLE 3. Size and yield index of prey flesh. Diameter of *Semibalanus balanoides* measured in July 1985; yield indices (dry flesh weight/total dry weight) were obtained in August 1985

| | Substratum | \bar{x} | <i>n</i> | <i>F</i> | <i>P</i> | Test |
|-------------------|------------|-----------|----------------|----------|----------|--------|
| (i) Diameter (cm) | | | | | | |
| Juveniles | Smooth | 0.497 | 320 } 320 } | 4.52 | <0.04 | ANCOVA |
| | Rough | 0.528 | | | | |
| Adults | Smooth | 1.40 | 274 } 314 } | 13.26 | 0.003 | ANCOVA |
| | Rough | 1.28 | | | | |
| (ii) Yield index | | | | | | |
| Juveniles | Smooth | 0.109 | 17 } 22 } | 6.69 | <0.02 | ANCOVA |
| | Rough | 0.173 | | | | |
| Adults | Smooth | 0.104 | 25 } 25 } | 4.62 | <0.04 | ANOVA |
| | Rough | 0.114 | | | | |

($F=4.2$, $P=0.04$, $n=341$, pooled results; nested ANOVA). Similar results were obtained for adult dogwhelks ($F=60.9$, $P<0.0001$, $n=917$, pooled results; nested ANOVA), suggesting selection for large prey by all dogwhelks. However, when the relative abundance of each juvenile prey size-class in the predator's diet was compared with the relative area covered (i.e. relative encounter likelihood) by each prey size-class on the substratum, the results clearly indicated that for immature dogwhelks there was no divergence between consumption frequency and encounter likelihood of barnacle size-classes (Fig. 3a, $P=0.55$, $n=341$, *N.* of size-classes = 19, Mann-Whitney *U*-test; Conover 1980). The same calculations showed that adult dogwhelks selected large juvenile barnacles (Fig. 3b, $P<0.02$, $n=917$, *N.* of size-classes = 22, Mann-Whitney *U*-test).

Adult prey. The average size of adult barnacles was smaller on heterogeneous than on homogeneous substrata (Table 3). Yield indices of adult barnacles, however, were higher on heterogeneous substrata (Table 3). Too few adult barnacles were consumed by immature dogwhelks to apply appropriate tests. For adult dogwhelks, however, the average shell diameter of adult prey consumed was not significantly different from that of

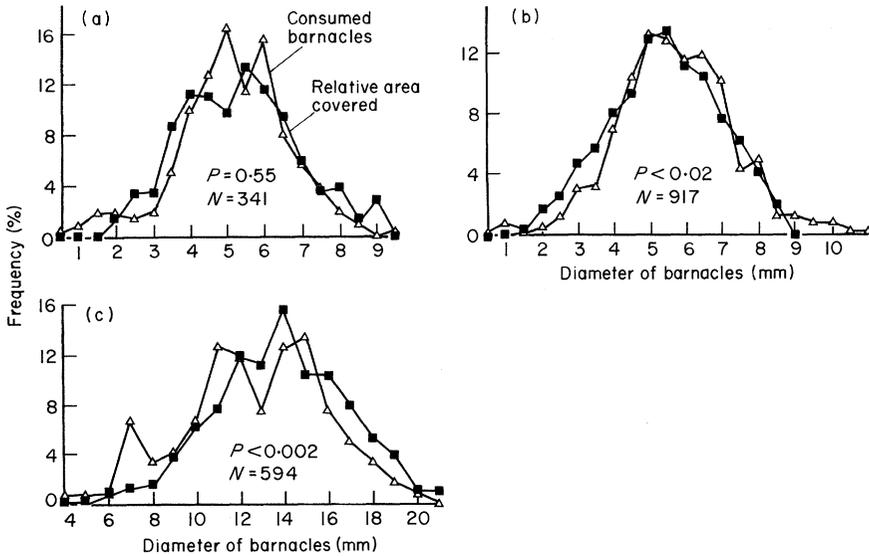


FIG. 3. Abundance (relative area covered) and consumption frequency (amount of individuals consumed by *Thais lapillus*) of different sizes of *Semibalanus balanoides*. (a) Predation on juvenile barnacles by immature *Thais*; (b) predation on juvenile barnacles by adult *Thais*; (c) predation on adult barnacles by adult *Thais*.

