Ecological Monographs, 55(4), 1985, pp. 421–445

REFUGES, BIOLOGICAL DISTURBANCE, AND ROCKY SUBTIDAL COMMUNITY STRUCTURE IN NEW ENGLAND[1]

JON D. WITMAN[2]
Zoology Department, University of New Hampshire,
Durham, New Hampshire 03824 USA

Abstract. The effects of two sources of biological disturbance—predation and sea urchin grazing—on the structure of benthic communities inside and outside beds of the horse mussel, *Modiolus modiolus,* were examined in the rocky subtidal zone off the Isles of Shoals, New Hampshire, USA. Multivariate analysis revealed three major communities between 8 and 30 m in depth: (1) a *Modiolus* community; (2) a 30 m community; and (3) an 8–18 m community. At all depths, mussel beds contained significantly higher densities of infauna than did other subtidal habitats.

The hypothesis that *Modiolus* beds provide a refuge from predation for the associated community was tested in five manipulative field experiments. Three members of the mussel bed community, the bivalve *Hiatella arctica,* the sea urchin *Strongylocentrotus droebachiensis,* and the ophiuroid *Ophiopholis aculeata,* were used as experimental prey. Consumption of these prey by a guild of generalist predators was observed outside but not inside mussel beds, which indicates that subtidal *Modiolus* beds provide a spatial refuge from predation. Deaths from predation were significantly higher at night than during the day for *Hiatella* but not for *Strongylocentrotus.* At night, crab (*Cancer borealis, Cancer irroratus*) and lobster (*Homarus americanus*) predation accounted for all attacks that were directly witnessed, while fish (*Tautoglabrus adspersus, Pseudopleuronectes americanus*) predation accounted for 71% of the total prey consumed during the day. Such diel differences in predation corresponded with predator abundance patterns.

The sea urchin *Strongylocentrotus droebachiensis* was the most significant agent of biological disturbance during the 1979–1984 study period. *Strongylocentrotus* intensively grazed the benthos at 8 m in 1982, causing a 79% reduction (from predisturbance levels) in the mean population density of invertebrates outside the mussel beds. This event served as a natural experiment in which to test the hypothesis that *Modiolus* beds function as a refuge from severe grazing disturbance. Re-sampling of communities inside and outside mussel beds immediately after the grazing disturbance indicated that the *Modiolus* community exhibited less change in species composition, dominance, and diversity than communities outside the mussel beds. Such comparisons indicate that *Modiolus* beds afford protection from severe grazing disturbance for infaunal invertebrates.

Long-term photographic monitoring of marked mussel beds at 8, 18, and 30 m depth showed that *Modiolus* beds at all depths persisted for more than 5 yr. Mortality rates of adult *Modiolus* were low; however, mortality was highest at the shallow site (8 m). Mussel beds successfully resisted the grazing disturbance which eliminated all other biogenic habitats except those created by crustose coralline algae. *Modiolus* beds are effective refuges because they persist for many years and resist biotic disturbance.

In the subtidal communities examined here, lower levels of disturbance inside mussel beds can account for the abundance and spatial distribution of *Modiolus*-community species. These results demonstrate the functional significance of mussel beds in cold-temperate subtidal regions where predation and sea urchin grazing are major determinants of community organization.

Key words: benthos; community structure; disturbance; Modiolus modiolus; *mussel; New England; predation; refuge; resistance; sea urchin grazing; subtidal.*

INTRODUCTION

Disturbance plays a key role in the determination of species abundance, distribution, and diversity in many terrestrial and marine communities (reviewed in Bazzaz 1983, Sousa 1984, Connell and Keough 1985). Disturbance is used here to mean any process that removes biomass (Grime 1977); biological disturbance refers to the effects of grazing and predation (Dayton 1971). Spatial refuges can isolate organisms from disturbance (Woodin 1978) and reduce the success of prey capture by predators (Huffaker 1958, Ware 1972, Heck and Thoman 1981, Menge and Lubchenco 1981, Woodin 1981, Peterson 1982, Coull and Wells 1983, Kaiser 1983, Watanabe 1984). Because of the prevalence of disturbance, it is clear that habitats which provide refuge from disturbance will have a disproportionately large influence on community structure (e.g., abundance and distribution of species). Thus, our understanding of processes shaping and maintaining community structure will benefit both from the identification of refuges and from the elucidation of their function.

---

[1] Manuscript received 17 September 1984; revised 1 February 1985; accepted 17 March 1985.

[2] Present address: Marine Science and Maritime Studies Center, Northeastern University, East Point, Nahant, Massachusetts 01908 USA.

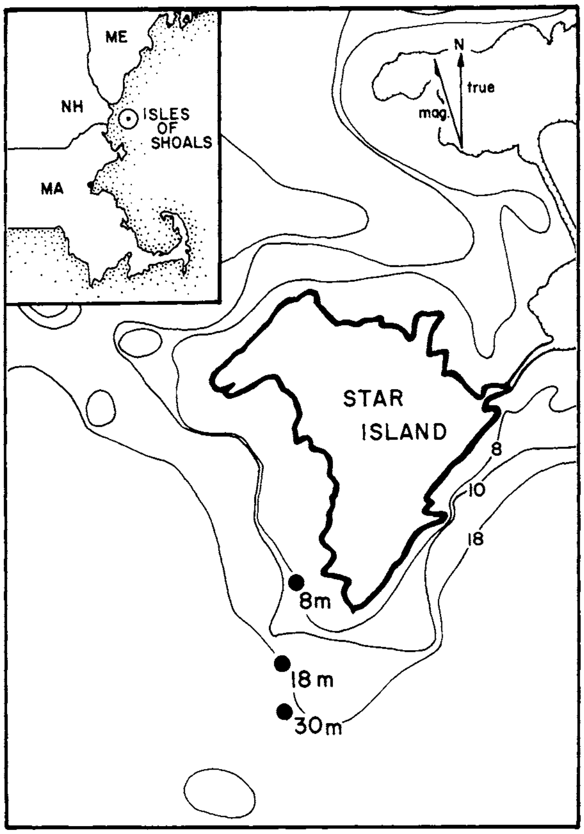


FIG. 1. Map showing the location of study sites at 8, 18, and 30 m depth off Star Island, Isles of Shoals. Depth contours in metres. Inset map shows location of Isles of Shoals in relation to New England coast.

While the effects of disturbance have been extensively studied in the rocky intertidal zone (Paine 1966, Dayton 1971, 1973, Levin and Paine 1974, Menge 1976, 1978, Sousa 1979, Lieberman et al. 1979, Paine and Levin 1981, Dethier 1984), little is known about how disturbance and the existence of refuges affect hard-bottom communities in the subtidal zone, particularly in cold-temperate regions. In temperate subtidal encrusting communities, as in rocky intertidal communities (Paine and Vadas 1969, Lubchenco 1978), coral reefs and rain forests (Connell 1978), and plant communities (Fox 1979, Grime 1979), species diversity is often maximized at intermediate levels of disturbance (Ayling 1981, Sebens 1985). As a group, echinoderms are probably the most important agents of biological disturbance in hard-bottom subtidal communities. For example, sea urchins cause catastrophic changes in the state of marine benthic ecosystems by consuming large algal stands and transforming productive kelp communities into denuded areas dominated by encrusting coralline algae (reviewed in Lawrence 1975; but see Moreno and Sutherland 1982). Sea stars influence subtidal communities both directly by consuming dominant prey organisms (Birkeland 1974, Dayton et al. 1974, Sloan and Aldridge 1981) and indirectly by creating grazer-free patches (Duggins 1984) and by restricting prey distribution to refuges (Watanabe 1984). In a study of the disturbance roles of fish, urchins, gastropods, and sponge disease in a warm-temperate subtidal community, Ayling (1981) ranked sea urchin grazing as the most important source of disturbance. In general, the role of fish predation in modifying temperate subtidal communities has not received wide attention (Choat 1982).

In this paper, I examine the effects of biological disturbance and the influence of a biologically generated refuge on the structure and dynamics of subtidal communities living on upper rock surfaces at the Isles of Shoals, New Hampshire, USA. I address three main questions. (1) Does biological disturbance affect the abundance, distribution, and diversity of benthic species in the subtidal zone? (2) Do aggregations of the large, structure-producing mussel *Modiolus modiolus* (L.) provide a spatial refuge from biological disturbance for the associated community of benthic invertebrates? (3) If so, what characteristics of *Modiolus* beds contribute toward their effectiveness as refuges? First, I recorded patterns of community structure at three depths (8, 18, 30 m) and in two types of habitat (inside and outside *Modiolus* beds), since the communities have not previously been quantitatively described. By conducting manipulative field experiments and documenting the results of a large-scale natural grazing experiment, I then demonstrated that subtidal mussel beds modify community structure by buffering the impact of two sources of biotic disturbance. Long-term photographic monitoring techniques have enabled me to show that *Modiolus* beds at all depths persisted for >5 yr and that shallow mussel beds resisted intensive grazing by sea urchins. The effectiveness of *Modiolus* beds as refuges is related to their persistence and their ability to resist the biotic disturbing forces that modify the distribution and abundance of other benthic organisms on upper rock surfaces.

STUDY AREA AND ORGANISMS

This study was conducted at three subtidal sites off the southwest corner of Star Island, at the Isles of Shoals (42°58′27″ N, 70°36′54″ W; Fig. 1). The sites are located on the most exposed side of the island and are impacted by oceanic swells originating from northeast, southeast, and southwest sectors. Wave heights range from 0.5 to 2.0 m in summer and from 0.5 to 7.0 m in winter (J. Witman, *personal observation*). Three sites were established at depths of 8, 18, and 30 m below mean low water on a sloping shelf composed of granitic gneiss. The bottom topography is heterogeneous, with large areas of rock dissected by small cracks and crevices.

Depth zonation of hard-bottom communities at Star Island is described in Witman (1984). Briefly, the shallowest subtidal zone (≈1–10 m) is dominated by a three-layered algal assemblage: a canopy of the kelp *Laminaria digitata* and *Laminaria saccharina* 1–2 m above the substratum, a 5–20 cm thick understory of red algae primarily composed of *Chondrus crispus, Phycodrys rubens, Phyllophora* spp., and *Corallina officinalis,* and a pavement of crustose coralline algae which covers, on average, 51% of the rock surface beneath fleshy red algae (L. Harris, *personal communication*).

The kelp-dominated zone ends abruptly at 10–12 m, where it is bordered by dense aggregations of *Strongylocentrotus.* Grazing by *Strongylocentrotus* controls the lower depth limit of kelp (Witman 1984). *Modiolus* forms spatially complex beds on upper rock surfaces throughout the New England subtidal, but is most abundant at intermediate depths (mean cover: 26.0% at 18 m at Star Island, 57.1% from 17 m at Murray Rock, a ledge 12 km north of Star Island; Table 1). *Agarum cribosum,* a kelp low on the preference hierarchy of sea urchins (Vadas 1977), and the red alga *Ptilota serrata* are the most conspicuous upright algae between 10 and 25 m. The primary substratum in this depth range is monpolized by crustose coralline algae.

Algal cover thins out between 25 and 30 m, probably as a result of poor light penetration to these depths (0.1% of surface irradiance at 27 m; J. Witman, *personal observation*). Deep subtidal communities (≈30 m) are characterized by a marked increase in the abundance of sessile invertebrates on upper rock surfaces (the sponge *Polymastia infrapilosa,* the octocoral *Clavularia modesta,* and ascidians). A 1–2 cm thick mat of amphipod tubes covers most nonvertical (upper) rock surfaces at 30 m depth.

This study focuses on factors controlling community structure at a given depth. Factors maintaining differences in community structure between depths (vertical zonation) are not considered here.

METHODS

All sampling and experimentation were carried out in situ using SCUBA. Disruptive sampling techniques were used to quantify the species composition of multispecies assemblages living on upper rock surfaces inside and outside *Modiolus* beds. At each of three depths (8, 18, and 30 m) five 0.25-m^2 quadrat samples were randomly taken inside and outside of mussel beds. All organisms within the quadrat were removed by scraping with a putty knife and simultaneously vacuuming with an airlift. Disruptive sampling was completed within one season in spring 1979. Samples were preserved in 10% buffered formaldehyde and sorted under a dissecting microscope to ensure that small specimens were not overlooked. With the exception of foraminifera and nematodes, all invertebrates were identified to species and counted. All upright algae were identified to species. Crustose coralline and fleshy red crustose algae encrusted mussel shells and rock substrata; they were omitted because the crusts on rock substrata were impossible to sample by the airlift method.

TABLE 1. Percent cover of *Modiolus modiolus* in 0.25-m^2 quadrats photographed at Star Island (42°58′27″ N, 70°36′54″ W) and at Murray Rock (43°04′15″ N, 70°37′20″ W), a ledge 12 km to the north. (See Witman 1984 for photographic sampling methods.)

Depth (m)	No. quadrats	*Modiolus* percent cover Mean	SD
Star Island			
4	32	0.3	0.2
8	32	5.0	15.4
12	32	22.0	31.5
18	32	26.0	35.4
24	32	3.8	5.2
32	32	1.6	3.6
Murray Rock			
8	40	7.8	10.0
11	40	29.1	24.2
14	40	33.6	21.7
17	40	57.1	30.2

To determine the appropriate quadrat size for sampling, a series of airlift samples of progressively larger sizes were collected from *Modiolus* beds and analyzed for species richness. The following five quadrat sizes were used: 156, 625, 1600, 2500, and 5000 cm^2. Species richness (S, the total number of species) and quadrat area (A, in square centimetres) were related as:

$$S = -11.81 + 10.28 \ln A,$$

with $r^2 = 0.96$. A plot of species richness vs. quadrat area revealed that the asymptote occurred between 1600 and 2500 cm^2, indicating that each 0.25-m^2 sample was near local species saturation; doubling the quadrat size from 2500 cm^2 to 5000 cm^2, added only three species ($S = 70$ at 2500 cm^2, $S = 73$ at 5000 cm^2). Consequently, the samples provided an adequate basis for comparisons of species richness between habitats.

Multivariate analysis

Cluster analysis was used to classify species into groups with similar patterns of distribution. Species density data were input as a two-way data matrix consisting of 80 species (rows) × 30 samples (columns) into the CLUSTAN 2.1 computer program (Wishart 1982). The matrix analyzed was a subset of the original data matrix, which contained 171 invertebrate species. Ninety-one species were excluded from the analysis because they occurred in <3 of the 10 samples at a single depth. Rare species are commonly deleted from large data sets prior to cluster analysis because their co-occurrence is primarily due to chance rather than similar habitat requirements (Boesch 1977:12). Because encrusting bryozoans and macroalgae fragmented during the sampling process, distinct individuals could not be recognized. Therefore, these taxa were excluded from cluster analysis but were included in calculations of species richness. *Modiolus* was omitted from the analysis to avoid biasing the calculation of group similarities. Densites ranged from 0 to 2164 individuals/0.25 m^2. To prevent the loss of information on species distributions, the data were square-root transformed prior to analysis, which reduced the obscuration of the clustering of the less abundant species by the dominant species clusters (Gauch 1982:22).

The analytical procedure consisted of two steps: (1) product-moment correlation coefficients were calculated to determine the level of similarity among species in the data matrix; (2) a group-average linkage algorithm constructed a dendrogram. In combination, these techniques provided an objective basis for revealing patterns of community structure. Product-moment correlation provides an objective criterion for deciding which clusters are similar. With this technique, coefficients are constrained between -1 (complete dissimilarity) and $+1$ (complete similarity). Clusters linked at positive nonzero values are considered similar (Bush 1980, Humphrey et al. 1983). Group average linkage minimizes the distortion of relationships in the similarity matrix during the construction of the dendrogram (Boesch 1977:51).

