ECOLOGY OF ROCKY SUBTIDAL COMMUNITIES: THE ROLE OF MODIOLUS MODIOLUS (L) AND THE INFLUENCE OF DISTURBANCE, COMPETITION, AND MUTUALISM

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ECOLOGY OF ROCKY SUBTIDAL COMMUNITIES: THE ROLE OF MODIOLUS MODIOLUS (L.) AND THE INFLUENCE OF DISTURBANCE, COMPETITION, AND MUTUALISM

Abstract
This study presents an analysis of physical and biological processes regulating the structure of rocky subtidal communities off coastal New Hampshire and southern Maine, USA, with emphasis on the ecology of the horse mussel Modiolus modiolus (L.). Quantitative sampling and multivariate analysis revealed 3 communities: (1) Modiolus community; (2) 30 m community of species with highest densities outside mussel beds; (3) 8-18 m community of species with maximal densities outside mussel beds.

Controlled field experiments, a natural grazing experiment, and long-term photographic monitoring (5 yrs) enabled patterns of Modiolus community structure to be related to the processes maintaining them. Bivalve, ophiuroid, and echinoid prey outside, but not inside, Modiolus beds were consumed by fish, crab, and lobster predators demonstrating that Modiolus beds provide a refuge from predation. The sea urchin Strongylocentrotus droebachiensis was the most significant agent of biological disturbance; urchin aggregations overgrazed the 8 m benthos causing radical changes in species composition, dominance, species richness, and diversity outside mussel beds. Infaunal assemblages within Modiolus beds changed the least because mussel bed structure damped the impact of overgrazing.

At exposed offshore sites, dense populations of Modiolus modiolus occurred at intermediate depths (11-18 m) but not at shallow depths (4-8 m) dominated by kelp (Laminaria digitata, Laminaria saccharina). Experiments indicated that chronic storm-generated disturbance caused massive dislodgement of mussels competitively overgrown by kelp, and could account for the scarcity of Modiolus at shallow depths. The hypothesis that by grazing kelp off mussels urchins decrease the risk of mussel dislodgement was tested by an urchin removal experiment. The removal of urchins from mussel beds led to exponential kelp recruitment, resulting in a 30-fold increase of mussel mortality (via kelp-induced dislodgement), compared to control beds with urchins. The Modiolus-Strongylocentrotus interaction is mutualistic, as mussels provide a refuge from predation for urchins. Thus, coexistence of kelp and mussel competitors is facilitated by mutualism. Patch recolonization experiments showed that kelps dominated all algal turf patches and 47% of mussel patches within 7 months. In contrast, Modiolus did not recover from simulated dislodgement disturbance, suggesting that the ability of kelps to bounce back from disturbance enhances their competitive superiority.

Keywords
Biology, Ecology

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ECOLOGY OF ROCKY SUBTIDAL COMMUNITIES:
THE ROLE OF MODIOLUS MODIOLUS (L) AND
THE INFLUENCE OF DISTURBANCE, COMPETITION, AND MUTUALISM

BY

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DISSERTATION

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in
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September, 1984
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THE INFLUENCE OF DISTURBANCE, COMPETITION, AND MUTUALISM

by

JON D. WITMAN

University of New Hampshire, September, 1984

This study presents an analysis of physical and biological processes regulating the structure of rocky subtidal communities off the coast of New Hampshire and southern Maine, USA, with particular emphasis on the ecology of the horse mussel Modiolus modiolus (L.). Quantitative sampling and multivariate analysis revealed 3 communities along an 8-30 m depth gradient off Star Island, Isles of Shoals: (1) a Modiolus community; (2) a 30 m community consisting of species with highest densities outside mussel beds; and (3) an 8-18 m community composed of species attaining maximal densities outside mussel beds.

A combination of methods: controlled field experiments, a natural grazing experiment, and long-term photographic monitoring (5 yrs) enabled patterns of Modiolus community structure to be related to the processes maintaining them. Bivalve, ophiuroid, and echinoid prey outside, but not inside, Modiolus beds were consumed by fish, crab, and lobster predators indicating that Modiolus beds are a spatial refuge from predation. The sea urchin Strongylocentrotus droebachiensis was the most significant agent of biological disturbance; motile urchin aggregations overgrazed the 8 m benthos in 1982 causing radical changes...
in species composition, rank order of dominance, species richness, diversity and evenness outside the mussel beds. Infaunal assemblages within Modiolus beds changed the least because the mussel bed structure damped the impact of overgrazing on the associated fauna.