the barnacles available ($F = 1.47$, $P = 0.23$, $n = 501$, nested ANOVA). However, comparison of the relative abundance of each adult prey size-class in the adult predator's diet with the relative area covered by each size-class of prey available to the predator in the enclosures (Fig. 3c) indicated the various sizes were not consumed proportionally to their likelihood of encounter by adult *Thais* ($P < 0.002$, $n = 594$, N of size-classes = 18, Mann-Whitney U -test). Adult dogwhelks selected small adult prey.

Predation rates

Number and total dry weight of each prey type as well as total dry weight of all prey consumed were determined for immature and adult *Thais* (Table 4). Whereas most predation rates did not differ significantly between substratum types, adult dogwhelks consumed juvenile barnacles at a significantly higher rate on flat than on heterogeneous substrata. Nevertheless, they did not obtain a larger amount of juvenile prey flesh or a larger total amount of prey flesh than adult dogwhelks on heterogeneous surfaces.

Protection against high temperatures

At an ambient air temperature of 21 °C the average body temperature of dogwhelks, on smooth and on rough vertical surfaces, was similar, at 22.0 °C ($s = 1.4$ °C) and 21.8 °C ($s = 1.5$ °C), respectively ($P = 0.40$, $n = 58$, Wilcoxon's signed ranks test; Sokal & Rohlf 1981).

Protection against desiccation

Mortality of *Thais* in conditions favouring high desiccation stress over a 30-day period, on flat and on uneven substrata, were 50% and 52%, respectively ($F = 0.53$, $P = 0.77$, $n = 14$, randomized complete blocks ANOVA; Sokal & Rohlf 1981).

TABLE 4. *Thais lapillus* (immatures and adults) predation rates on *Semibalanus balanoides* (juveniles and adults) on uniform and heterogeneous substrata

| Predator | Prey | Substratum | \bar{x} (per <i>Thais</i> /30 d) | <i>n</i> | <i>F</i> | <i>P</i> | Test |
|---------------------------|--|------------|------------------------------------|----------|----------|----------|--------------|
| (i) Immature <i>Thais</i> | Number of juveniles | Smooth | 18.92 | 2 | 0.38 | 0.68 | ANCOVA |
| | | Rough | 17.95 | 2 | | | |
| | Juvenile dry flesh weight (mg) | Smooth | 29.26 | 2 | 0.86 | 0.45 | Nested ANOVA |
| | | Rough | 45.86 | 2 | | | |
| | Number of adults | Smooth | 0.543 | 2 | 0.29 | 0.68 | ANCOVA |
| | | Rough | 0.642 | 2 | | | |
| | Adult dry flesh weight (mg)* | Smooth | 3.21 | 2 | 1.74 | 0.41 | ANCOVA |
| | | Rough | 3.87 | 2 | | | |
| | Total flesh weight: juveniles + adults | Smooth | 50.10 | 2 | 0.05 | 0.85 | ANCOVA |
| | | Rough | 56.05 | 2 | | | |
| (ii) Adult <i>Thais</i> | Number of juveniles | Smooth | 10.13 | 8 | 6.22 | <0.03 | ANCOVA |
| | | Rough | 5.04 | 8 | | | |
| | Juvenile dry flesh weight (mg) | Smooth | 21.91 | 8 | 1.48 | 0.24 | ANCOVA |
| | | Rough | 13.79 | 8 | | | |
| | Number of adults | Smooth | 1.32 | 8 | 0.10 | 0.76 | ANCOVA |
| | | Rough | 1.51 | 8 | | | |
| | Adult dry flesh weight (mg)* | Smooth | 6.17 | 8 | 0.08 | 0.78 | ANCOVA |
| | | Rough | 7.10 | 8 | | | |
| | Total flesh weight: juveniles + adults | Smooth | 68.35 | 8 | 0.01 | 0.94 | ANCOVA |
| | | Rough | 70.34 | 8 | | | |

* Adult flesh weights normalized by the Box-Cox method.