Postclustering statistics identified the common distribution pattern among members of a cluster. For each species, two-way ANOVA was conducted to assess the effect of depth (8, 18, or 30 m) and habitat (inside or outside *Modiolus* beds) on species density. Means, standard deviations, and significance levels are listed in the Appendix. To eliminate heteroscedasticity, the data were $\log(x + 1)$-transformed before analysis. $F_{\max}$ tests (Sokal and Rohlf 1969) were nonsignificant for all 80 species, indicating that the assumptions of homoscedasticity had not been violated. Where the interaction of depth and habitat were nonsignificant, differences among depth and habitat means were compared by a Student-Newman-Keuls test (as in Underwood 1981).

Predation experiments

The hypothesis that the *Modiolus* beds function as a spatial refuge from predation was tested for a selected group of invertebrates by controlled experimentation at the 8 m depth. By definition, a habitat represents a spatial refuge for an organism if its likelihood of death is reduced by the habitat structure (Woodin 1978). Accordingly, the experiments described below were designed to monitor the mortality rates of invertebrates inside and outside *Modiolus* beds.

A large steel rack was constructed to hold eight 0.1-m^2 plexiglass panels flat against the substratum. Mussel beds were created on half of the panels prior to the experiments by transplanting 10 live *M. modiolus* to each panel and allowing byssal attachments to form. Thus, there were four panels for each of two treatments: presence or absence of mussel bed structure. Treatment panels were interspersed in a systematic design (Hurlburt 1984). The general experimental procedure consisted of placing equal densities of invertebrate prey in the two treatments and in two 0.5-m^2 predator exclusion cages (controls). Predation attacks were monitored by direct observation and time-lapse photography with a Nikon F2 motor-drive camera equipped with a 250-exposure magazine and an intervalometer. The null hypothesis of no difference in the mortality of experimental prey inside and outside mussel beds was to be rejected if deaths by predation differed between treatments.

Three species of invertebrates (the bivalve *Hiatella arctica,* and sea urchin *Strongylocentrotus droebachiensis,* and the ophiuroid *Ophiopholis aculeata*) were selected as prey because they are abundant inside *Modiolus* aggregations (Appendix). Data on the population structure of these species were utilized to select a range of naturally occurring sizes and densities for use in the experiments (Witman 1984). Movement of the prey organisms was restricted so that they remained at position inside or outside of the mussel beds. This was accomplished for *Hiatella arctica* by gluing small Velcro pads (hooks) to the shells of live individuals and placing them on reciprocal Velcro pads (rugs) on the plexiglass panels. The rugs had been glued to each panel in a random pattern prior to the initiation of the experiment. Eight of the Velcro *Hiatella* were attached to Velcro rugs on each panel (for a total of 32 *Hiatella* per treatment). On the mussel bed panels, Velcro *Hiatella* occupied positions at the base of the aggregation, between the mussels. Two trials were conducted with *Hi. arctica* prey. The first trial began on 12 August 1982 and was monitored by diving at approximately 4-h intervals for a 29-h period. Trial 2 began on 30 September 1982 and ran for 32 h; predation attacks were monitored by time-lapse photography.

Sea urchins were prevented from leaving the experimental habitat by tethering individual urchins to a central eyebolt in each panel. Five urchins were tethered to each panel by tying fine monofilament around the tests (total: 20 urchins with mussels, 20 without mussels). The size of sea urchins used in the experiments (29 mm mean test diameter) corresponded to the secondary mode of the bimodal size distribution of urchins from *Modiolus* beds at 8 m (28 mm; Witman 1984). An additional eight panels, each with five tethered sea urchins, were placed inside predator exclusion cages as controls. The urchin trial began on 2 October 1982. Rates of predation on *Strongylocentrotus* were slower than on *Hiatella* and *Ophiopholis,* so the survival of sea urchins was monitored by diving at ≈6-h intervals for 45 h.

Ophiuroids were sewn and tied to small lead sinkers with fine monofilament. The aboral surface of the disc was pierced with a fine needle through the mouth and a knot was tied around the disc. No ophiuroids died as a result of this procedure. An experiment was conducted to test the hypothesis that pierced ophiuroids incurred artifically high predation rates due to the attraction of chemosensory predators. In this experiment, two sets of six sinkers, with four tethered ophiuroids per sinker, were placed on the bottom 6 m apart. One set of ophiuroids were sutured as described above and the other group was tethered by double-tying each ophiuroid with monofilament (which is very laborious). Survival of ophiuroids was monitored by diving.

The design of the *Ophiopholis* experiments differed from the experiments with *Hiatella* and *Strongylocentrotus.* Instead of placing prey on panels, tethered ophiuroids were placed inside and outside a natural *M. modiolus* bed to simulate the natural habitat of *Ophiopholis.* Six sinkers with four *Ophiopholis* each were placed between mussels in the mussel bed, and another six sinkers were placed on the substratum (1 m away). The time-lapse camera was focused on the experiment and photographs were taken at 5-min intervals during the two trials. Trial 1 began at night on 6 October 1982 and continued for 8.5 h. In contrast, trial 2 began during the day on 7 October 1982, but was terminated after 6 h due to a northeast storm.

Band transects were used to determine the densities of predators in the vicinity of the 8 m site where the predation refuge experiments were conducted. A 25-m transect line was randomly dropped onto the substratum and all predatory fish and invertebrates within a 1-m band along the line were counted. To evaluate diel and seasonal variation in predator abundance, three replicate transects were conducted during the day and night in September 1982 and February 1983.

Natural grazing experiment

Multispecies assemblages at the 8 m study site were radically altered when a dense front of large *Strongylocentrotus droebachiensis* (46.3 mm mean test diameter; maximum density 70 individuals/0.25 m^2) advanced into the study area in December 1981 (Witman et al. 1982). This served as a large natural experiment in which to evaluate the hypothesis that the *Modiolus* beds provide a refuge from intense grazing by sea urchins. The abundance and distribution of benthic invertebrates and macroalgae had been quantified in April 1979, when this site was a kelp bed. At that time, the kelps *Laminaria digitata* and *Laminaria saccharina* formed a canopy above a dense understory of red algae. During April 1982, 1 mo after the kelp forest had been denuded and transformed into a community dominated by crustose coralline algae, the communities were re-sampled using the same techniques as in 1979. As before, five 0.25-m^2 quadrats were airlifted inside and outside *Modiolus* beds (n = 10 samples). Because the 1979 samples had been collected before severe grazing occurred, it was assumed that differences in species composition between the 1979 and 1982 samples were primarily due to urchin grazing effects. There was no perceptible change between 1979 and 1982 in the species composition of communities in nearby kelp beds that escaped urchin damage (J. Witman, *personal observation*). After the disturbance event, care was taken to sample in the same month as before (April), to mitigate against the effect of seasonality on species composition. The term "coralline flats" (Ayling 1981) is used here to describe areas where sea urchins have consumed all understory and canopy-forming algae, leaving communities dominated by crustose coralline algae ("urchin-dominated barren grounds" of Lawrence 1975, "Isoyake areas" of Hagen 1983).

Quantitative comparisons of communities before and after urchin disturbance were made by cluster analysis, by rank analysis, and by calculating species diversity indices. For cluster analysis, species density data were entered into the CLUSTAN 2.1 computer program (Wishart 1982) as a matrix of 20 rows (samples) × 74 columns (species). Half of the rows represented samples from 1979; the other half were 1982 samples. The data were reduced and transformed prior to analysis by the methods described above (see Multivariate Analysis). Product-moment correlation and group average linkage were performed. This time, however, samples were clustered to compare faunas from pre- and postdisturbance periods. Rank analysis (Fager 1957) was used to examine the effect of urchin disturbance on the rank order of dominant species in the 8 m community. Two measures of species diversity were used: (1) the Shannon-Wiener information theory index (H') with the evenness component (J') and (2) species richness (S). Shannon-Wiener and evenness indices were calculated using natural logarithms according to the formulas in Pielou (1974:290, 301). Species richness represents the total number of species in the community. This index has the advantage of being intuitively simple, and may be a better indicator of biological change than H' (Green 1977).

The 8 m species were classified into four functional groups: infauna, epifauna, mobile fauna (see Appendix), and upright algae (Witman 1984). The interpretation of the effect of severe grazing was facilitated by making comparisons within functional groups before and after urchin disturbance. Upright algae included all foliose, filamentous, corticated, and leathery algae (divisions of Steneck and Watling 1982). Infauna were defined as species living in sediments or cryptic habitats, while mobile fauna were those species that moved freely throughout the mussel aggregation. Epifauna were attached to mussels or rock substrata.

Monitored mussel beds

The persistence of individual *Modiolus* beds at different depths was determined by long-term photographic monitoring. Underwater epoxy marked four corners of each 0.25-m^2 plot around *Modiolus* beds. Beginning in January 1979, four mussel beds were monitored at each of three depths (8, 18, and 30 m; n = 12 beds). The epoxy marks served as alignment guides for a fixed aluminum camera frame (quadrapod)

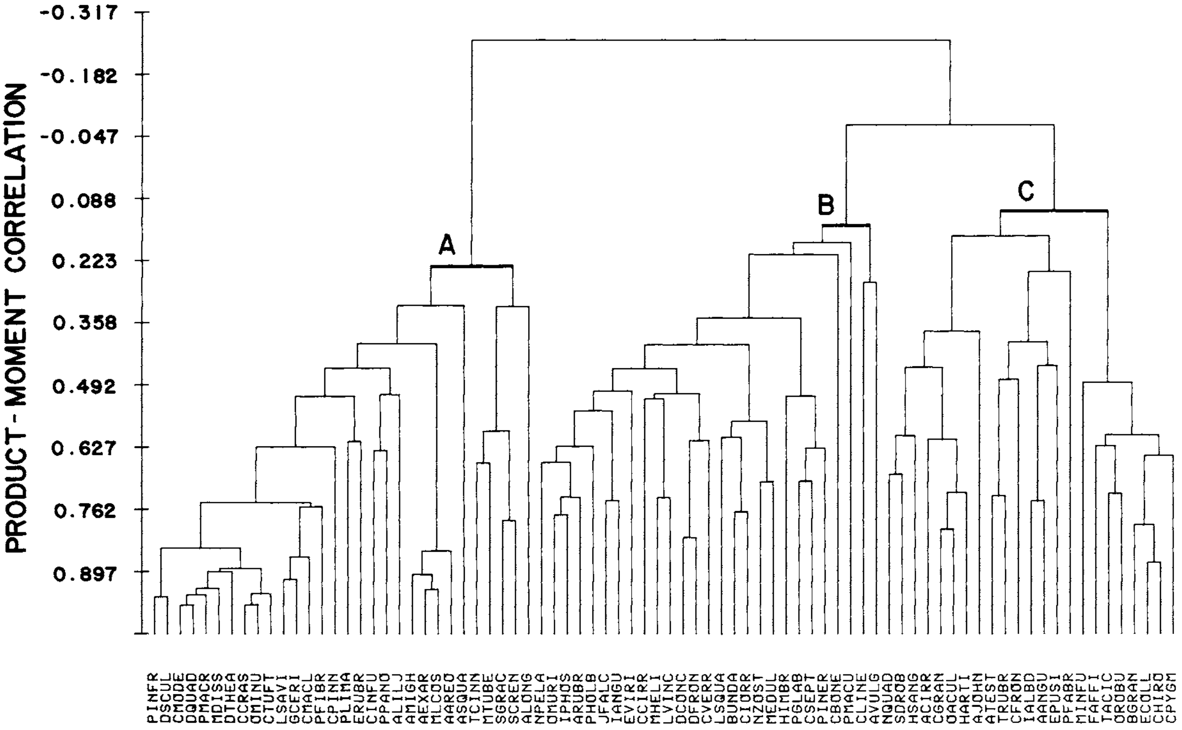


FIG. 2. Dendrogram resulting from group average clustering of 80 invertebrate species. Species are indicated by code at bottom, which can be matched with species names and densities in the Appendix. Group A represents substrate community at 30 m depth outside *Modiolus* beds, group B a substrate community at 8–18 m outside *Modiolus* beds, and group C the *Modiolus* community.

specially designed for the photography of 0.25-m^2 quadrats. A Nikonos camera with a 15 mm wide-angle lens and two electronic strobes were all mounted on the quadrapod. Marked mussel beds were photographed 3–6 times/yr for 5 yr. Mussels were easily counted from the photographs; individual mussels were identified by specific patterns of crustose coralline algae encrusting the shells and by their position within the bed. No mussels emigrated from the monitored beds, since *Modiolus* is incapable of breaking byssus threads and crawling away once attached (Stanley 1970). Each time the beds were photographed (and on many other dives) notes were taken on specific sources of mussel mortality. In conjuction with the photographs, these observations enabled three sources of mortality to be differentiated: (1) dislodgement of mussels following overgrowth by kelp; (2) predation by *Asterias vulgaris*; and (3) shell-crushing predation by crabs and lobsters. Ten percent of mussel deaths could not be attributed to a specific source of mortality. Two unexplained categories were (1) gaping mussels and (2) disappearance of individual mussels. Mortality rates of *Modiolus* were calculated from the photographic record.

RESULTS

Benthic communities

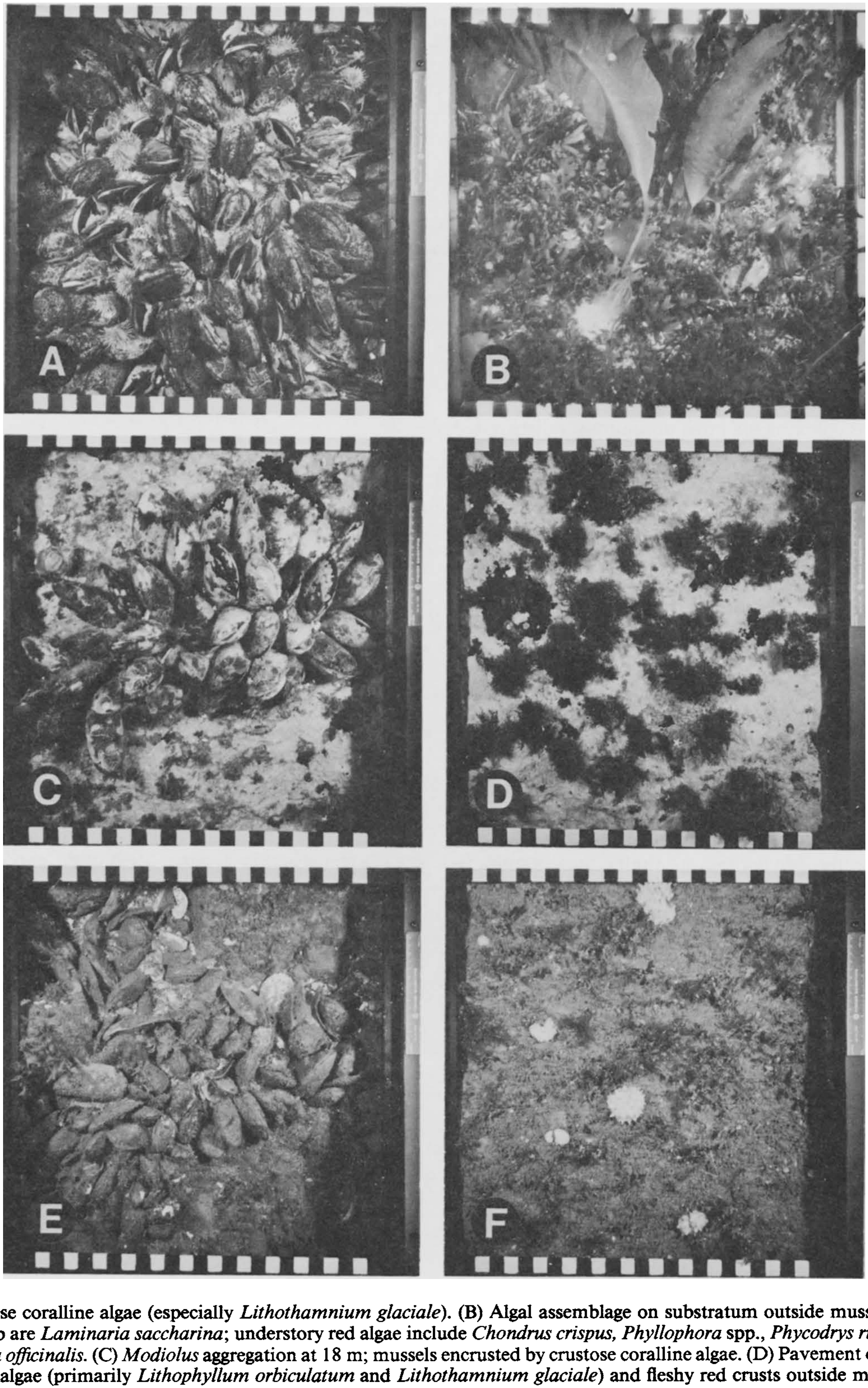
Cluster analysis separated the 80 common species of benthic invertebrates into three major groups (Fig. 2). The species composition of each of these groups is listed in the Appendix. Two-way analysis of variance indicated that there was a significant effect of both depth and habitat on the distributions of all species in groups A, B, and C (Appendix).