At two exposed offshore sites, dense populations of Modiolus modiolus occurred at intermediate depths (11-18 m) but not at shallow depths (4-8 m) that were dominated by the kelp Laminaria digitata and Laminaria saccharina. Experiments and surveys indicated that chronic storm-generated disturbance caused massive dislodgement of mussels competitively overgrown by kelp, and could account for the scarcity of Modiolus at shallow depths. The hypothesis that sea urchins increase Modiolus survivorship by grazing kelp off mussels and decreasing the risk of dislodgement was tested by an urchin removal experiment. The removal of sea urchins from mussel beds led to an exponential recruitment of kelp resulting in a 30-fold increase of mussel mortality (via kelp-induced dislodgement), compared to control beds with resident sea urchins. The Modiolus-Strongylocentrotus interaction is mutualistic, as mussels provide a refuge from predation for resident sea urchins. It is suggested that the coexistence of kelp and mussel competitors is facilitated by facultative mutualism. Patch recolonization experiments evaluated the ability of kelp and mussels to recover from dislodgement disturbance. Kelps recolonized and dominated all algal turf patches and 47% of mussel patches within 7 months. In contrast, Modiolus did not recover from simulated dislodgement disturbance despite dense mussel recruitment, suggesting that the ability of kelps to bounce back from dislodgement disturbance enhances their competitive superiority.
CHAPTER I

THE EFFECTS OF BIOLOGICAL DISTURBANCE AND MUSSEL BED REFUGES
ON SUBTIDAL COMMUNITY STRUCTURE

INTRODUCTION

On rocky shores, much of the structure of marine benthic communities is produced by sessile organisms (Dayton, 1971; Jackson, 1977; Paine and Suchanek, 1984). Since sessile organisms are permanently attached to the substratum, attachment space is an important limiting resource in rocky shore environments (Connell, 1961; Paine, 1966; Dayton, 1971; Menge, 1976). Thus, competition for attachment space frequently determines the abundance and distribution of hard substrate organisms such as macroalgae (Dayton, 1975; Lubchenco, 1980; Santileces et al., 1981), barnacles (Connell, 1961a,b; Menge, 1976), mussels (Paine, 1966, 1974; Harger, 1972), cheilostome ectoprocts (Buss and Jackson, 1979; Jackson, 1979; Rubin, 1982), sea anemones (Francis, 1973), sponges (Rutzler, 1970; Sara, 1970), and assemblages of sponges, ectoprocts, and ascidians (Russ, 1982; Sebens, 1984a). Another consequence of epifaunal existence is that communities of sessile organisms are exposed to large, potentially destructive disturbances. There is a considerable amount of evidence that physical and/or biological disturbances are major determinants of community structure in the rocky intertidal zone (Paine, 1966; Dayton, 1971, 1973; Levin and Paine, 1974; Osman, 1977; Paine, 1979; Sousa, 1979; Lieberman et al., 1979; Paine and Levin, 1981; Dethier, 1984; reviewed
in Sousa, 1984). Disturbance refers to an extrinsic, deleterious event that causes a rapid modification in a population or community (Levinton, 1982). Dayton (1971) demonstrated that disturbance can mediate competitive interactions by forestalling competitive exclusion; this process increases species diversity by enabling competitively inferior species to coexist with competitive dominants (Levin and Paine, 1974). As shown by Connell (1978) and Lubchenco (1978), diversity is maximized at intermediate levels of disturbance. A major implication of disturbance studies in intertidal communities is that mosaic patterns of species distribution may be attributed to the influence of biological interactions (predation, competition) among suites of species that have colonized disturbance-generated patches (Dayton, 1971; Levin and Paine, 1974; Sousa, 1979; Paine and Levin, 1981; Dethier, 1984).