Protection against wave action

Escape rates (number of whelks exiting from control arenas, per tide) were low, ranging from 0 to 13%, and were null for most tidal cycles (60%). When necessary, data were corrected for escape rate differences between substratum types. Percentages of dogwhelks missing from exposed arenas (pooled data, smooth and rough surfaces) were plotted over a subjective evaluation of the intensity of wave action made during the previous low tide (Fig. 4). The close fit of these two data sets strongly suggests that the missing dogwhelks had effectively been dislodged by wave action. Actual dislodgement rates averaged 42.8% per tide on smooth surfaces, which was significantly greater than 32.2% for heterogeneous surfaces ($t = 2.92$, $P < 0.007$, $n = 33$ pairs, t -test for paired comparisons; Sokal & Rohlf 1981).

Relation between structural heterogeneity and performance

Thais condition indices

Condition indices (dry flesh weight/shell length) of dogwhelks after 60 days in the predation enclosures averaged 102 mg cm⁻¹ ($s = 4$, $n = 25$) on smooth substrata, which was not significantly different from 110 mg cm⁻¹ ($s = 4$, $n = 25$) for those on uneven substrata ($F = 1.64$, $P = 0.21$, ANCOVA; Huitema 1980).

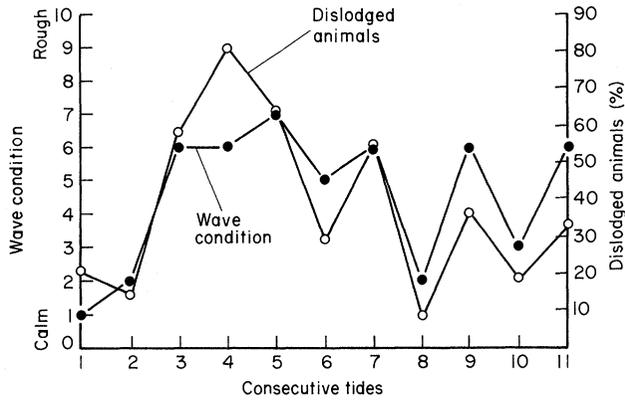


FIG. 4. Wave condition, subjectively evaluated at low tide, and the percentage dislodgement of *Thais lapillus* as observed on the following low tide. Dislodgement arenas were inspected over eleven consecutive tides, September 1986.

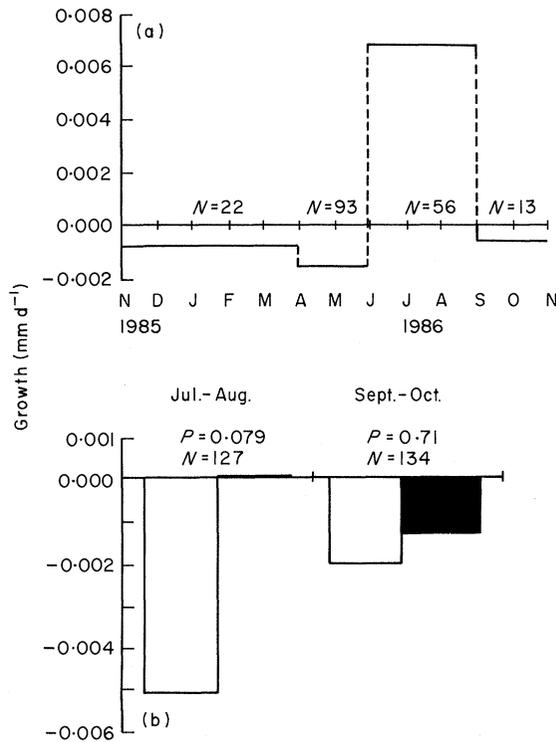


FIG. 5. Growth rate (mm days⁻¹) of *Thais lapillus* at Ste-Anne-des-Monts, Quebec. Negative growth rates indicate reduction in length due to shell erosion. (a) Growth rate of dogwhelks larger than 2.7 cm length released in the intertidal zone and recaptured four times over 1 year. (b) Growth rate of adult dogwhelks (length between 2.8 and 3.0 cm in July 1985) in predation enclosures during two consecutive periods in 1985.