Group A consists of species that were most abundant at 30 m depth outside the mussel beds (Fig. 3F). In terms of both number of species and number of individuals, group A was dominated by gammarid amphipods. Most of the habitat structure in this community was created by the numerically dominant gammarid *Photis macrocoxa*, which constructs a matrix of tubes on the rock surface. The most abundant encrusting invertebrates were a demosponge *Polymastia infrapilosa*, an octocoral *Clavularia modesta*, and the ascidians *Chelyosoma macleayanum* and *Polycarpa fibrosa*. The interaction of depth and habitat factors in two-way ANOVA was significant for all but eight

---

→

FIG. 3. Photoquadrats (0.25 m^2) of benthic habitats sampled. Increments at top and bottom of each quadrat are 2 cm wide. (A) *Modiolus* aggregation at 8 m; note *Strongylocentrotus droebachiensis* in between mussels. Mussel shells are encrusted



by crustose coralline algae (especially *Lithothamnium glaciale*). (B) Algal assemblage on substratum outside mussel beds at 8 m. Kelp are *Laminaria saccharina*; understory red algae include *Chondrus crispus, Phyllophora* spp., *Phycodrys rubens,* and *Corallina officinalis.* (C) *Modiolus* aggregation at 18 m; mussels encrusted by crustose coralline algae. (D) Pavement of crustose coralline algae (primarily *Lithophyllum orbiculatum* and *Lithothamnium glaciale*) and fleshy red crusts outside mussel beds at 18 m. Tufts of upright algae are *Ptilota serrata.* (E) *Modiolus* aggregation at 30 m. (F) Substratum outside mussel beds at 30 m covered by a matrix of amphipod tubes (*Photis macrocoxa*). Sponges are *Polymastia infrapilosa*; upright algae are primarily *Ptilota serrata.* Cluster group A (in Fig. 2) composed of species from habitat depicted in photoquadrat (F); cluster group B composed of species occurring in habitats illustrated in photoquadrats (B) and (D); cluster group C composed of species inhabiting mussel beds shown in photoquadrats (A), (C), and (E).

TABLE 2. Mean densities of infauna in 0.25-m² quadrats inside and outside *Modiolus* beds.

Depth (m)	Habitat	No. of quadrats	Density (no./0.25 m²) $\bar{X}$ ± SE	One-way ANOVA results F	P
8	*Modiolus* bed	5	374 ± 69.7	10.2	<.025
	Outside substratum	5	161 ± 25.5		
18	*Modiolus* bed	5	541 ± 77.8	34.9	<.001
	Outside substratum	5	65 ± 21		
30	*Modiolus* bed	5	308 ± 35.2	7.7	<.025
	Outside substratum	5	191 ± 27.5		

species. The results of Student-Newman-Keuls (SNK) tests on densities of these eight species indicated that they were significantly more abundant outside the mussel beds at 30 m (Appendix).

Group B contains the most ubiquitously distributed species, which attained maximum densities outside the mussel bed at either 8 or 18 m depth. This is supported by SNK tests on the 14 species without significant interaction terms; all these species were significantly more abundant outside mussel beds (Appendix). Within the group B assemblage of 27 species, polychaetes and amphipods had high species richness (eight and seven species, respectively). The three most abundant species in group B were the amphipods *Ischyrocerus anguipes* and *Pontogenia inermis,* and the herbivorous gastropod *Lacuna vincta.* All three dominants principally inhabited algal assemblages outside the mussel beds at 8 or 18 m (Fig. 3B, D).

Members of group C were all most abundant within the mussel beds, at either 8, 18, or 30 m depth (Appendix, Fig. 3A, C, E). Consequently, group C was designated the *Modiolus* community. It was numerically dominated by the ophiuroid *Ophiopholis aculeata,* which lived between mussels at the base of the aggregation. Other numerically important (>30 individuals per 0.25-m² sample) taxa inhabiting the base of the mussel bed included the polychaetes *Cistenides granulata, Nainereis quadricuspida, Amphitrite cirrata, Amphitrite johnstoni,* the ophiuroid *Ophiura robusta,* and the hiatellid bivalve *Hiatella arctica. Strongylocentrotus droebachiensis* was abundant in the upper portion of the mussel bed. SNK tests conducted on the 13 species without significant interaction terms indicated that the mean densities of all these taxa were significantly higher inside the mussel beds than on the substratum outside the mussel beds (Appendix). Although all 23 species in group C were most abundant in mussel bed habitats, the majority of these species (18) were also present in other habitats sampled, at low densities. The five species that only occurred inside *Modiolus* beds were the polychaetes *Cistenides granulata, Myxicola infundibulum,* and *Brada granosa,* and the holothuroids *Cucumaria frondosa* and *Chiridota laevis.* One-way ANOVA was performed on log(x + 1)-transformed data to compare mean densities of infaunal invertebrates inside and outside mussel beds. Table 2 shows that there were significantly higher densities of infauna in the mussel beds than on the substratum outside the beds at each of the three depths.

Predation experiments

Two characteristics of *Modiolus* community structure were: (1) 23 species showed their greatest abundance in the mussel beds and (2) overall densities of infaunal organisms were higher in *Modiolus* beds than elsewhere. To search for the mechanisms maintaining these patterns of community structure, five predation experiments were carried out.

Hiatella arctica: *trial 1.*—Predation on *Hiatella* outside the experimental mussel beds was dramatic (Fig. 4). Within an hour, three *Hiatella* outside the beds were consumed by predators. In 29 h, mobile predators had consumed all 32 *Hiatella* outside the mussel beds, while only two *Hiatella* were eaten inside the mussel beds.

The predator guild consisted of the crabs *Cancer irroratus* and *Cancer borealis,* the lobster *Homarus americanus,* the neogastropod *Buccinum undatum,* and the sea star *Asterias vulgaris.* Most of the exposed *Hiatella* were eaten by *Cancer borealis,* which foraged nocturnally, as did *Ho. americanus* (Fig. 4). *Buccinum undatum, Asterias vulgaris,* and *C. irroratus* fed on *Hiatella* during the day. *Hiatella* outside the mussel beds were devastated by nocturnal predation; between 1900 and 0100, 21 exposed individuals were consumed. Ten of these predation events were witnessed during the 0100 dive. At this time, four large *C. borealis* were seen eating a total of nine *Hiatella,* and one lobster was observed with a Velcro *Hiatella* in its crusher claw. The remaining 11 attacks were not witnessed. All that remained on the outside panels were crushed *Hiatella* shells and 10 Velcro pads from the prey. It is suspected that the crushed shells indicated crab or lobster predation, since rock crabs and lobsters are known to crush bivalve and sea urchin prey (Elner 1980, J. Witman, *personal observation*), and both *Asterias* and *Buccinum* left empty, intact shells still attached to the panels after predation. *Asterias* was the only predator that penetrated the mussel bed, consuming two *Hiatella* (Fig. 4).

Hiatella arctica: *trial 2.*—Nineteen hours of the second *Hiatella* trial were monitored by time-lapse photography, to follow the sequence of predation directly.

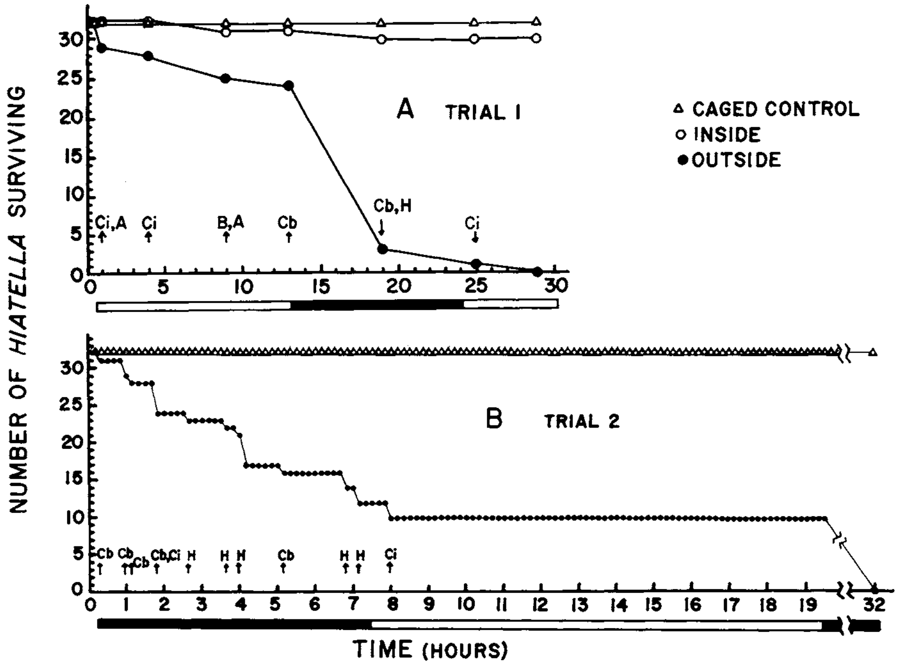


FIG. 4. Results of predation experiments with the bivalve *Hiatella arctica* as prey inside and outside *Modiolus* beds. (A) Trial 1, monitored directly by diving. Note high predation at night. (B) Trial 2, monitored remotely by time-lapse photography for 19 h; break in X axis indicates that remainder of trial was monitored by diving. Predators responsible for attacks represented as Ci = *Cancer irroratus*; A = *Asterias vulgaris*; B = *Buccinum undatum*; Cb = *Cancer borealis*; H = *Homarus americanus*; T = *Tautogolabrus adspersus*; P = *Pseudopleuronectes americanus*. Light and dark bars below X axis indicate hours of daylight and darkness.

The camera was placed 2.5 m from the center of the experiment to photograph the entire rack at 10-min intervals. Unlike the first trial, which was started in the morning, the second trial was begun at night. This permitted diel variation in the intensity of predation to be evaluated.

Fig. 4 shows that, as in trial 1, deaths from predation were greater outside the mussel beds. The camera ran out of film after 19 h and 40 min. Consequently, the survivorship of the remaining prey had to be monitored by diving. Between 1830 and 0600 the last 10 *Hiatella* outside the mussel beds were eaten. As before, crushed shells were left on the panels, implicating crab or lobster predators. None of the *Hiatella* inside the mussel beds was consumed during the 32-h experiment; thus, the experimental mussel beds were as effective as the predator exclusion cages in deterring predation (Fig. 4).

Crabs and lobsters accounted for all the predation directly observed in trial 2. The majority of Velcro *Hiatella* (10) were eaten by three small lobsters. *Cancer borealis* was a significant predator, consuming eight of the exposed *Hiatella.*

Data from the first and second trial were pooled to evaluate diel variation in predation intensity. This analysis was possible because the hours of daylight and darkness were approximately equivalent (30 h day, 29.5 h night). Chi-square analysis indicated that predation mortality was significantly higher at night than during the day ($\chi^2 = 28.8$, 1 df, $P < .005$ with Yates' correction for sample size).

Strongylocentrotus droebachiensis trial. —Fig. 5 shows that there was a striking difference in the survivorship of urchins inside and outside *Modiolus* beds. Within 44 h, all exposed urchins were consumed by crabs, cunner (*Tautogolabrus adspersus*), and a lobster. In contrast, no urchins were eaten inside the mussel beds or in the control cages.

There was evidence of a temporal pattern of pred-

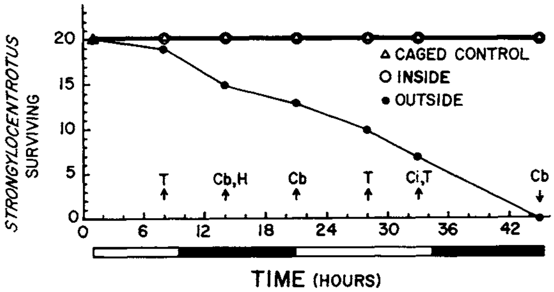


FIG. 5. Results of predation experiment with *Strongylocentrotus droebachiensis* as prey inside and outside *Modiolus* beds. Survival of sea urchin prey monitored directly by diving; predator symbols as in Fig. 4.

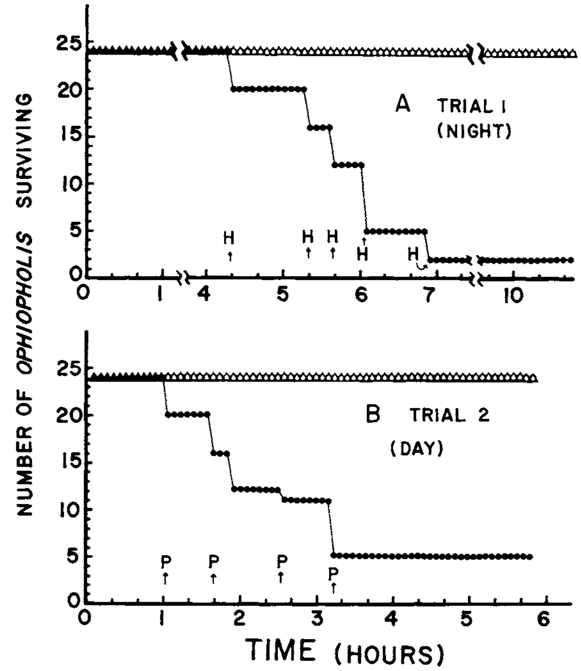


FIG. 6. Results of predation experiments with *Ophiopholis aculeata* as prey inside and outside *Modiolus* beds. △ = caged control; ○ = inside; ● = outside. Note that ○ and △ are superimposed at all times. (A) Trial 1, conducted at night; note that *Homarus americanus* accounted for all attacks. (B) Trial 2, conducted during the day; all attacks were by *Pseudopleuronectes americanus*. Both trials monitored remotely by time-lapse photography; predator symbols as in Fig. 4.

TABLE 3. Experimental comparison of predation on *Ophiopholis aculeata* tethered by two different methods: ophiuroid disk pierced and sewn vs. monofilament double-tied around disk (nonpierced).

	No. *Ophiopholis* remaining*	
Time	Pierced	Nonpierced
1900	24	24
2330	19†	17‡
0700	0	0

* The number of *Ophiopholis* remaining on the substratum was determined by direct observation.

† *Cancer borealis* observed feeding on four tethered *Ophiopholis.*

‡ *Homarus americanus* observed feeding on four tethered *Ophiopholis.*

ators on exposed urchins. With the exception of one attack by *Cancer irroratus* during the day, crab predation was greatest at night because *C. borealis* preyed on urchins only at night. Cunner were important predators during the day, consuming six urchins. The feeding behavior of these fish consisted of an initial strike to damage the urchin test and to expose the viscera, which were subsequently picked out. The only lobster attack occurred at midnight when a juvenile lobster was seen moving away from the experimental site with two tethered urchins in its claw.