Less is known about how disturbance affects community structure in the subtidal zone, particularly in cold temperate and subarctic regions (reviewed in Connell and Keough, 1984). As a group, echinoderms are probably the most significant agents of biological disturbance in hard substrate subtidal communities. For example, sea urchins cause catastrophic changes in the state of benthic ecosystems by transforming productive kelp communities into barren grounds dominated by encrusting coralline algae (Kitching and Ebling, 1961; Leighton et al., 1966; Jones and Kain, 1967; Paine and Vadas, 1969; Pearse et al., 1970; Himmelman and Steele, 1971; Dayton, 1975; Breen and Mann, 1976; Forman, 1977; Pearse and Hines, 1979; Duggins, 1980; Hagen, 1983; reviewed in Lawrence, 1975). A major exception occurs in Chilean kelp forests where sea urchin grazing does not affect kelp communities (Moreno and
Sutherland, 1982). In addition to sea urchins, the sea stars Asterias rubens and Asterias vulgaris play an important disturbance role in North Atlantic subtidal communities. Massive aggregations of A. rubens (in Europe) and A. vulgaris (in North America) devastate extensive Mytilus edulis beds in the shallow subtidal zone (Sloan and Aldridge, 1981; personal observations). On Pacific coral reefs, the crown of thorns sea star Acanthaster planci causes radical changes in community structure by severely grazing vast tracts of coral (Chesher, 1969; Endean, 1973). In perhaps the most complete investigation of biological disturbance in any temperate subtidal community to date, Ayling (1981) evaluated the disturbance roles of fish, gastropods, sea urchins, and sponge disease in encrusting communities in northern New Zealand. The effect of sea urchin grazing, which was ranked as the most important source of disturbance, was to clear patches of free space in sponge-ascidian assemblages encrusting subtidal rock surfaces. Ayling (1981) and Sebens (1984b) found that the species diversity of subtidal encrusting invertebrates was highest at intermediate levels of disturbance.

A sessile organism that determines much of the structure of subtidal communities on both sides of the North Atlantic Ocean is the horse mussel, Modiolus modiolus. Essentially a subtidal species, Modiolus creates physically complex aggregations on a wide range of hard substrata including solid rock, boulder and gravel floors, and clay pavements from the low intertidal zone to a depth of 280 meters (Peterson, 1913; Shelford, 1935; Spark, 1935; Wiborg, 1946; Rowell, 1967; Roberts, 1975; Comely, 1978). Early on, Petersen (1913, 1918) recognized that Modiolus beds supported a rich community of marine
invertebrates. Thorson (1971) stated that the *Modiolus* community was "... as far as species are concerned, the most luxuriant society these seas (cold-temperate northeast Atlantic) can offer." The species composition of *Modiolus* communities have not been quantitatively described, even though *M. modiolus* forms the basis of a major North Atlantic subtidal community. Qualitative descriptions of *Modiolus* communities have been published by Roberts (1975), Hiscock and Mitchell (1980), and Comely (1981). Warwick and Davies (1977) sampled *Modiolus* communities in the Bristol Channel, England with a bottom grab, however, they adopted a loose definition of the community as < 20% of their samples included *Modiolus*. The lack of information on the ecology of subtidal *Modiolus* communities reflects the general absence of information on the ecological roles of mussels in subtidal communities. In one of the few ecological investigations of subtidal mussel beds, Paine (1976) documented the depth and size distribution of *Mytilus californianus* and observed that a species rich community was associated with the subtidal mussel beds.

In this chapter, I examine the structure and dynamics of subtidal communities living on upper rock surfaces at the Isles of Shoals, New Hampshire. First, I describe variation in community structure between depths (8, 18, and 30 m) and habitats (inside and outside *Modiolus* beds). By conducting controlled field experiments and documenting the results of a large, natural grazing experiment, I then demonstrate that subtidal mussel beds modify community structure by buffering the impact of both types of biological disturbance (predation and grazing; Dayton, 1971). Long-term photographic monitoring techniques have enabled me to show that *Modiolus* beds at all depths persisted for > 5 years, and that
shallow mussel beds resisted a large overgrazing disturbance. The effectiveness of *Modiolus* beds as refuges is related to their persistence, and their ability to resist the biotic disturbing forces which largely determine the distribution and abundance of other benthic organisms on upper rock surfaces.
METHODS

Study Area and Sampling Methods

This study was conducted at three subtidal sites off the southeast corner of Star Island, at the Isles of Shoals, NH (42°58'30"N:70°37'W; Fig. 1). The sites are located on the most exposed side of the island (Kingsbury, 1976) and are impacted by oceanic swells originating from northeast, southeast, and southwest sectors. Wave heights range from .5 to 2 m in summer and from .5 to 7 m in winter (personal observations). Three sites, which are described in Hulbert (1980), were established at depths of 8, 18, and 30 meters 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. Of particular interest here is the occurrence of dense aggregations of *Modiolus modiolus* on upper rock surfaces throughout the study area (Witman, 1980; *M. modiolus* abundance in Chapter 2).