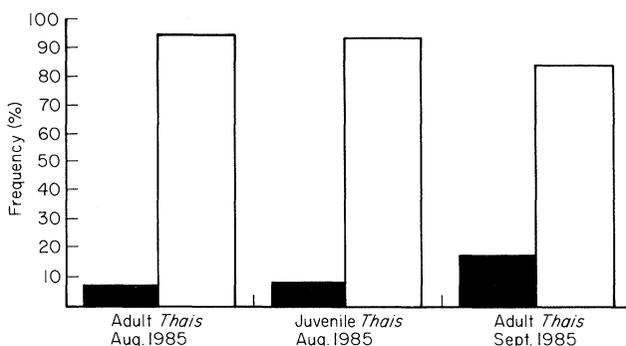


FIG. 6. Frequency counts of *Thais lapillus* observed daily on either heterogeneous (□) or uniform (■) substratum in cages bearing equal areas of each substratum type. Differences between proportions of dogwhelks on each substratum type were significant for each period ($P < 0.001$).

Thais growth rates

The total annual shell growth of marked dogwhelks in 1986 occurred over approximately 4 months during the summer. For the remaining 8 months, a net decrease in shell length was observed. These growth and erosion periods correspond to periods of active foraging and inactivity, respectively.

Growth of dogwhelks in the predation enclosures was monitored for 1 month during the critical growth period and 1 month during the passive erosion period. Growth of juvenile *Thais* could not be compared due to insufficient data (two enclosures per substratum type). However, growth of adults (eight enclosures per substratum type) during August 1985 (Fig. 5b) proceeded at a higher rate on heterogeneous than on homogeneous substrata, though the difference was not significant ($F = 3.14$, $P = 0.079$, $n = 127$, ANCOVA). On average, dogwhelks on heterogeneous surfaces exhibited a small increase in shell length while the length of those on flat surfaces decreased. Whelks on both substratum types showed a decrease in shell length during September 1985. The rates of shell erosion on the two substrata did not differ significantly during September ($F = 0.13$, $P = 0.71$, $n = 134$; ANCOVA).

Substratum selection by Thais

The substratum selection experiment, which was carried out three times in 1985, revealed that *Thais* were found 4.8 (adults, September) to 13.3 (adults, August) times more often on heterogeneous than on smooth surfaces (Fig. 6). The null hypothesis, no selection for substratum type (equal number of dogwhelks on both substrata), was rejected for all three periods ($P \ll 0.001$; G -test) indicating that adult and immature *Thais* preferred heterogeneous substrata.

DISCUSSION

A large mesh size (1 cm) was used to build enclosures and cages in order to minimize interference with natural conditions. Whereas all enclosures probably had some slight influence on ambient conditions, this bias was the same for experiments on both substratum types. Tagging and manipulations in general do not appear to affect dogwhelks significantly (personal observation; also see Chapman 1986). In any case, all animals used for each experiment were treated similarly.

TABLE 5. Summary of results from experiments on the influence of various factors on the performance of *Thais lapillus* in the intertidal zone of the Northwestern gulf of St Lawrence

| Factor | Most advantageous substratum with regard to the listed factor | |
|--|---|-------|
| | Smooth | Rough |
| Structural heterogeneity and components of performance | | |
| Prey abundance | — | — |
| Prey abundance variability (predictability) | — | X |
| Prey size (juveniles & adults) | — | X |
| Prey yield index | — | X |
| Predation rates | — | — |
| Protection against high temperatures | — | — |
| Protection against desiccation | — | — |
| Protection against wave action | — | X |
| Structural heterogeneity and overall performance | | |
| Performance indicators: | | |
| <i>Thais</i> condition index | — | — |
| <i>Thais</i> growth rates | — | X |
| Predator behaviour: | | |
| Substratum selection | — | X |

At first, prey size-selection by *Thais* was examined by comparing average size of available barnacles with average size of consumed barnacles. Subsequent reanalysis of data accounted for predator-prey encounter likelihoods. The results indicate that numbers of prey in each size-class are not necessarily good indicators of encounter likelihoods. Adequate estimations of encounter likelihoods of prey by the predator must account for the predator's search behaviour and for the prey's body shape. Few studies on *Thais lapillus* have adequately accounted for the encounter likelihood of different prey.