There was no significant difference between the number of urchins preyed on at night and the number eaten during the day ($\chi^2 = 1.5$, 1 df, $P > .05$ with Yates' correction for sample size).

Ophiopholis aculeata: *trial 1.*—Although crabs and lobsters were present 65 min after the experiment began, no *Ophiopholis* were attacked until 3 h later, when a small lobster dragged away four tethered ophiuroids from outside the mussel beds (Fig. 6). Lobsters continued to prey on exposed ophiuroids throughout the night. By 0215, all but two *Ophiopholis* were consumed by three different lobsters. None of the ophiuroids in

TABLE 4. Densities of predatory fish and invertebrates at the site of the predation experiments, 8 m depth. Summer survey conducted in September 1982, winter survey in February 1983. $n = 3$ transects, each 25.0 m^2.

	Predator density (no./25.0 m^2; $\bar{X}$ ± SD)						
	Summer			Winter			Summer vs. winter
	Day	Night	P*	Day	Night†	P*	P
		Fish					
Tautogolabrus adspersus	21.6 ± 2.0	0.3 ± 0.6	<.05	0	0		Not seen in winter
Pseudopleuronectes americanus	3.0 ± 1.0	0	<.05	0	0		Not seen in winter
Gadhus morhua	0	1.6 ± 0.5	NS	0	0		Not seen in winter
Pollachius virens	0	22.6 ± 2.5	<.05	0	0		Not seen in winter
Macrozoaraces americanus	0.3 ± 0.5	0.6 ± 0.5	NS	1.3 ± 0.5	1.0 ± 1.0	NS	NS
		Invertebrates					
Asterias vulgaris	152.6 ± 23.7	172 ± 8.2	NS	105.6 ± 6.1	106.3 ± 11.8	NS	NS
Buccinum undatum	8.6 ± 2.5	6.6 ± 1.5	NS	9.6 ± 1.5	9.3 ± 2.5	NS	NS
Cancer irroratus	2.6 ± 1.5	6.3 ± 1.5	<.05	0.3 ± 0.6	3.6 ± 0.6	<.05	NS
Cancer borealis	6.0 ± 1.0	15.3 ± 2.5	<.05	3.0 ± 1.0	8.3 ± 1.5	<.05	NS
Homarus americanus	2.6 ± 0.6	8 ± 1	<.05	0.7 ± 0.6	4.3 ± 0.5	<.05	NS

* Results of Wilcoxon two-sample tests comparing daytime and nighttime densities. NS = not significant.
† 1800; dark, but not late at night.

the mussel beds was eaten throughout the 10.5-h experiment.

Ophiopholis aculeata: *trial 2.*—A second trial was initiated during the day. In contrast to trial 1, in which lobsters accounted for all nocturnal predation, all of the daytime predation was by winter flounder, *Pseudopleuronectes americanus* (Fig. 6). Most of the predation was by a single large flounder (35 cm total length) that fed on exposed *Ophiopholis* for 70 min. Later, a small flounder (20 cm total length) consumed seven ophiuroids. As in the first trial, no ophiuroids in the *Modiolus* beds were consumed.

The results of the experiment testing for artifacts associated with the method of tethering *Ophiopholis* are presented in Table 3. The result was the same for pierced and nonpierced individuals; all ophiuroids were eaten by morning. During the 2330 dive, a *Cancer borealis* was seen feeding on pierced *Ophiopholis* and a lobster was observed with four nonpierced ophiuroids in its claw. These results falsify the hypothesis that the intensity of predation is higher on pierced *Ophiopholis.*

In summary, virtually all the prey organisms placed in the experimental mussel beds escaped predation during the five refuge experiments, clearly supporting the hypothesis that the mussel beds are refuges from predation for the dominant species of the *Modiolus* community.

Predator abundance

Table 4 shows diel and seasonal variation in the abundance of major predators in the vicinity of the experimental site at 8 m depth. Common predatory fish included the cunner, *Tautogolabrus adspersus,* winter flounder *Pseudopleuronectes americanus,* and pollock, *Pollachius virens.* Eelpout, *Macrozoaraces americanus,* were present in low densities and cod, *Gadhus morhua,* were rare. Eelpout were present during summer and winter. Other fish were seen only in summer transects. During the summer, both cunner and flounder were significantly more abundant during the day than during the night (Table 4). Pollock showed the opposite trend, and were commonly observed feeding on planktonic organisms at night.

In contrast, there was no seasonality in the abundance of invertebrate predators. All of the five major predators (*Asterias vulgaris, Buccinum undatum, Cancer irroratus, Cancer borealis,* and *Homarus americanus*) were present at the 8 m study site during the winter as well as the summer. All three crustacean predators (*C. irroratus, C. borealis,* and *Ho. americanus*) were significantly more abundant at night than in the day (Table 4). *Asterias* and *Buccinum* were present in high densities, and showed no significant diel or seasonal variation in abundance.

Effect of sea urchin disturbance

Species composition.—The dendrogram in Fig. 7 is the result of cluster analysis of samples from the 8 m community before and after it was intensively grazed by sea urchins. The analysis designated four major groups. Group A includes four *Modiolus* bed samples from before urchin disturbance; these clustered out together, along with one predisturbance substratum sample. Group B is the combination of one predisturbance and four postdisturbance *Modiolus* bed samples. In contrast with the *Modiolus* samples, samples from the community on the substratum outside the mussel beds separated into distinct predisturbance (group C) and postdisturbance (group D) clusters. Group C represents the invertebrate community associated with the kelp bed before it was severely grazed by urchins. All samples from the coralline flats clustered out in group D, which was characterized by the highest degree of internal similarity (samples linked at 0.30). This reflects the extreme change in community composition that was brought about by intensive grazing. The inclusion of both pre- and postdisturbance samples in *Modiolus* cluster B indicates that urchin disturbance caused less change in species composition inside the mussel beds than on the substratum outside the mussel beds.

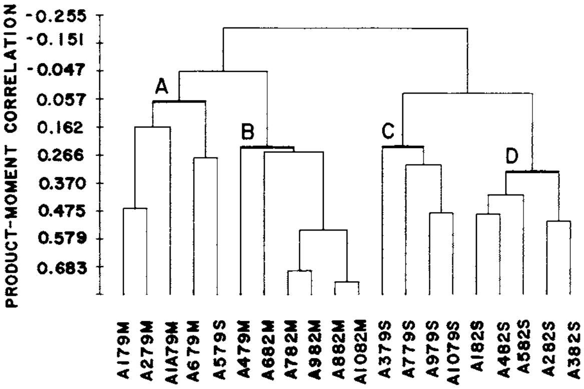


FIG. 7. Dendrogram resulting from group average clustering of 20 samples collected at 8 m study site before and after severe urchin grazing. Group A consists of four predisturbance *Modiolus* bed samples and one predisturbance outside substratum sample; group B composed of pre- and postdisturbance *Modiolus* bed samples; group C composed of predisturbance outside substratum samples (kelp forest community); and group D consists of postdisturbance outside substratum samples (coralline flats community).

Dominant species: outside substratum community.—Before disturbance, multispecies assemblages associated with the kelp beds were dominated by the herbivorous gastropod *Lacuna vincta* (Table 5A). Of the 10 top-ranked species, 6 are gammarid amphipods. A majority of the dominant amphipods (*Ischyrocerus anguipes, Corophium bonelli, Ampithoe rubricata,* and *Jassa falcata*) are tube dwellers (Bousfield 1973, Dickenson and Wigley 1981). *Pontogenia inermis* is pelagic and epibenthic, while *Pleusymtes glaber* is epibenthic on hard substrata (Bousfield 1973). Of significant note are the high densities of herbivores (*L. vincta, A. rubri-*

TABLE 5. Rank analysis of abundances of dominant species inside and outside the mussel beds before and after urchin disturbance. Maximum score is 50.

A) Samples collected from substratum outside mussel beds; $n = 5$ quadrats, each 0.25 m^2

Species (group)*	Rank	Score	Density (no./0.25 m^2; $\bar{X}$ ± SD)
	Before disturbance		
Lacuna vincta (G)	1	45	255 ± 163
Pontogeneia inermis (A)	2	43	199 ± 82.4
Ischyrocerus anguipes (A)	3	34	386 ± 593
Pleusymtes glaber (A)	4	32	120.4 ± 70.7
Corophium bonelli (A)	5	29	142.2 ± 122.8
Ampithoe rubricata (A)	6	27	116.6 ± 97.4
Jassa falcata (A)	7	24	188 ± 254
Ophiopholis aculeata (O)	8	15	61.2 ± 34.3
Caprella linearis (C)	9	8	64.2 ± 61.5
Idotea phosphorea (I)	10	7	38.2 ± 27.6
	After disturbance		
Pontogeneia inermis (A)	1	50	294 ± 126.8
Ischyrocerus anguipes (A)	2	37	19.2 ± 10.5
Strongylocentrotus droebachiensis (E)	3	36	15.6 ± 11.5
Tonicella rubra (CH)	4	30	16.6 ± 7.9
Asterias vulgaris (AS)	5	27	15.6 ± 7.4
Pleusymtes glaber (A)	6	24	14.4 ± 13.8
Onchidoris muricata (NU)	7	16	12.8 ± 21
Corophium bonelli (A)	8	13	9.8 ± 11.2
Ampithoe rubricata (A)	9	12	9.8 ± 11.9
Nereis pelagica (P)	10	10	5.6 ± 3.8

B) Samples collected inside mussel beds; $n = 5$ quadrats, each 0.25 m^2

Species (group)	Rank	Score	Density (no./0.25 m^2; $\bar{X}$ ± SD)
	Before disturbance		
Ophiopholis aculeata (O)	1	50	273 ± 137.5
Nainereis quadricuspida (P)	2	40	59.8 ± 36.1
Strongylocentrotus droebachiensis (E)	3	38	54 ± 10
Lacuna vincta (G)	4	34	28 ± 23
Amphitrite cirrata (P)	5	31	20.4 ± 28.8
Tonicella rubra (CH)	6	28	15.2 ± 5.2
Hiatella arctica (B)	7	21	12.4 ± 9
Ischyrocerus anguipes (A)	8	20	10 ± 12.2
Amphitrite johnstoni (P)	9	19	8.8 ± 13.9
Cistenides granulata (P)	10	10	7.4 ± 3.4
	After disturbance		
Ophiopholis aculeata (O)	1	50	199 ± 140
Nainereis quadricuspida (P)	2	39	44.6 ± 21.5
Strongylocentrotus droebachiensis (E)	3	35	24.4 ± 4
Tonicella rubra (CH)	4	34	22.4 ± 14.8
Amphitrite cirrata (P)	5	30	18.6 ± 8.6
Amphitrite johnstoni (P)	6	24	14.6 ± 6.1
Hiatella arctica (B)	7	18.5	8.6 ± 6.8
Eualus pusiolus (D)	8	11	7 ± 3.4
Nereis pelagica (P)	9	7	5.8 ± 2.5
Cistenides granulata (P)	10	6	5.6 ± 1.8

* (P) = polychaete, (G) = gastropod, (B) = bivalve, (NU) = nudibranch, (CH) = chiton, (A) = amphipod, (C) = caprellid, (I) = isopod, (D) = decapod, (AS) = asteroid, (E) = echinoid. (O) = ophiuroid.

cata, Idotea phosphorea) in the predisturbance community.

Intensive grazing by *Strongylocentrotus* caused a major shift in the rank order of dominance; none of the community dominants was ranked the same before and after the perturbation (Table 5A). Pre- and postdisturbance densities of the dominant species were compared by one-way ANOVA (1, 8 df). The postdisturbance community was overwhelmingly dominated by the amphipod *Pontogeneia inermis*. *Pontogeneia* densities were not significantly different before and after urchin grazing ($F = 1.97$, $P > .05$). The population densities of other dominant amphipods were, however, an order of magnitude lower after disturbance (*Is. anguipes*: $F = 8.2$, $P < .025$; *Co. bonelli*: $F = 16$, $P < .005$; *J. falcata*: $F = 28.7$, $P < .001$; *Pl. glaber*: $F = 21.8$, $P < .005$; *A. rubricata*: $F = 16.8$, $P < .005$; all data $\log[x + 1]$-transformed). Populations of tube-dwelling amphipods (*A. rubricata, Is. anguipes, J. falcata, Co. bonelli*) were decimated because amphipod

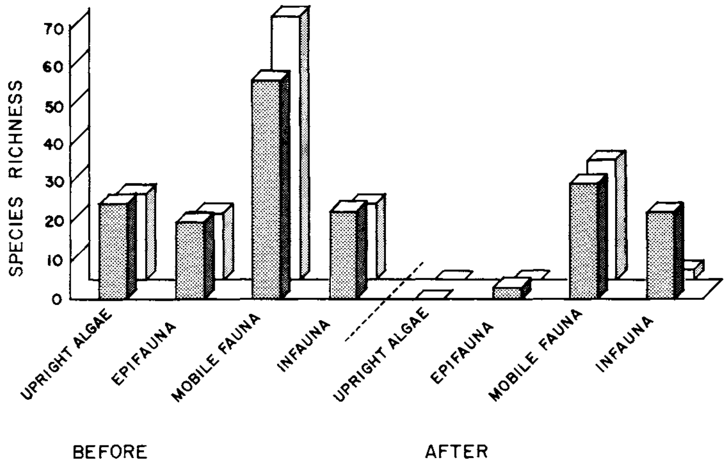


FIG. 8. Species richness of macrobenthic taxa within functional groups before and after sea urchins severely grazed the 8 m study site. Dark bars in front represent *Modiolus* bed samples; light bars in rear represent samples from the substratum outside mussel beds.

tube networks were grazed off the substratum by sea urchins. It is suggested that the ability of *Po. inermis* to occupy pelagic habitats and rapidly recolonize enabled it to escape the benthic-oriented disturbance. As expected, population densities of dominant herbivores were significantly lower after urchin disturbance (*L. vincta:* $F = 66.1$, $P < .001$; *Id. phosphorea:* $F = 9.6$, $P < .025$). Other herbivores that incurred significant density reductions as a result of intensive grazing but were not ranked as dominants in the postdisturbance community were *Margarites helicinus* ($F = 18.7$, $P < .005$) and *Idotea balthica* ($F = 6.1$, $P < .05$). I attributed such reductions in herbivore population densities to the loss of algal food resources and habitats.

Dominant species: mussel bed community. —In striking contrast to the outside substratum community, the rank order of dominant species in the *Modiolus* community was nearly the same before and after urchin disturbance. The rank order of 6 of the top 10 species was not changed by the perturbation (Table 5B). *Ophiopholis aculeata* dominated the *Modiolus* community before and after disturbance. Eight of the species listed as dominants in the predisturbance community remained among the 10 top-ranked species after the disturbance.

Densities of the dominant species were compared before and after disturbances by one-way ANOVA. Pre- and postdisturbance densities were not significantly different for 7 of the 10 top-ranked species (*Ophiopholis aculeata*: $F = 0.87$; *Na. quadricuspida*: $F = 0.3$; *Amphitrite cirrata*: $F = 1.1$; *To. rubra*: $F = 0.11$; *Hi. arctica*: $F = 1.37$; *Amphitrite johnstoni*: $F = 1.63$; *Cistenides granulata*: $F = 5.0$; all P values $> .05$, data $\log[x + 1]$–transformed). Densities of *Str. droebachiensis* were significantly lower after the urchin front passed over the mussel beds ($F = 41.8$, 1, 8 df, $P < .001$). As in the outside community, densities of *L. vincta* and *Is. anguipes* were significantly lower in the postdisturbance mussel bed community (*L. vincta*: $F = 6.46$, $P < .05$; *Is. anguipes*: $F = 7.89$, $P < .05$; both 1, 8 df).