All sampling and experimentation was 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 meters) a 0.25 m² quadrat was randomly dropped onto the substratum. All organisms within the quadrat were removed by scraping with a putty knife and simultaneously vacuuming with an airlift. Organisms were sucked into a nylon bag (0.5 mm mesh size) at the end of the airlift. This procedure was repeated until 5 samples were collected from *Modiolus* aggregations and 5 samples were collected on
the substratum outside the mussel aggregations for a total of ten 0.25 m² samples per depth (thirty 0.25 m² quadrats overall depths; 7.5 m² total sampling area). Disruptive sampling was completed within 1 season; spring, 1979. Samples were preserved in 10% buffered formalin 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.

In order 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 5 quadrat sizes were used: 156 cm², 625 cm², 1600 cm², 2500 cm², and 5000 cm². Species richness (the total number of species) and area were related as:

\[ S = -11.81 + 10.28 \ln A \]

where \( S \) = species richness and \( A \) = quadrat area in cm², and \( R^2 = 0.96 \). A plot of species richness vs. quadrat area revealed that the asymptote occurred between 1600 and 2500 cm², indicating that each 0.25 m² sample was near local species saturation. This was evident when doubling the quadrat size (from 2500 cm² to 5000 cm²) added only 3 species (\( S = 70 \) at 2500 cm²; \( S = 73 \) at 5000 cm²). 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 of species with similar patterns of distribution. Species density data were input as a two way data matrix consisting of 80 species (rows) X 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. 91 species were excluded from the analysis because they occurred in < 3 out of 10 samples per 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. *M. modiolus* was omitted from the analysis to avoid biasing the calculation of inter-entity similarities. Densities ranged from 0 to 2164 individuals/0.25 m². It was evident that unless the data were transformed, the clustering of the less abundant species would be obscured by the dominant species clusters. Consequently, the data were square-root transformed prior to analysis to eliminate the effect of overwhelming dominance by very abundant species (Gauch, 1982:22).

The analytical procedure consisted of the following two steps:

1. Product moment correlation coefficients were calculated to determine the level of similarity in all possible combinations of entities 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 was selected in preference to other similarity measures because it provides an objective criterion for deciding which clusters are similar. With this technique, coefficients are constrained between -1 and + 1, with -1 representing complete
dissimilarity and +1 representing complete similarity. Clusters linked at positive non-zero values are considered similar (Bush, 1980; Humphrey et al., 1983). Group average linkage is hierarchical and agglomerative. It was chosen because it minimizes the distortion of inter-entity relationships in the original similarity matrix during the construction of the dendrogram (Boesch, 1977:51).

Post-clustering statistics were performed to identify 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 Appendix I. To eliminate heteroscedasticity, the data were log (x + 1) transformed before analysis. F-max tests (Sokal and Rohlf, 1969) were non-significant for all 80 species, indicating that the assumptions of homoscedasticity had not been violated. Where the interaction of depth and habitat were non-significant, 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 site. 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 m² plexiglas
panels. The rack was secured to the bottom so that it lay flat against the substratum. Before the experiments began, mussel beds were created on half of the panels by transplanting 10 live *M. modiolus* to each panel and allowing byssal attachments to form. Thus, there were two treatments; presence and absence of mussel bed structure. The general experimental procedure consisted of placing equal densities of invertebrate prey in the two treatments and in two 0.5 m² predator exclusion cages which served as 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 intervolometer. The null hypothesis of no difference in the mortality of experimental prey inside and outside mussel beds will be rejected if deaths by predation differ between treatments.

Three species of invertebrates were selected as prey because they are normally very abundant inside *Modiolus* aggregations (Appendix 1). They were the bivalve *Hiatella arctica*, the ophiuroid *Ophiopholis aculeata*, and the sea urchin *Strongylocentrotus droebachiensis*. Data on the population structure of these 3 species was utilized to select a range of naturally occurring sizes and densities for use in the experiments (Appendix 2). It was necessary to restrict the movement of the prey organisms so that they remained at positions inside and 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 plexiglas panels. Pieces of velcro rugs were 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, in between the mussels. Two trials were conducted with H. arctica prey. The first trial began on August 12, 1982 and was monitored by diving at approximately 4 hour intervals for a 29 hour period. Trial 2 began on September 30, 1982 and ran for 32 hours. In the second trial, predation attacks were monitored by time lapse photography.