Structural heterogeneity and the components of performance

Prey densities were not significantly different between substratum types (Table 5). However, the variability in prey density on uniform surfaces was twice as high as on rough surfaces. Since *Thais* is a non-visual predator, higher variability entails lower predictability of prey abundance. Prey size and the prey yield index were both more favourable to the predator on irregular surfaces (Table 5).

The three abiotic factors examined in relation to the influence of structural heterogeneity on *Thais* are those most documented and generally recognized as imposing major physical constraints on intertidal organisms: desiccation (Yamada 1977; Menge 1978b), temperature (Menge, Ashkenas & Matson 1983; Garrity 1984) and wave action (Dayton 1971; Moran 1985; Shanks & Wright 1986). In contrast to previous discussions (Spight 1982) and experiments (Garrity 1984) we did not detect any enhanced protection against high temperatures or desiccation on heterogeneous substrata. We suspect this was due to the relatively cool and damp conditions prevailing during our study (at low tide, air temperature rarely exceeded 20 °C). Heterogeneous surfaces did, however, offer enhanced protection against wave action (Table 5), as suggested by Feare (1971). We did not examine whether irregular surfaces impede dogwhelk movements or cause greater travel costs (or less travel).

Relation between substratum topography and performance

Although growth rate is probably the simplest and most accurate indicator of performance, other variables, such as the condition index or tissue quality (energy content), may also be considered. In any case the life history of the species must be considered in choosing the appropriate variable(s), the season and the duration of the study.

We determined the performances of dogwhelks by examining growth rates and condition indices. Mortality rates of *Thais*, an important component of performance, were not examined. However, *Thais* did not have any apparent natural predators at our site (the crab *Cancer irroratus*, say, may have preyed on small dogwhelks (< 1.0 cm in shell length) but no actual case of such predation was observed), and other known mortality sources during the summer (warm temperatures, desiccation and wave action), were found to affect individuals similarly on either substratum type or were less harsh on heterogeneous surfaces (in the case of wave action).

Comparison of *Thais*' condition indices following different treatments (Table 5) indicates flesh content did not vary as a consequence of the predator being maintained on different substratum types. The summer growth period is apparently shorter at our study site than on the coast of Nova Scotia (Hughes 1972). Growth rates during the critical summer season were higher on heterogeneous surfaces (Table 5), suggesting performance is higher on heterogeneous surfaces. This corroborates well our previous results.

If we assume that dogwhelks are able to distinguish between substratum types, then our results support the hypothesis that they should select heterogeneous surfaces during their active season. Substratum type selection results (Table 5) confirm both the assumption and the hypothesis. The ability of intertidal gastropods to assess costs, benefits and risks have already been documented (Menge 1974; Leviten & Kohn 1980; Spight 1982; Hughes & Dunkin 1984). This suggests they behave in such a way as to optimize overall costs and benefits. The substratum selection by *Thais* which we report in this study supports this hypothesis. Garrity (1984) also reports that ten species of intertidal gastropods preferred surface irregularities over smooth surfaces, at least during low tide in stressful periods.

*Ecological implications**Prey selection and the energy maximization premise*

Thais chose the barnacle type offering the highest yield. Young barnacles, in addition to having higher yield indices, could be attacked by a quicker and probably energetically cheaper method than adult barnacles, since *Thais* pries open their opercular valves rather than boring through their shell (Hughes & Dunkin 1984), and probably injects a narcotic causing the prey to relax sufficiently to introduce its proboscis (Palmer 1982). Size selection, only detected among adult *Thais*, may have conformed to energy maximization or time minimization strategies. Indeed, yield indices did not correlate with adult prey size, but small adult barnacles are more susceptible to the prising technique than large ones (Dunkin & Hughes 1984), involving less time and probably lower costs.