Severe grazing caused dramatic changes in both the rank order and abundance of dominant species outside, but not inside, the mussel beds. The species that changed the least were associated with *Modiolus* beds. These contrasting results indicate that the mussel beds were effective refuges from the destructive effects of grazing for a majority of the dominant species inhabiting them.

Species richness. —Fig. 8 indicates that for three of the four functional groups, the effect of urchin disturbance on species richness was the same inside and outside the mussel beds. Comparisons were carried out by one-way ANOVA (1, 8 df). Intensive grazing caused a significant reduction in the species richness of upright algae, epifauna, and mobile fauna in both habitats (upright algae: $F = 190$, $P < .001$, outside; $F = 200$, $P < .001$, inside; epifauna: $F = 241$, $P < .001$, outside; $F = 180$, $P < .001$, inside; mobile fauna: $F = 135$, $P < .001$, outside; $F = 52.6$, $P < .001$, inside). A major exception to this trend was demonstrated by the infauna. While infaunal species richness was significantly reduced outside the mussel beds ($F = 109$, $P < .001$), there was no significant difference in the species richness of mussel bed infauna before and after urchin disturbance ($F = 0.3$, $P > .05$). This result suggests that the destructive effect of grazing was restricted to the upper portion of the mussel bed. Upright algae and virtually all epifauna attached to the mussel shells were grazed off as the urchin front passed over the surface of the mussel bed. Infauna living at the base of the mussel matrix were not impacted because they were spatially isolated from the disturbance. After urchin disturbance, mean species richness (all functional groups pooled) was significantly higher inside the mussel beds ($\bar{X} = 34.2$) than on the substratum outside the beds ($\bar{X} = 24.6$; $F = 38.4$, $P < .001$).

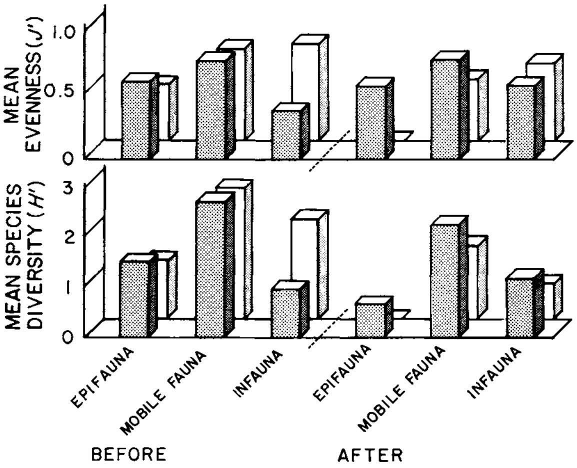


FIG. 9. Mean species diversity and mean eveness per quadrat of invertebrate functional groups before and after severe sea urchin grazing for *Modiolus* bed samples (dark bars in front) and outside substratum samples (light bars in rear).

Species diversity and evenness.—Mean values of Shannon-Wiener diversity (H') and evenness (J') were computed by functional groups (Fig. 9). Between-habitat comparisons of mean species diversity and mean evenness before and after disturbance were made by the Wilcoxon two-sample test (Sokal and Rohlf 1969: 392).

1. *Epifauna.*—Prior to disturbance, epifaunal species diversity did not differ inside and outside the mussel beds. This pattern was also evident for mean evenness (Fig. 9). After urchin disturbance, however, both mean species diversity and mean evenness of epifauna were higher inside the mussel beds. This was due to the elimination of all epifauna attached to rock and to crustose coralline algae outside the mussel beds.

2. *Mobile fauna.*—There was no significant difference in either mean species diversity or mean evenness of mobile fauna inside and outside *Modiolus* beds before urchin disturbance. After the disturbance, mean species diversity was significantly higher inside the mussel beds ($U = 25$, $P < .01$). This was primarily a response to changes in mean evenness, which was significantly higher inside the mussel beds ($U = 25$, $P < .01$). The low mean evenness outside the mussel beds was due to the overwhelming dominance of the amphipod *Pontogeneia inermis* in the postdisturbance coralline flats community (Table 5A).

3. *Infauna.*—Patterns of infaunal species diversity were reversed by the disturbance event. The mean species diversity of infauna was significantly greater outside the mussel beds prior to disturbance ($U = 25$, $P < .01$). Correspondingly, mean evenness was significantly greater in the outside substratum community before it was intensively grazed ($U = 25$, $P < .01$). Low mean evenness in the *Modiolus* infauna was due to the dominance of *Ophiopholis aculeata.* After urchin disturbance, the mean species diversity of infauna was significantly greater inside the mussel beds ($U = 26$, $P < .005$). Since mean evenness was not significantly different between habitats, this result is attributed to the significant reduction of infaunal species richness in exposed habitats outside *Modiolus* beds (Fig. 8).

In summary, urchin grazing eliminated all upright algae, a majority of the species inhabiting algal habitat structures, and most species of encrusting invertebrates. Local species diversity of invertebrates was significantly lower in the postdisturbance coralline flats community than in the predisturbance kelp bed community. The coralline flats community has low species richness, with a high concentration of dominance among few species; consequently, it has a low value of H' and low evenness.

Resistance and mortality of Modiolus.—The predation experiment and the natural grazing experiment indicated that the *Modiolus* beds are short-term refuges from biological disturbance. How persistent are these beds in the long term? This question was addressed by monitoring mussel beds for 5 yr.

All of the *Modiolus* beds persisted for 5 yr. Moreover, net gains from recruitment exceeded deaths of resident mussels in 9 out of the 12 monitored beds (Fig. 10). Consequently, the majority of the mussel beds increased in size. Three of the monitored beds showed no net change in *Modiolus* density (one each at 8, 18, and 30 m). An opportunity to evaluate the resistance stability (sensu Connell and Sousa 1983) of the shallow mussel beds occurred when the benthic community at 8 m was impacted by urchin grazing disturbance. Severe urchin grazing represented a disturbance to *Modiolus* in addition to other sessile species because large *Str. droebachiensis* can consume mussels (K. Sebens, *personal communication*). Changes in the mussel beds were documented for 2 yr after the urchin front passed over the monitored beds between December 1981 and February 1982. Fig. 10 shows that the *Modiolus* beds remained intact after the disturbance. Since a disturbance force was applied and resisted (Type 1 perturbation of Sutherland 1981), the *Modiolus* populations at 8 m are characterized by a high degree of resistance stability for intense grazing disturbance. Deeper mussel beds were not subjected to a major disturbance during the 5-yr period. Thus, the constancy of the mussel beds at 18 and 30 m depths is a result of the longevity of *Modiolus.*

As shown in Table 6, mortality rates of adult *Modiolus* were low, but were strongly dependent on depth. Overall percent mortality (all mortality sources pooled) was highest at the shallow 8 m site (8 m > 18 m, $\chi^2 = 24.5$, $P < .005$; 8 m > 30 m, $\chi^2 = 18.2$, $P < .005$; chi-square analysis). For example, the mortality rate at 8 m was 7 times higher than at 18 m, and 4.5 times higher than at 30 m. This was primarily a function of the high frequency of deaths following overgrowth and dislodgement by kelp at 8 m. Kelp-induced dislodgement was the most important source of mortality, ac-

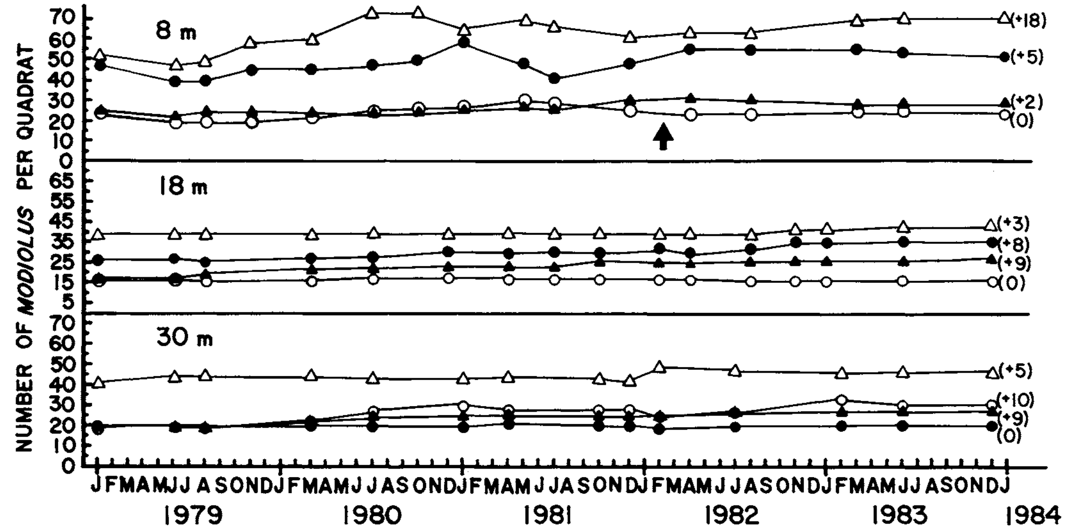


FIG. 10. The number of *Modiolus modiolus* in four monitored mussel beds (each 0.25 m^2 in area) at each of three depths (8, 18, and 30 m). Arrow indicates when the sea urchin front passed over the 8 m mussel beds; note lack of change in mussel density after urchin disturbance. Net change in each monitored mussel bed over the period is given in parentheses at right.

counting for 76% of the deaths at 8 m (all deaths pooled), prior to the urchin disturbance. By grazing kelp off mussel shells, sea urchins eliminated mortality from kelp-induced dislodgement. This caused a reduction in the percent mortality of *Modiolus* from 31.2% prior to severe urchin grazing to 5.2% after the disturbance. Because the 18 and 30 m sites are below the lower limit of the kelp zone, *Modiolus* populations at the deeper sites were not affected by dislodgement mortality. The intensity of predation by *Asterias* was greatest at 8 m and decreased with depth (8 m > 18 m, $\chi^2 = 4.2$, $P < .05$; 8 m > 30 m, $\chi^2 = 3.9$, $P < .05$; Table 6). Deaths from shell-crushing predators (crabs and lobsters) were a minor source of mussel mortality and did not vary with depth.

DISCUSSION

The results demonstrate the functional significance of *Modiolus* beds as spatial refuges from predation and grazing, two types of biological disturbance (sensu Dayton 1971) identified as major determinants of community structure in the New England subtidal zone. The observed distribution and abundance patterns of mussel bed fauna reflect differential survival inside and outside the mussel matrix. Open rocky substrata with little structural complexity represent high-risk habitats where the probability of death from predation is high. Thus, many species escape predation and severe grazing disturbance by occupying structurally complex mussel beds, where they attain population densities significantly higher than those attained in exposed habitats.

As competitive dominants on marine rocky shores, mussels play major roles in community organization (reviewed in Suchanek 1985). This study demonstrates a new functional role of mussel beds: protection from predation. This role, which is a by-product of mussel bed spatial complexity, has been hypothesized for *Mytilus californianus* beds (Suchanek 1979) but has not been explicitly demonstrated. The effect of the *Modiolus* predation refuge on species diversity is consis-

TABLE 6. Major sources of *Modiolus* mortality in monitored mussel beds as a function of depth, based on photographic monitoring from January 1979 to January 1984. n = four 0.25-m^2 beds per depth.

	Mussels killed in 5 yr					
	8 m		18 m		30 m	
Mortality source	No.	%	No.	%	No.	%
Initial number	153		101		98	
Dislodgement by kelp	43	28	0		0	
Asterias vulgaris predation	10	6.5	1	0.9	1	1.0
Crab and lobster predation	2	1.3	1	0.9	3	3.0
Gaping mussels*	1	0.6	0		2	2.0
Mussel disappearances*	0		3	2.9	2	2.0
Total mortality	56	36.4	5	4.7	8	8.0

* Mortality source unknown.

tent with the prediction that habitat structural complexity reduces predation intensity (Huffaker 1958), thereby increasing species diversity (Menge and Sutherland 1976). *Modiolus modiolus* is a foundation species (sensu Dayton 1972) in rocky subtidal communities because it provides the structural habitat complexity that serves as a refuge from biotic disturbance for other species. As a large matrix-forming species, *Modiolus* apparently plays a role similar to that of *Mytilus californianus* and the tunicate *Pyura praeputialis* in Chile (Paine and Suchanek 1983). All three species are major space occupiers on rocky substrata, and each is solitary but forms dense, structurally complex habitats that harbor diverse communities.

An alternate hypothesis to the predation refuge effect is that observed patterns of community structure may be explained by differences in sedimentation inside and outside mussel beds. Mussel beds accumulate large amounts of organic and inorganic sediment from the production of feces and pseudofeces by live mussels, and from the deposition of sediment particles (Suchanek 1979, Tsuchiya 1980). The hypothesis has particular relevance for the deposit-feeding members of the *Modiolus* community: the polychaetes *Cistenides granulata, Amphitrite johnstoni, Amphitrite cirrata, Flabelligera affinis,* and *Brada granosa* and the holothuroid *Chirodota laevis.* High densities of these deposit-feeders might reflect increased availability of food resources in mussel beds. While sedimentation may be an important factor affecting the composition of *Modiolus* communities, it is very clear from the predation experiments that deposit-feeding polychaetes and holothuroids could not survive high levels of predation outside mussel beds without spatial refuges. Thus, I view sedimentation as a secondary community-structuring factor, but it is really inseparable from the predation refuge effect.

Disturbance and community organization

Two scales of biological disturbance influence community organization in the New England subtidal zone. Predation represents a recurrent, small-scale disturbance that modifies the spatial distribution and abundance of prey. Unlike predator disturbances, which occur frequently and vary in intensity on a diurnal and seasonal basis, biological disturbance by intensively grazing sea urchins is comparatively infrequent, occurs on a large scale, and causes major shifts in community structure. For example, shallow subtidal communities were severely grazed only once in a 5-yr period; however, community-wide reductions in species abundance, diversity, and richness ensued.

Small-scale predator disturbance.—By preying heavily on epibenthos outside mussel beds, the predators *Cancer borealis, Cancer irroratus, Homarus americanus, Asterias vulgaris, Buccinum undatum, Tautogolabrus adspersus,* and *Pseudopleuronectes americanus* play an important role in the distribution and abundance of species. Data on the diets of *As. vulgaris* at the Isles of Shoals (Hulbert 1980) and other members of the predator guild at Nahant, Massachusetts (K. Sebens, *personal communication*) suggest that these seven predators are dietary generalists.

It is clear from field experiments and predator abundance surveys that nocturnal predation by crabs and lobsters has a major effect on the spatial distribution of benthic prey. For example, 66% of the total number of prey available in the predation experiments were consumed at night by *Cancer borealis* and *Homarus americanus* (data pooled for all five trials). This result reflects the nocturnal foraging behavior of crustacean predators, as *C. borealis, C. irroratus,* and *Ho. americanus* were significantly more abundant at night (Table 4). Moreover, all *C. borealis* and *Ho. americanus* enumerated during night transects were actively foraging, while during the day they were hidden in crevices, burrows, or at the base of undercut rock ledges. Bernstein et al. (1981) suggested that in Nova Scotian subtidal communities, predation pressure from crabs and lobsters was comparatively less important than fish predation (e.g., by wolffish *Anarhichas lupus* and plaice *Hippoglossoides platessoides*). However, Bernstein et al. (1981) may have underestimated the importance of crabs in natural communities because they did not evaluate the effects of crab predation in the field. In the shallow subtidal communities examined here, fish predation only occurred during the day, and cunner and flounder were present at the experimental site only during the day (Table 4). This result is consistent with the observations of Bernstein et al. (1981) that fish predation is most intense during the day. Edwards et al. (1982) hypothesized that predation by cunner plays an important role in structuring sheltered, mid-intertidal rocky shore communities in New England.

Although the hypothesis has not been tested experimentally, it is likely that the level of predator disturbance in the shallow New England subtidal zone is lower in winter than in summer, because demersal fish leave nearshore subtidal regions in winter and move offshore into deeper water (Bigelow and Schroeder 1953). Cooper et al. (1975) found no seasonal difference in population densities of lobsters in shallow (<24 m) nearshore regions of the Gulf of Maine. Choat (1982) stressed the importance of understanding variation in predator distribution patterns in order to properly interpret experimental evaluations of the effects of predators on community structure. Predator abundance surveys indicated that the *Modiolus* refuge experiments were conducted during a period of high predator abundance (summer, Table 4). It is important to consider how the experimental results might differ if the experiments were conducted during the winter, when overall predator densities are lower. I expect that the same experimental conclusions—that predators control prey spatial distribution and that *Modiolus* beds provide a refuge from predation—would be reached, because crabs and lobsters were common at the study site during the winter and were observed actively foraging at night. Although the rate of predation would probably be lower in winter experiments, I expect that predation pressure from a combination of invertebrate predators, from *Asterias, Buccinum,* crabs, and lobsters, is high enough to restrict the distribution of *Modiolus* community species to mussel bed refuges during the winter.

The utilization of mussel bed habitats by *Ophiopholis aculeata, Hiatella arctica,* and *Strongylocentrotus droebachiensis* is interpreted as a response to avoid predation. Major predators of *Ophiopholis* were winter flounder and juvenile lobsters. Carter and Steele (1982) found that juvenile lobsters showed positive prey selection for *Ophiopholis aculeata* in the shallow subtidal zone off Newfoundland, suggesting tht predation pressure may also cause selection for cryptic habitats in subarctic subtidal regions. Cod, *Gadhus morhua,* is another predator species that preys heavily on *Ophiopholis* in the New England subtidal. For instance, the stomachs of 10 cod feeding on the benthos of upper rock surfaces at 33 m depth at Pigeon Hill (30 km southeast of Star Island) contained 453 *Ophiopholis aculeata* (J. Witman, *personal observation*). An analogue to the interhabitat differences in ophiuroid population densities documented here occurs on Caribbean coral reefs with three congeneric species of *Ophiothrix* (Hendler 1984). *Ophiothrix lineata, O. angulata,* and *O. suensoni* are significantly more abundant inside sponges than elsewhere, and Hendler (1984) demonstrated that the sponges protect these ophiuroids from fish predation. In subtidal communities off the coast of Nova Scotia, Bernstein et al. (1981) attributed the tendency of *Str. droebachiensis* to remain "hidden" in kelp-dominated communities as a response to crab and lobster predation. They showed that the presence of *Cancer irroratus* caused small *Strongylocentrotus* to seek shelter among rocks in laboratory conditions. At Star Island, *Cancer borealis* and *Tautogolabrus adspersus* had the greatest effect on small *Strongylocentrotus. C. borealis* is a major predator on *Str. droebachiensis* in subtidal communities off northern Massachusetts (K. Sebens, *personal communication*). It is suggested that populations of *Hiatella arctica* outside the mussel beds are maintained at low levels by intense predation from the entire predatory guild.

Large-scale grazing disturbance.—No matter what criterion is used to compare the impact of disturbance from severe urchin grazing in the two shallow subtidal habitats, the same pattern emerges. Communities outside the mussel beds underwent major changes in species composition, rank order of dominance, species richness, diversity, and evenness as a result of intense grazing. Mussel bed communities changed the least because the mussel bed structure damped the impact of severe grazing on the associated fauna. Thus, infaunal assemblages within the mussel matrix were not altered by the disturbance.

Intense grazing by aggregated *Strongylocentrotus* denuded the substratum of all species of upright algae and nearly all encrusting invertebrates, leaving *Modiolus* beds (Fig. 10) and crustose coralline algae (mean cover 66.7%, 12.4% SD, $n = 30$ 0.25-m² quadrats). Associated with the destruction of algal habitat structure and loss of algal food resources was the near elimination of herbivore populations and a drastic reduction in species density. Herbivores particularly affected were the gastropods *Lacuna vincta, Margarites helicinus,* and *Acmaea testudinalis,* the amphipod *Ampithoe rubricata,* and the isopods *Idotea phosphorea* and *Idotea balthica.* In addition to *Strongylocentrotus,* the major herbivores remaining in the coralline flats community were the chitons *Tonicella rubra* and *Tonicella marmorea.* Chitons were not immediately impacted by the disturbance because they graze coralline algal surfaces and did not depend on the algal food resources destroyed by intensively grazing urchins (Langer 1978, Steneck and Watling 1982). The abundance of invertebrates in the community outside the mussel beds underwent a 79% reduction in population density (mean density: 2164 individuals/0.25 m² predisturbance, 453 individuals/0.25 m² postdisturbance). In the St. Lawrence estuary, Himmelman et al. (1983) demonstrated that the removal of urchins from barren areas caused the reestablishment of macroalgae, which led to significant increases in population densities of herbivorous molluscs: *Acmaea testudinalis, Margarites helicinus, Lacuna vincta,* and *Littorina obtusata.*

In the present study, sea urchin grazing represented a large, relatively nonselective disturbance; consequently, it brought about a significant community-wide reduction in species richness and diversity of all functional groups of benthic invertebrates except mussel bed infauna. Algal species richness was similarity affected. The coralline flats community outside the mussel beds was characterized by low species diversity ($H' = 2.14$, all functional groups pooled) and low species richness ($S = 22$ species), which is typical of communities following a severe disturbance (Connell 1978, Lubchenco 1978, Fox 1979).

Despite considerable work on the effects of urchin grazing on algal species diversity (Lawrence 1975), few studies have evaluated the effect of intense urchin grazing on the species diversity of invertebrates. Vance (1979) showed that grazing by *Centrostephanus coronatus* reduced the taxonomic diversity of invertebrates within localized foraging areas. However, no data were given on the effect of grazing at the species level because the photographic sampling methods employed did not enable all organisms to be identified to species. Importantly, Himmelman et al. (1983) demonstrated that intense *Strongylocentrotus* grazing severely reduced invertebrate species richness in the shallow subtidal zone of the St. Lawrence estuary. The effect was not examined on the entire macrobenthic community, however, because gammarid amphipods were not identified to species. In the present study, amphipods were an extremely important community component, dominating both pre- and postdisturbance communities at the 8 m site. A unique aspect of this study was that the analysis of sea urchin grazing effects on community structure was based on the knowledge of the distribution and abundance patterns of all macrobenthic species in the community.

Because species richness and diversity were significantly greater inside mussel beds after the urchin disturbance, *Modiolus* bed communities represent species-rich patches set in a species-poor landscape. When viewed on a large spatial scale, the pattern that emerges is a mosaic of high- and low-diversity patches corresponding to the patchy spatial distribution of *Modiolus* beds in the shallow coralline flats.

Role and effectiveness of spatial refuges

The significance of spatial refuges in natural communities rests in their potential to (1) stabilize predator-prey relationships (Huffaker 1958); (2) affect the evolution of habitat selection (Woodin 1978); and (3) reduce predation or disturbance-caused mortality (Huffaker 1958, Ivlev 1961, Ware 1972, Woodin 1981). Field manipulations have shown that the ability of spatially complex structures to provide refuge from disturbance or predation is sufficient to explain local patterns of animal distribution and abundance in aquatic communities (Crowder and Cooper 1982) and in many marine habitats, including sea grass beds (Stoner 1979, Heck and Thoman 1981, Peterson 1982), intertidal sand flats (Woodin 1978, 1981), intertidal algal assemblages (Coull and Wells 1983), tropical rocky intertidal habitats (Menge and Lubchenco 1981, Menge et al. 1983) and benthic subtidal habitats (Watanabe 1984 and the present study). Taitt et al. (1981) showed that the removal of protective vegetation led to increased bird predation on microtine rodents. However, experimental tests of spatial refuges in natural terrestrial communities are rare (Hassell 1978). Woodin (1978) pointed out that the effectiveness of spatial refuges depends on the severity of the disturbance, the size and spatial complexity of the refuge, and, for biologically generated refuges, the longevity of the refuge-forming organism and its susceptibility to disturbance. Coull and Wells (1983) suggested that there may be a threshold of structural complexity that must be attained before a refuge effect can be achieved.

The effectiveness of mussel bed refuges in New England rocky subtidal communities is linked to several life history features of the refuge-forming species. The results of age and growth studies indicate that *Modiolus modiolus* is a slow-growing, long-lived species with an average life-span of 17–30 yr (Wiborg 1946, Rowell 1967, Brown and Seed 1977, Comely 1978, Seed and Brown 1978). Maximum life-spans of 36 and 65 yr have been extrapolated from growth ring data for *Modiolus* in Norway (Wiborg 1946) and New Brunswick (Rowell 1967), respectively. In the present study, where mortality rates were determined by direct monitoring, *Modiolus* beds persisted for >5 yr. In deep subtidal habitats (18 and 30 m) where disturbance-caused mortality is low (Table 6), *Modiolus* beds may persist for several decades. The persistence of mussel beds at shallow depths (8 m) depends on the ability of *Modiolus* to escape both predation by *Asterias vulgaris* and death from dislodgement by attached kelp, which depends on the level of grazing by resident sea urchins (Witman 1984) and the amount of drag imparted by kelp (Witman and Suchanek 1984). Monitoring revealed that the mussel bed framework was able to withstand severe grazing disturbance that caused community-wide mortalities in other benthic assemblages. As a consequence of this ability to resist biological disturbance, and its considerable longevity, *Modiolus* beds represent persistent habitat structures that are predictable in space and time. These characteristics should make them particularly effective refuges from biological disturbance for other species in the community. They also suggest that in the rocky subtidal zone of the northwestern North Atlantic Ocean, where intense grazing by *Strongylocentrotus* is a major mortality source (Breen and Mann 1976, Himmelman et al. 1983), *Modiolus* bed refuges play a large role in the distribution, abundance, and diversity of species in coralline flat communities. Since *Modiolus* beds are the only large, biogenic habitat providing shelter in coralline flats, they may be an important nursery area for many species of marine invertebrates. Additionally, populations of invertebrates living in postdisturbance *Modiolus* beds may produce more gametes than their counterparts in the heavily grazed habitats outside the mussel beds, and thus contribute more toward maintaining overall population levels of benthic invertebrates in coralline flat communities.

There are undoubtedly other, less disturbance-resistant habitat structures in the rocky subtidal zone of New England that serve as spatial refuges from fish and invertebrate consumers for their associated fauna. Vertical rock walls can be a refuge from consumers for encrusting invertebrate assemblages (Sebens 1985). Spatial refuges may be particularly common in kelp beds that have not been subjected to high levels of urchin grazing. Possible refuges include various elements of algal habitat structure such as kelp holdfasts and canopies, understory red algae (*Chondrus, Phyllophora, Phycodrys*) and *Corallina officinalis* mats at the 8 m site, tufts of the red alga *Ptilota serrata* at 18 and 30 m, and the undersurface microhabitats of coralline crusts (*Lithothamnium glaciale*) at all depths. Although not experimentally demonstrated, the ability of such algal habitat structures at the Isles of Shoals to afford assemblages of amphipods, polychaetes, and gastropods associated with them (Fig. 2, Appendix) protection from predation can be inferred from other studies. For instance, Watanabe (1984) showed that turfs of fleshy red algae provide a spatial refuge for gastropods from crab and sea star predation in subtidal hard-bottom communities off central California. Prey mortality was higher in deep (11 m) habitats than shallow (4 m) ones because predators were more abundant at the deeper sites and the cover of protective algae was lower in deep habitats. Coull and Wells (1983) demonstrated that mats of *Corallina officinalis* were the most effective structures deterring fish predation on associated meiofauna in the New Zealand rocky intertidal zone. In this study, *Corallina officinalis* was an abundant component of understory algae outside the mussel beds at the 8 m site, with a mean (±SD) dry biomass of 25.3 ± 28.4 g/0.25 m^2 ($n = 5$) prior to urchin disturbance, and it is presumed to provide predation refuge. Unlike *Modiolus* beds, *Corallina* mats were removed from the rock surface by severe urchin grazing; consequently they have less of a long-term impact on prey distribution than *Modiolus* beds.

An understanding of the effectiveness of biogenic refuges should include measures of the disturbances impacting the organism that generates the refuge. Resistance stability of the refuge-forming organism, which refers to the ability of a population or assemblage to resist perturbation (Sutherland 1981, Connell and Sousa 1983) should be a major determinant of refuge effectiveness. Clearly, refuges formed by resistant organisms should make better refuges than those formed by organisms more vulnerable to disturbance. However, little is known about the relationship between resistance and refuge effectiveness, because direct demonstrations of resistance in natural communities are rare (Connell and Sousa 1983). This study represents one of the few demonstrations that the ability of a species to resist disturbance contributes towards its capability to serve as a refuge. Another example is apparently provided by the refuge-forming polychaete *Diopatra cuprea,* which can withstand crab predation (Woodin 1981).

In the New England rocky subtidal zone, the principal effects of biological disturbance are (1) to bring about major shifts in the system state of shallow subtidal communities, accompanied by massive reductions in species richness, diversity, and population densities of marine invertebrates; (2) to cause significant mortality of benthic invertebrates outside mussel beds; and (3) to restrict the spatial distribution of species to habitats where the level of biological disturbance is reduced. Mussel bed refuges are thus important between-habitat determinants of species distribution, abundance, and diversity on upper rock surfaces in the New England subtidal zone.

ACKNOWLEDGMENTS

This paper is part of a dissertation submitted in partial fulfillment of the requirements for a Ph. D. in Zoology at the University of New Hampshire, Durham. I thank my advisor, L. Harris, for the unfailing enthusiasm with which he supported my work, and for his friendship. Thanks to my other committee members, D. Hartzband, A. Mathieson, K. Sebens, J. Taylor, and C. Walker, for their significant contributions to my research. The manuscript was improved by comments from L. Harris, K. Sebens, T. Suchanek, A. Mathieson, T. Lee, D. Duggins, R. Steneck, J. Sutherland, and an anonymous reviewer. I am grateful for taxonomic assistance provided by W. Hartman (sponges), B. Spracklin (hydroids), N. Blake (polychaetes), R. Turner (gastropods), L. Harris (nudibranchs), J. Dickinson (amphipods), D. Denniger (caprellids), and H. Plough (ascidians). Algal identifications were kindly provided by A. Mathieson and P. Busse. Benthic sorters M. Nickerson and S. Craig helped immeasurably. I thank divers A. Hulbert, L. Harris, P. Lavoie, P. Pelletier, S. Craig, M. Lesser, and others for many cold hours of assistance underwater. I am especially grateful for the excellent seamanship of Captain N. MacIntosh, Captain P. Pelletier, and Diving Safety Officer P. Lavoie on board the R.V. *Jere Chase.* Without their dedicated help offshore, none of this research would have been possible. Special thanks to P. Pelletier and P. Lavoie for putting up with me through six winters of diving in the Gulf of Maine. Most of all, I am grateful to my partner, M. Hardwick-Witman, for her indispensable assistance and support throughout every aspect of this study. Financial assistance was provided by the University of New Hampshire Marine Program, the Lerner-Gray Fund for Marine Research, and by grants to L. Harris from the Dreyfus Foundation and from the Northeast Pollution Monitoring Program (NOAA, number NA-79-FAC-0013). This is University of New Hampshire Marine Program Contribution Series Number UNHMP-JR-SG-85-4.

LITERATURE CITED

Ayling, A. M. 1981. The role of biological disturbance in temperate subtidal encrusting communities. Ecology **62**: 830–847.