Resource utilization

Substratum irregularities reduce habitat exploitation costs related to wave action, and probably mortality during storms as well. Heterogeneous surfaces also allow dogwhelks to forage on surfaces otherwise too exposed to wave action. Surface heterogeneity might equally act to extend the range of *Thais* upward (Menge 1976), providing a greater access to barnacles.

Predator-prey relation

The data on value, distribution and abundance of barnacles with respect to substratum topography did not indicate any predator avoidance or low yield strategy by *Semibalanus*. This may be because climatic factors exert a much greater selective pressure on barnacles than dogwhelk predation. Ice scouring in particular is a major constraint on sessile organisms which settle on uniform surfaces (Wetthey 1979; Bergeron & Bourget 1986). Menge (1978a) noted that the density of *Thais* was greater in and near crevices, in areas exposed to wave action on the coast of New England. Chabot & Bourget (1988) show that on the southern coast of New Brunswick (Passamoquoddy Bay), barnacles (*Semibalanus balanoides*) settle more densely outside cracks and crevices than inside, while the opposite was observed at our study site. Ice scouring in the New Brunswick coast is much less frequent and is not as intense as at our study site. These observations and results suggest that settling barnacles avoid microhabitats most used by *Thais* in regions where ice scouring is rare or absent (see Bourget 1988).

Our results are not consistent with the classic view that structural heterogeneity is a source of refuges from predators. Surface depressions of the scale studied here did not impede or prevent *Thais* from reaching barnacles, on the contrary. Similarly, in experimental studies of juvenile fish predation on meiobenthos, Marinelli & Coull (1987) report that structural heterogeneity of the sediment increased rather than reduced predation and disturbance effects. Such results underline the importance of a case-by-case study approach.

Significance of structural heterogeneity to Thais

In our study there was no evidence indicating that uniform substrata were more advantageous to *Thais* than heterogeneous substrata (Table 5). Although amounts of consumed prey flesh were similar for dogwhelks on both substrata, suggesting similar benefits to dogwhelks, heterogeneous surfaces seem to impose lower overall exploitation costs (Table 5), therefore allowing higher performances.

In this subarctic environment, *Thais* is inactive during approximately 8 months of the year. However, during the remaining 4 months, they must obtain sufficient energy and essential nutrients to satisfy growth, reproduction and annual maintenance needs. Maximum performance during the summer period is thus essential. By taking advantage of surface irregularities, patchily distributed in its natural habitat, *Thais* attains a higher performance due to the particular conditions prevailing there (Table 5). The observed consistent selection by *Thais* of heterogeneous over uniform surfaces shows it can and suggests it actually does take advantage of small-scale structural heterogeneity.

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REFERENCES

- Arnold, S. J. (1986). Laboratory and field approaches to the study of adaptation. *Predator-Prey Relations* (Ed. by M. E. Feder & G. V. Lauder), pp. 157-169. University of Chicago Press, Chicago and London.
- Bayne, B. L. (Ed.) (1976). *Marine Mussels: Their Ecology and Physiology*. Cambridge University Press, London.