Bazzaz, F. A. 1983. Characteristics of populations in relation to disturbance in natural and man-modified ecosystems. Pages 259–275 *in* H. A. Mooney and M. Godron, editors. Disturbance and ecosystems. Springer-Verlag, Berlin, Germany.

Bernstein, B. B., B. E. Williams, and K. H. Mann. 1981. The role of behavioral responses to predators in modifying urchins' (*Strongylocentrotus droebachiensis*) destructive grazing and seasonal foraging patterns. Marine Biology (Berlin) **63**:39–49.

Bigelow, H. B., and W. C. Schroeder. 1953. Fishes of the Gulf of Maine. United States Fish and Wildlife Service Fishery Bulletin **53**.

Birkeland, C. 1974. Interactions between a sea pen and seven of its predators. Ecological Monographs **44**:211–232.

Boesch, D. F. 1977. Application of numerical classification in ecological investigations of water pollution. EPA-600/3-77-033. United States Environmental Protection Agency, Corvallis, Oregon, USA.

Bousfield, E. L. 1973. Shallow-water Gammaridean Amphipoda of New England. Cornell University Press, Ithaca, New York, USA.

Breen, P. A., and K. H. Mann. 1976. Destructive grazing of kelp by sea urchins in Eastern Canada. Journal of the Fisheries Research Board of Canada **33**:1278–1283.

Brown, R. A., and R. Seed. 1977. *Modiolus modiolus* (L.)—an autecological study. Pages 93–100 *in* B. F. Keegan, P. O. Cleidigh, and P. J. S. Boodin, editors. Biology of benthic organisms. Pergamon, Oxford, England.

Bush, A. O. 1980. Faunal similarity and infracommunity structure in the helminths of Lesser Scaup. Dissertation. University of Alberta, Edmonton, Alberta, Canada.

Carter, J. A., and D. H. Steele. 1982. Stomach contents of immature lobsters (*Homarus americanus*) from Placentia

Bay, Newfoundland. Canadian Journal of Zoology **60**:337–347.

Choat, J. H. 1982. Fish feeding and the structure of benthic communities in temperate waters. Annual Review of Ecology and Systematics **13**:423–429.

Comely, C. A. 1978. *Modiolus modiolus* (L.) from the Scottish West Coast. I. Biology. Ophelia **17**:167–193.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science **199**:1302–1310.

Connell, J. H., and M. J. Keough. 1985. Disturbance and patch dynamics of subtidal marine animals on hard substrata. Pages 125–152 *in* S. T. A. Pickett and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, New York, New York, USA.

Connell, J. H., and W. P. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. American Naturalist **121**:789–824.

Cooper, R. A., R. A. Clifford, and C. D. Newell. 1975. Seasonal abundance of the American lobster *Homarus americanus* in the Boothbay Region of Maine. Transactions of the American Fisheries Society **104**:669–674.

Coull, B. C., and J. B. J. Wells. 1983. Refuges from fish predation: experiments with phytal meiofauna from the New Zealand rocky intertidal. Ecology **64**:1599–1609.

Crowder, L. B., and W. E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology **63**:1802–1813.

Dayton, P. K. 1971. Competition, disturbance, and community orgnaization: the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs **41**:351–389.

———. 1972. Toward an understanding of community resilience and the potential effects of enrichment to the benthos at McMurdo Sound, Antarctica. Pages 81–95 *in* B. C. Parker, editor. Proceedings of the Colloquium on Conservation Problems in Antarctica. Allen Press, Lawrence, Kansas, USA.

———. 1973. Dispersion, dispersal, and persistence of the annual intertidal alga, *Postelsia palmaeformis* Ruprecht. Ecology **54**:433–438.

Dayton, P. K., G. A. Robilliard, R. T. Paine, and L. B. Dayton. 1974. Biological accommodation in the benthic community at McMurdo Sound, Antarctica. Ecological Monographs **44**:105–128.

Dethier, M. 1984. Disturbance and recovery in intertidal pools: maintenance of mosaic patterns. Ecological Monographs **54**:99–118.

Dickenson, J. J., and R. L. Wigley. 1981. Distribution of Gammaridean Amphipoda (Crustacea) on Georges Bank. Technical Report, United States Department of Commerce, National Oceanic and Atmospheric Administration, Rockville, Maryland, USA.

Duggins, D. O. 1983. Starfish predation and the creation of mosaic patterns in a kelp-dominated community. Ecology **64**:1610–1619.

Edwards, D. C., D. O. Conover, and F. Sutter. 1982. Mobile predators and the structure of marine intertidal communities. Ecology **63**:1175–1180.

Elner, R. W. 1980. Predation of the sea urchin (*Strongylocentrotus droebachiensis*) by the American lobster (*Homarus americanus*) and the rock crab (*Cancer irroratus*). Pages 48–65 *in* J. D. Pringle, G. J. Sharp, and J. F. Caddy, editors. Proceedings of the workshop on the relationship between sea urchin grazing and commercial plant/animal harvesting. Canadian Technical Report of Fisheries and Aquatic Sciences **954**.

Fager, E. W. 1957. Determination and analysis of recurrent groups. Ecology **38**:586–595.

Fox, J. F. 1979. Intermediate-disturbance hypothesis. Science **204**:1344–1345.

Gauch, H. G., Jr. 1982. Multivariate analysis in community ecology. Cambridge University Press, New York, New York, USA.

Green, R. H. 1977. Some methods for hypothesis testing and analysis with biological monitoring data. Pages 200–211 *in* J. Cairns, Jr., K. L. Dickson, and G. F. Westlake, editors. Biological monitoring of water and effluent quality. American Society for Testing and Materials, Philadelphia, Pennsylvania, USA.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist **111**:1169–1194.

———. 1979. Plant strategies and vegetation processes. John Wiley and Sons, New York, New York, USA.

Hagen, N. T. 1983. Destructive grazing of kelp beds by sea urchins in Vestfjorden, northern Norway. Sarsia **68**:177–190.

Hassell, M. P. 1978. The dynamics of Arthropod predator-prey systems. Princeton University Press, Princeton, New Jersey, USA.

Heck, K. L., and T. A. Thoman. 1981. Experiments on predator-prey interactions in vegetated aquatic habitats. Journal of Experimental Marine Biology and Ecology **53**: 125–134.

Hendler, G. 1984. The association of *Ophiothrix lineata* and *Callyspongia vaginalis*: a brittle star–sponge cleaning symbiosis? Marine Ecology (Pubblicazioni della Stazione Zoologica di Napoli) **5**:138–150.

Himmelman, H. J., A. Cardinal, and E. Bourget. 1983. Community development following removal of urchins, *Strongylocentrotus droebachiensis*, from the rocky subtidal zone of the St. Lawrence Estuary, Eastern Canada. Oecologia (Berlin) **59**:27–39.

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

Hulbert, A. W. 1980. The functional role of *Asterias vulgaris* Verrill (1866) in three subtidal communities. Dissertation. University of New Hampshire, Durham, New Hampshire, USA.

Humphrey, S. R., F. J. Bonaccorso, and T. L. Zinn. 1983. Guild structure of surface-gleaning bats in Panama. Ecology **64**:284–294.

Hurlburt, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs **54**: 187–211.

Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Connecticut, USA.

Kaiser, H. 1983. Small scale spatial heterogeneity influences predation success in an unexpected way: model experiments on the functional response of predatory mites (Acarina). Oecologia (Berlin) **56**:249–256.

Langer, P. D. 1978. Some aspects of the biology of three northwestern Atlantic chitons: *Tonicella rubra, Tonicella marmorea,* and *Ischnochiton albus* (Mollusca: Polyplacophora). Dissertation. University of New Hampshire, Durham, New Hampshire, USA.

Lawrence, J. M. 1975. On the relationships between marine plants and sea urchins. Oceanography and Marine Biology, an Annual Review **13**:213–286.

Levin, S. A., and R. T. Paine. 1974. Disturbance, patch formation, and community structure. Proceedings of the National Academy of Sciences (USA) **71**:2744–2747.

Lieberman, M., D. M. John, and D. Lieberman. 1979. Ecology of subtidal algae on seasonally devastated cobble substrates off Ghana. Ecology **60**:1151–1161.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. American Naturalist **112**:23–39.

Menge, B. A. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. Ecological Monographs **46**: 355–393.

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

Menge, B. A., L. R. Ashkenas, and A. Matson. 1983. Use of artificial holes in studying community development in cryptic marine habitats in a tropical intertidal region. Marine Biology (Berlin) **77**:129–142.

Menge, B. A., and J. Lubchenco. 1981. Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. Ecological Monographs **51**:429–450.

Menge, B. A., and J. P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. American Naturalist **110**:351–369.

Moreno, C. A., and J. P. Sutherland. 1982. Physical and biological processes in a *Macrocystis pyrifera* community near Valdivia, Chile. Oecologia (Berlin) **55**:1–6.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist **100**:65–75.

Paine, R. T., and S. A. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. Ecological Monographs **51**:145–178.

Paine, R. T., and T. H. Suchanek. 1983. Convergence of ecological processes between independently evolved competitive dominants: a tunicate-mussel comparison. Evolution **37**:821–831.

Paine, R. T., and R. L. Vadas. 1969. The effects of grazing by sea urchins, *Strongylocentrotus* spp,. on benthic algal populations. Limnology and Oceanography **14**:710–719.

Peterson, C. H. 1982. Clam predation by whelks (*Busycon* sp.): experimental tests of the importance of prey size, prey density, and seagrass cover. Marine Biology (Berlin) **66**: 159–170.

Pielou, E. C. 1974. Population and community ecology. Gordon and Breach, New York, New York, USA.

Rowell, T. W. 1967. Some aspects of the ecology, growth, and reproduction of the horse mussel *Modiolus modiolus*. Thesis. Queens University, Kingston, Ontario, Canada.

Sebens, K. P. 1985. Community ecology of vertical walls in the Gulf of Maine, USA: small scale processes and alternative community states. Pages 346–371 *in* P. G. Moore and R. Seed, editors. The ecology of rocky coasts. Hodder and Stoughton, Kent, England.

Seed, R., and R. A. Brown. 1978. Growth as a strategy for survival in two marine bivalves, *Cerastoderma edule* and *Modiolus modiolus*. Journal of Animal Ecology **47**:283–292.

Sloan, N. A., and T. H. Aldridge. 1981. Observations on an aggregation of the starfish *Asterias rubens* L. in Morecambe Bay, Lancashire, England. Journal of Natural History **15**:407–418.

Sokal, R. R., and F. G. Rohlf. 1969. Biometry. W. H. Freeman, San Francisco, California, USA.

Sousa, W. P. 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecological Monographs **49**:227–254.

———. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics **15**:353–391.

Stanley, S. M. 1970. Relation of the shell form to life habits of the Bivalvia (Mollusca). Memoirs of the Geological Society of America **125**.

Steneck, R. S., and L. Watling. 1982. Feeding capabilities and limitation of herbivorous molluscs: a functional group approach. Marine Biology (Berlin) **68**:299–319.

Stoner, A. W. 1979. Species specific predation on amphipod Crustacea by pinfish (*Lagodon rhomboides*): mediation by macrophyte standing crop. Marine Biology (Berlin) **56**:239–246.

Suchanek, T. H. 1979. The *Mytilus californianus* community: studies on the composition, structure, organization, and dynamics of a mussel bed. Dissertation. University of Washington, Seattle, Washington, USA.

———. 1985. Mussels and their role in structuring rocky intertidal communities. Pages 70–96 *in* G. Moore and R. Seed, editors. The ecology of rocky coasts. Hodder and Stoughton, Kent, England.

Sutherland, J. P. 1981. The fouling community of Beaufort, North Carolina: a study in stability. American Naturalist **118**:499–519.

Taitt, M. J., J. H. W. Gipps, C. J. Krebs, and Z. Duneljerski. 1981. The effect of extra food and cover on declining populations of *Microtus townsendii*. Canadian Journal of Zoology **59**:1593–1599.

Tsuchiya, M. 1980. Biodeposit production by the mussel *Mytilus edulis* L. on rocky shores. Journal of Experimental Biology and Ecology **47**:203–222.

Underwood, A. J. 1981. Techniques of analysis of variance in experimental marine biology and ecology. Oceanography and Marine Biology, an Annual Review **19**:513–605.

Vadas, R. L. 1977. Preferential feeding: an optimization strategy in sea urchins. Ecological Monographs **47**:337–371.

Vance, R. R. 1979. Effects of grazing by the sea urchin, *Centrostephanus coronatus*, on prey community composition. Ecology **60**:537–546.

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

Watanabe, J. M. 1984. The influence of recruitment, competition, and benthic predation on the spatial distributions of three species of kelp forest gastropods (Trochidae: *Tegula*). Ecology **65**:920–936.

Wiborg, K. F. 1946. Undersokelser over oskjellet (*Modiola modiolus*) (L.). Alminnelig biologi, vekst og okonomisk betydning. Reports on Norwegian Fishery and Marine Investigations **8**(5).

Wishart D. 1982. Clustan 2.1 User Manual. Edinburgh University Press, Edinburgh, Scotland.

Witman, J.D. 1984. Ecology of rocky subtidal communities: the role of *Modiolus modiolus* and the influence of disturbance, competition, and mutualism. Dissertation. University of New Hampshire, Durham, New Hampshire, USA.

Witman, J. D., A. H. Hulbert, and L. G. Harris. 1982. Morphology of a sea urchin front (*Strongylocoentrotus droebachiensis*) at the Isles of Shoals, N.H. Page 205 *in* J. M. Lawrence, editor. Proceedings of the International Echinoderm Conference. A. A. Balkema, Rotterdam, The Netherlands.

Witman, J. D., and T. H. Suchanek. 1984. Mussels in flow: drag and dislodgement by epizoans. Marine Ecology Progress Series **16**:259–268.

Woodin, S. A. 1978. Refuges, disturbance, and community structure: a marine soft-bottom example. Ecology **59**:274–284.

———. 1981. Disturbance and community structure in a shallow water sandflat. Ecology **62**:1052–1066.

APPENDIX

TABLE A1. Species group identified by cluster analysis (depicted in Fig. 2). Post-clustering analyses by two-way ANOVA and Student-Newman-Keuls (SNK) test identified the major distribution pattern shared among taxa in clusters A, B, and C in Fig. 2. The effect of depth (8, 18, or 30 m) and habitat (outside or inside *Modiolus* bed) on species density was tested

Taxon†	Code‡	Functional group§	Density (no./0.25 m²)‖ 8 m IN	8 m OUT
		Group A: 30-m community outside *Modiolus* bed		
Polymastia infrapilosa (S)	PINFR	EPI	0	0
Diastylis sculpta (CU)	DSCUL	MOB	0	0
Clavularia modesta (OC)	CMODE	EPI	0	0
Diastylis quadrispinosa (CU)	DQUAD	MOB	0	0
Photis macrocoxa (A)	PMACR	MOB	0	0
Mitrella dissimilis (G)	MDISS	MOB	0	0
Dexamine thea (A)	DTHEA	MOB	0	1.0 (1.7)
Corophium crassicorne (A)	CCRAS	MOB	0	0
Orchomene minuta (A)	OMINU	MOB	0	0
Chirodotea tuftsi (I)	CTUFT	MOB	0	0.2 (0.4)
Leptochelia savignyi (TA)	LSAVI	MOB	0	0
Gnathia cerina (I)	GCERI	MOB	0	0
Chelysoma macleayanum (T)	CMACL	EPI	0	0
Polycarpa fibrosa (T)	PFIBR	EPI	0	1.2 (2.6)
Cerastoderma pinnulatum (B)	CPINN	INF	0	5.2 (1.3)
Philine lima (OP)	PLIMA	MOB	0	0
Erichthonius rubricornis (A)	ERUBR	MOB	0	0
Chone infundibuliformis (P)	CINFU	INF	0.6 (1.3)	0
Pleustes panoplus (A)	PPANO	MOB	0	0
Anonyx liljeborgi (A)	ALILJ	MOB	0	0
Alvania mighelsii (G)	AMIGH	MOB	0.2 (0.4)	0
Alvania exarta (G)	AEXAR	MOB	0	0
Molleria costulata (G)	MLCOS	MOB	0	0.2 (0.4)
Alvania areolata (G)	AAREO	MOB	0	0.4 (0.9)
Axiognathus squamata (O)	ASQUA	INF	13.0 (13.9)	18.0 (11.2)
Thelepus cincinnatus (P)	TCINN	INF	0	1.4 (2.6)
Monoculodes tuberculatus (A)	MTUBE	INF	0	0
Stenopleustes gracilis (A)	SGRAC	MOB	0	0
Syrrhoe crenulata (A)	SCREN	MOB	0	0
Aeginna longicuris (C)	ALONG	MOB	0	4.4 (8.8)
		Group B: 8- and 18-m community outside *Modiolus* bed		
Nereis pelagica (P)	NPELA	MOB	9.2 (9.8)	60.0 (21.9)
Onchidoris muricata (NU)	OMURI	MOB	5.2 (6.9)	42.6 (19.8)
Idotea phosphorea (I)	IPHOS	MOB	0.4 (0.6)	38.2 (27.6)
Ampithoe rubricata (A)	ARUBR	MOB	14.2 (9.6)	116.6 (97.4)
Phoxocephalus holboli (A)	PHOLB	MOB	2.4 (2.3)	21.6 (21.0)
Jassa falcata (A)	JFALC	MOB	4.0 (4.0)	188.0 (254.0)
Ischyrocerus anguipes (A)	IANGU	MOB	20.0 (33.0)	386.0 (593.0)
Eualia viridis (P)	EVIRI	MOB	2.0 (2.4)	13.6 (8.5)
Cirratulus cirratus (P)	CCIRR	INF	0.8 (1.8)	22.0 (21.8)
Margarites helicinus (G)	MHELI	MOB	1.8 (1.5)	37.2 (19.0)
Lacuna vincta (G)	LVINC	MOB	28.0 (23.0)	255.0 (164.0)
Dodecaceria concharum (P)	DCONC	INF	0.4 (0.9)	12.0 (5.6)
Dendronotus frondosus (NU)	DFRON	MOB	0	4.2 (6.6)
Coryphella verrucosa (NU)	CVERR	MOB	0	4.2 (.2)
Lepidonotus squamatus (P)	LSQUA	MOB	17.8 (14.0)	34.0 (24.7)
Buccinum undatum (G)	BUNDA	MOB	0.8 (0.4)	1.8 (1.1)
Cancer irroratus (D)	CIORR	MOB	0.8 (1.6)	4.6 (1.4)
Nicolea zostericola (P)	NZOST	MOB	4.8 (6.9)	18.2 (14.6)
Mytilus edulis (B)	MEDUL	EPI	6.0 (4.9)	24.0 (12.5)
Harmothoe imbricata (P)	HIMBR	MOB	3.8 (2.8)	10.2 (3.8)
Pleusymtes glaber (A)	PGLAB	MOB	28.8 (21.4)	120.4 (60.7)
Caprella septentrionalis (C)	CSEPT	MOB	7.8 (6.1)	45.4 (35.0)
Pontogeneia inermis (A)	PINER	MOB	22.8 (21.6)	199.0 (82.4)
Corophium bonelli (A)	CBONE	MOB	11.6 (19.9)	142.2 (122.8)
Phyllodoce maculata (P)	PMACU	MOB	4.4 (6.2)	32.4 (26.0)
Caprella linearis (C)	CLINE	MOB	10.8 (4.7)	64.2 (51.5)
Asterias vulgaris (AS)	AVULG	MOB	12.8 (4.2)	25.8 (8.9)

by two-way ANOVA. Where the interaction of depth and habitat was nonsignificant (NS), mean densities were compared by SNK tests.

Density (no./0.25 m²)‖				Significance level (by ANOVA)			SNK
18 m		30 m					
IN	OUT	IN	OUT	Effect of depth	Effect of habitat	Inter-action	Highest density#
Group A: 30-m community outside *Modiolus* bed							
0	0	0	5.8 (2.1)	***	***	***	
0	0	0.2 (0.4)	17.6 (5.2)	***	***	***	
0	0	0	3.4 (1.5)	***	***	***	
0	0	0.2 (0.4)	19.2 (5.6)	***	***	***	
0	0	0	357.0 (65.6)	***	***	***	
0	0	0.4 (0.5)	47.2 (17.1)	***	***	***	
0	0.2 (0.4)	0	12.4 (4.5)	***	***	***	
0	0	0	84.6 (55.8)	***	***	***	
0	0	0.4 (0.9)	28.2 (20.1)	***	***	***	
0	0	0	20.6 (15.7)	**	**	**	
0	0	0	63.2 (60.0)	***	***	***	
0	0	0	6.4 (4.5)	***	***	***	
0	0	0	4.8 (3.9)	***	***	***	
0	0	0.2 (0.4)	12.4 (10.4)	**	**	**	
0.8 (0.8)	0	9.2 (7.0)	61.4 (44.0)	***	***	***	
0	0	0	2.6 (2.1)	**	**	**	
0.6 (0.8)	3.4 (5.2)	0	13.8 (12.0)	**	**	*	
0.2 (0.4)	0.4 (0.5)	0.4 (0.5)	14.4 (6.6)	**	**	**	
0	0	0	4.4 (7.6)	*	*	*	
0	0	0.2 (0.4)	8.0 (7.3)	**	**	**	
4.0 (4.4)	12.2 (3.0)	37.8 (27.6)	75.2 (31.0)	**	*	NS	30 M OUT
0	0	4.4 (6.1)	18.2 (5.9)	***	*	NS	30 M OUT
0	0.6 (1.3)	7.8 (8.4)	24.0 (10.1)	**	*	NS	30 M OUT
0	0	8.1 (12.5)	31.4 (13.9)	**	*	**	
0.3 (0.2)	1.6 (2.6)	11.2 (8.9)	32.0 (17.5)	***	*	NS	30 M OUT
1.4 (2.1)	10.0 (13.0)	4.8 (4.2)	27.2 (12.4)	**	**	NS	30 M OUT
1.2 (1.3)	6.0 (5.1)	9.4 (6.6)	19.8 (8.1)	**	*	NS	30 M OUT
0	0	0.8 (1.3)	14.8 (11.0)	***	***	***	
0	0	1.8 (1.7)	11.8 (12.2)	**	*	NS	30 M OUT
8.2 (12.0)	21.2 (11.3)	9.4 (13.8)	23.8 (16.0)	*	*	NS	30 M OUT
Group B: 8- and 18-m community outside *Modiolus* bed							
6.0 (3.5)	10.6 (4.9)	0.8 (0.8)	5.2 (4.8)	***	**	**	
0.2 (0.4)	2.2 (2.9)	0	1.8 (4.0)	***	**	NS	8 M OUT
0	0.2 (0.4)	0	0	***	***	***	
8.0 (5.2)	14.6 (5.7)	0.2 (0.4)	8.0 (15.1)	***	***	NS	8 M OUT
0	0.2 (0.4)	0.6 (0.8)	2.8 (0.4)	***	***	*	
5.0 (5.0)	12.0 (10.0)	0	14.0 (20.0)	**	***	**	
6.0 (7.0)	25.0 (14.0)	1.0 (1.0)	8.0 (7.0)	**	***	NS	8 M OUT
1.2 (1.5)	2.0 (1.5)	0	2.0 (2.1)	**	**	**	
0.2 (0.4)	0	0	0.4 (0.8)	***	***	**	
1.2 (0.8)	16.2 (25.0)	1.4 (1.5)	2.9 (1.4)	**	***	**	
40.0 (30.0)	241.0 (231.0)	10.0 (8.0)	21.0 (14.0)	***	**	**	
0	0.2 (0.4)	0	0	***	**	**	
0	0	0	0	***	**	***	
0.2 (0.4)	0	0	0	*	*	*	
1.4 (1.1)	5.6 (2.6)	0.6 (0.9)	2.2 (1.2)	***	*	*	
5.6 (1.8)	12.6 (6.8)	1.0 (0.7)	3.4 (2.8)	***	**	NS	18 M OUT
0	0	0	0	***	*	NS	8 M OUT
0.8 (0.8)	2.6 (1.8)	1.8 (1.9)	4.2 (2.6)	***	*	NS	8 M OUT
1.0 (2.3)	3.0 (2.1)	0.8 (1.8)	1.4 (3.1)	***	*	NS	8 M OUT
2.0 (1.8)	6.2 (3.0)	0.8 (1.1)	3.1 (1.4)	*	*	NS	8 M OUT
58.2 (30.2)	68.8 (33.3)	1.4 (1.7)	3.8 (1.1)	***	*	*	
21.0 (22.7)	34.2 (12.6)	0	1.7 (1.4)	***	**	NS	8 M OUT
75.0 (73.7)	162.2 (114.5)	2.8 (5.6)	11.6 (6.5)	***	***	NS	8 M OUT, 18 M OUT
9.4 (8.3)	65.2 (88.8)	0.8 (1.3)	59.6 (48.0)	*	***	NS	8 M OUT
0.6 (0.9)	5.2 (2.5)	5.4 (6.5)	10.0 (11.1)	**	**	NS	8 M OUT
5.8 (6.2)	38.8 (34.2)	0.6 (0.9)	14.6 (12.8)	**	**	NS	8 M OUT
14.0 (9.0)	34.4 (21.7)	6.2 (3.9)	15.8 (7.7)	*	**	NS	8 M OUT

APPENDIX

Continued.

Taxon†	Code‡	Functional group§	Density (no./0.25 m²)‖ 8 m IN	Density (no./0.25 m²)‖ 8 m OUT
	Group C: *Modiolus* community			
Nainereis quadricuspida (P)	NQUAD	MOB	59.8 (36.1)	24.6 (18.4)
Strongylocentrotus droebachiensis (E)	SDROB	MOB	54.0 (10.4)	37.4 (6.1)
Henricia sanguinolenta (AS)	HSANG	MOB	9.8 (4.3)	5.4 (2.6)
Amphitrite cirrata (P)	ACIRR	INF	20.4 (28.8)	2.2 (2.3)
Cistenides granulata (P)	CGRAN	INF	7.4 (3.4)	0
Ophiopholis aculeata (O)	OACUL	INF	273.0 (137.5)	61.2 (34.3)
Hiatella arctica (B)	HARTI	INF	12.4 (9.0)	4.0 (3.3)
Amphitrite johnstoni (P)	AJOHN	INF	8.8 (13.9)	0.2 (0.4)
Acmaea testudinalis (G)	ATEST	MOB	8.2 (4.7)	0.2 (0.5)
Tonicella rubra (CH)	TRUBR	MOB	15.2 (5.2)	4.6 (6.0)
Cucumaria frondosa (H)	CFRON	INF	1.2 (0.4)	0
Ischnochiton albus (CH)	IALBD	MOB	0.2 (0.4)	0
Amphiphorus angulatus (N)	AANGU	MOB	7.2 (6.9)	1.8 (2.2)
Eualus pusiolus (D)	EPUSI	MOB	7.0 (7.6)	1.6 (3.0)
Psolus fabricii (H)	PFABR	EPI	1.9 (0.7)	0.2 (0.4)
Myxicola infundibulum (P)	MINFU	INF	0	0
Flabelligera affinis (P)	FAFFI	INF	1.6 (2.0)	0.2 (0.4)
Turritelopsis acicula (G)	TACIC	MOB	0	0.4 (0.5)
Ophiura robusta (O)	OROBU	INF	2.6 (1.2)	1.2 (4.7)
Brada granosa (P)	BGRAN	INF	0	0
Euclymene collaris (P)	ECOLL	INF	0.6 (1.3)	0
Chiridota laevis (H)	CHIRO	INF	0	0
Colus pygmaeus (G)	CPYGM	MOB	0	0

* $P < .05$; ** $P < .01$; *** $P < .001$.

† Taxonomic group abbreviations: (S) sponge, (OC) octocoral, (N) nemertean, (P) polychaete, (B) bivalve, (G) gastropod, (NU) nudibranch, (OP) opisthobranch, (CH) chiton, (A) amphipod, (C) caprellid, (I) isopod, (TA) tanaid, (CU) cumacean, (D) decapod, (AS) asteroid, (E) echinoid, (O) ophiuroid, (H) holothuroid, (T) tunicate.

‡ Code represents species abbreviation used in Fig. 2 dendrogram.

§ Functional group categories: epifauna (EPI), mobile fauna (MOB), infauna (INF).

‖ Mean densities (with standard deviations in parentheses) from samples inside *Modiolus* beds (IN) and on the substratum outside (OUT) at each depth.

\# Where 2 locations are listed, mean densities at both sites were greater than at the third and not significantly different from each other. The first-listed location had the greater density. All SNK results had $P < .05$.

APPENDIX

Continued.

Density (no./0.25 m^2)‖				Significance level (by ANOVA)			SNK
18 m		30 m		Effect of depth	Effect of habitat	Inter-action	Highest density#
IN	OUT	IN	OUT				
Group C: *Modiolus* community							
13.8 (12.0)	0	4.4 (2.5)	1.4 (0.9)	***	***	***	
28.0 (13.0)	14.0 (4.7)	14.8 (11.0)	9.2 (3.0)	***	**	NS	8 M IN
5.6 (3.6)	1.0 (1.7)	1.6 (1.3)	0.6 (0.7)	**	**	NS	8 M IN
41.6 (20.3)	2.0 (2.9)	6.8 (3.0)	1.8 (3.1)	**	**	**	
56.0 (26.9)	0	26.8 (14.3)	0	**	***	***	
357.2 (119.0)	31.6 (22.8)	148.8 (62.1)	19.0 (10.5)	**	***	NS	18 M IN, 8 M IN
34.0 (10.4)	0.8 (1.8)	3.8 (3.1)	4.2 (5.4)	***	***	NS	18 M IN, 8 M IN
4.0 (1.9)	0	0	0	*	*	NS	8 M IN
7.8 (3.4)	3.0 (1.4)	0.5 (0.2)	0	**	**	**	
38.2 (12.9)	20.0 (15.6)	5.6 (3.7)	3.0 (2.6)	***	**	NS	18 M IN, 8 M IN
4.8 (2.5)	0	2.3 (0.5)	0	**	**	NS	18 M IN, 8 M IN
0	0	3.6 (1.6)	0.2 (0.4)	***	***	NS	30 M IN
5.0 (6.4)	0.6 (0.8)	0.8 (1.3)	0	*	*	NS	8 M IN
16.2 (8.9)	3.6 (1.3)	12.6 (11.5)	0.6 (1.3)	**	*	NS	18 M IN
4.8 (1.2)	0	1.0 (0.7)	0.2 (0.4)	*	**	NS	18 M IN
3.6 (0.6)	0	5.2 (1.1)	0	***	***	NS	30 M IN
4.0 (3.3)	0	6.8 (4.0)	1.0 (1.2)	**	***	NS	30 M IN
7.2 (6.9)	0	18.6 (16.0)	3.6 (2.0)	***	***	**	
25.2 (19.3)	9.8 (8.7)	38.2 (20.4)	14.4 (8.9)	***	**	***	
2.2 (1.4)	0	5.8 (7.5)	0	***	**	***	
0.6 (0.8)	0	20.8 (10.6)	1.8 (3.4)	***	***	***	
0	0	3.8 (0.8)	0	***	***	***	
1.8 (1.3)	0	19.4 (4.4)	8.0 (1.4)	***	***	***	