- Bell, S. S. & Coen, L. D. (1982). Investigations on epibenthic meiofauna. II Influence of microhabitat and macroalgae on abundance of small invertebrates on *Diopatra cuprea* (Bosc) (Polychaeta: Onuphidae) tubecaps in Virginia. *Journal of Experimental Marine Biology and Ecology*, **61**, 175–188.
- Bergeron, P. & Bourget, E. (1984). Effet du froid et des glaces sur les peuplements intertidaux des régions nordiques, particulièrement dans l'estuaire du Saint-Laurent. *Océanis*, **10**, 279–304.
- Bergeron, P. & Bourget, E. (1986). Shore topography and spatial partitioning of crevice refuges by sessile epibenthos in an ice disturbed environment. *Marine Ecology Progress Series*, **28**, 129–145.
- Bourget, E. (1988). Barnacle larval settlement: The perception of cues at different spatial scales. *Behavioural Adaptations to the Intertidal Life* (Ed. by M. Vannini & G. Chelazzi) (in press). Plenum Press, New York.
- Bourget, E., Archambault D. & Bergeron, P. (1985). Effet des propriétés hivernales sur les peuplements épibenthiques intertidaux dans un milieu subarctique, l'estuaire du Saint-Laurent. *Naturaliste canadien: Revue d'écologie et de systématique*, **112**, 131–142.
- Brock, R. E. (1979). An experimental study on the effects of grazing by parrot-fishes and the role of refuges in benthic community structure. *Marine Biology*, **51**, 381–388.
- Carefoot, T. H. (1977). *Pacific Seashores*. J. J. Douglas Ltd., Vancouver.
- Chabot, R. & Bourget, E. (1988). The influence of substratum heterogeneity and settled barnacle density on the settlement of cypris larvae. *Marine Biology*, **97**, 45–56.
- Chapman, M. G. (1986). Assessment of some controls in experimental transplants of intertidal gastropods. *Journal of Experimental Marine Biology and Ecology*, **103**, 181–201.
- Connell, J. H. (1961). Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecological Monographs*, **31**, 61–104.
- Conover, W. J. (1980). *Practical Non-Parametric Statistics*, 2nd edn. Wiley, New York.
- Crowder, L. B. & Cooper, W. E. (1982). Habitat structural complexity and the interaction between bluegills and their prey. *Ecology*, **63**, 1802–1813.
- Dayton, P. K. (1971). Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs*, **41**, 351–389.
- Dunkin, S. de B. & Hughes, R. N. (1984). Behavioural components of prey selection by dogwhelks, *Nucella lapillus* (L.), feeding on barnacles, *Semibalanus balanoides* (L.), in the laboratory. *Journal of Experimental Marine Biology and Ecology*, **79**, 91–103.
- El-Sabh, M. I. (1979). The lower St Lawrence Estuary as a physical oceanographic system. *Naturaliste canadien: Revue d'écologie et de systématique*, **106**, 55–73.
- Emsen, R. H. & Faller-Fritsch, R. J. (1976). An experimental investigation into the effect of crevice availability on abundance and size-structure in a population of *Littorina rudis* (Maton): Gastropoda: Prosobranchia. *Journal of Experimental Marine Biology and Ecology*, **23**, 285–297.
- Feare, C. J. (1971). The adaptive significance of aggregation behaviour in the dogwhelk *Nucella lapillus* (L.). *Oecologia*, **7**, 117–126.
- Garrity, S. D. (1984). Some adaptations of gastropods to physical stress on a tropical rocky shore. *Ecology*, **65**, 559–574.
- Gilinski, E. (1984). The role of fish predation and spatial heterogeneity in determining benthic community structure. *Ecology*, **65**, 455–468.
- Hogue, E. W. & Miller, C. B. (1981). Effects of sediment microtopography on small-scale spatial distribution of meiobenthic nematodes. *Journal of Experimental Marine Biology and Ecology*, **53**, 181–191.
- Holt, R. D. (1984). Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *American Naturalist*, **124**, 377–406.
- Hughes, R. N. (1972). Annual production of two Nova-Scotian populations of *Nucella lapillus* (L.). *Oecologia*, **8**, 356–370.
- Hughes, R. N. & Dunkin, S. de B. (1984). Effects of dietary history on selection of prey, and foraging behaviour among patches of prey, by the dogwhelk *Nucella lapillus* (L.). *Journal of Experimental Marine Biology and Ecology*, **79**, 159–172.
- Huitema, B. E. (1980). *The Analysis of Covariance and Alternatives*. Wiley Interscience, New York.
- Kern, J. C. & Bell, S. S. (1984). Spatial heterogeneity in size structure of meiofaunal sized invertebrates on small spatial scales (meters) and its implications. *Journal of Experimental Marine Biology and Ecology*, **78**, 221–236.
- Kohn, A. J. & Leviten, P. J. (1976). Effects of habitat complexity on population density and species richness in tropical intertidal predatory gastropod assemblages. *Oecologia*, **25**, 199–210.
- Letourneux, F. & Bourget, E. (1988). The importance of physical and biological settlement cues used at different spatial scales by the larvae of *Semibalanus balanoides*. *Marine Biology*, **97**, 57–66.
- Leviten, P. J. & Kohn, A. J. (1980). Microhabitat resource use, activity patterns and episodic catastrophe: *Conus* on tropical intertidal reef rock benches. *Ecological Monographs*, **50**, 55–75.
- MacArthur, R. H. (1965). Patterns of species diversity. *Biological Review*, **40**, 510–533.
- Main, K. L. (1987). Predator avoidance in seagrass meadows: prey behaviour, microhabitat selection, and cryptic coloration. *Ecology*, **68**, 170–180.
- Marinelli, R.L. & Coull, B. C. (1987). Structural complexity and juvenile fish predation on meiobenthos: an experimental approach. *Journal of Experimental Marine Biology and Ecology*, **108**, 67–81.

- Menge, J. L. (1974). Prey selection and foraging period of the predaceous rocky intertidal snail, *Acanthina punctulata*. *Oecologia*, **17**, 293–316.
- Menge, B. A. (1976). Organization of the New-England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecological Monographs*, **46**, 355–395.
- Menge, B. A. (1978a). Predation intensity in a rocky intertidal community. Relation between predator foraging activity and environmental harshness. *Oecologia*, **34**, 1–16.
- Menge, B. A. (1978b). Predation intensity in a rocky intertidal community. Effect of an algal canopy, wave action and desiccation on predator feeding rates. *Oecologia*, **34**, 17–35.
- Menge, B. A., Ashkenas, L. R. & Matson, A. (1983). Use of artificial holes in studying community development in cryptic marine habitats in a tropical rocky intertidal region. *Marine Biology*, **77**, 129–142.
- Menge, B. A., Lubchenco, J. & Ashkenas, L. R. (1985). Diversity, heterogeneity and consumer pressure in a tropical rocky intertidal community. *Oecologia*, **65**, 394–405.
- Moran, M. J. (1985). Distribution and dispersion of the predatory intertidal gastropod *Morula marginalba*. *Marine Ecology Progress Series*, **22**, 41–52.
- Palmer, A. R. (1982). Predation and parallel evolution: recurrent parietal plate reduction in balanomorph barnacles. *Paleobiology*, **8**, 31–44.
- Palmer, A. R. (1983). Growth rate as a measure of food value to thaidid gastropods: assumptions and implications for prey morphology and distribution. *Journal of Experimental Marine Biology and Ecology*, **73**, 95–124.
- Pianka, E. R. (1966). Convexity, desert lizards, and spatial heterogeneity. *Ecology*, **47**, 1055–1059.
- Russ, G. R. (1980). Effects of predation by fishes, competition, and structural complexity of the substratum on the establishment of a marine epifaunal community. *Journal of Experimental Marine Biology and Ecology*, **42**, 55–69.
- Shanks, A. L. & Wright, W. G. (1986). Adding teeth to wave action: the destructive effects of wave-borne rocks on intertidal organisms. *Oecologia*, **69**, 420–428.
- Smith, F. E. (1972). Spatial heterogeneity, stability, and diversity in ecosystems. *Transactions of the Connecticut Academy of Arts & Sciences*, **40**, 309–335.
- Sokal, R. R. & Rohlf, F. J. (1981). *Biometry*, 2nd edn. Freeman, San Francisco.
- Spight, T. M. (1977). Diversity of shallow-water gastropod communities on temperate and tropical beaches. *American Naturalist*, **111**, 1077–1097.
- Spight, T. M. (1982). Risk, reward, and the duration of feeding excursions of a marine snail. *Veliger*, **24**, 302–308.
- Webb, P. W. (1986). Locomotion and predator-prey relationships. *Predator-Prey Relationships* (Ed. by M. E. Feder & G. V. Lauder), pp. 24–41. University of Chicago Press, Chicago.
- Wethey, D. S. (1979). *Demographic Variation in Intertidal Barnacles*. Unpublished Ph.D. thesis, University of Michigan.
- Woodin, S. A. (1981). Disturbance and community structure in a shallow water sand flat. *Ecology*, **62**, 1052–1066.
- Yamada, S. B. (1977). Geographic range limitation of the intertidal gastropods *Littorina sitkana* and *L. planaxis*. *Marine Biology*, **39**, 61–65.

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