The movement of sea urchins was restricted by tethering individual urchins to an eyebolt in the center of each panel. Tethering consisted of tying fine monofilament around the test. Five tethered urchins were tied to each panel (n = 20 per treatment). Urchins moved freely across the panel but were prevented from leaving the experimental habitat by the monofilament tether. The size of the sea urchins used in the experiments (29 mm mean test diameter) corresponded to the primary mode of the size distribution of urchins living in Modiolus beds at 8 m (20 to 30 mm). An additional 40 sea urchins were tethered to 8 panels and placed inside predator exclusion cages to serve as controls. Rates of predation on S. droebachiensis were slower than on H. arctica and O. aculeata, so the survival of sea urchins was monitored by diving at approximately 6 hour intervals for 45 hours. The sea urchin trial began on October 2, 1982.

Initial attempts to tether O. aculeata by tying monofilament around the central disc failed because the ophiuroids escaped. Consequently, ophiuroids were sewn and tied to small lead sinkers with fine monofilament. The aboral surface of the disc was pierced with a fine needle which was passed through the mouth so that a knot could be tied around the disc. None of the tethered ophiuroids died as a result
of this procedure. A separate experiment was conducted to test the hypothesis that pierced ophiuroids incurred artificially high predation rates due to the attraction of chemosensory predators. In this experiment, 2 sets of 6 sinkers with 4 tethered ophiuroids per sinker were placed on the bottom. One set of ophiuroids was sutured as above and the other group of ophiuroids was successfully tethered by double tying each ophiuroid with two lengths of monofilament (very laborious). The two treatment sets (pierced vs. non-pierced ophiuroids) were 6 m apart and Q. aculeata survival was monitored by diving.

The design of the Q. aculeata experiments differed from the experiments with M. arctica and G. droebachiensis. Instead of placing prey on panels, tethered ophiuroids were placed inside and outside a natural M. modiolus bed. Six sinkers with 4 Ophiopholis attached to each sinker were placed in between mussels in the established mussel bed and another 6 sinkers were placed on the substratum outside the bed (1 m away). The time lapse camera was focused on the mussel bed and the ophiuroids on the substratum. Photographs were taken at 5 min intervals during the two trials. Trial 1 began at night on October 6, 1982 and continued for 8.5 hours. In contrast, trial 2 began during the day on October 7, 1982. After 6 hours, the second trial was terminated due to a northeast storm.

Band transects were used to determine the densities of predators normally present 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 on one side of the line were counted. To evaluate diel and seasonal variation in predator abundance, 3 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, 70 individuals/0.25 m² maximum density) 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 overgrazing by sea urchins. The abundance and distribution of benthic invertebrates and macroalgae was quantified in April, 1979 when this site was a laminarian algal forest. At this time, the kelps *Laminaria digitata* and *Laminaria saccharina* formed a canopy 1–2 m above a dense understory of red algae. During April, 1982 which was 1 month after the kelp forest had been transformed into an urchin barrens (*sensu* Pearse et al., 1970), the communities were re-sampled using the same techniques as in 1979. As before, five 0.25 m² quadrats were airlifted inside and outside *Modiolus* beds (10 samples overall, 2.5 m² total sampling area), and the samples were processed in the lab. Because the 1979 samples were collected before overgrazing by urchins occurred, it was assumed that differences in species composition between the 1979 and 1982 samples were primarily due to urchin grazing effects. 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.
Quantitative comparisons of communities before and after urchin disturbance were made by cluster analysis and by calculating species diversity indices. Species density data were entered into the CLUSTAN 2.1 computer program (Wishart, 1982) as a matrix of 20 rows (samples) x 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 same methods described previously. Product moment correlation and group average linkage were performed. This time, however, samples were clustered based on the similarity of their faunas (Boesch, 1977). 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 logs 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 species from 8 m depths were classified into four functional groups; upright algae, infauna, epifauna, and mobile fauna (Appendix 1 and 3). The interpretation of the effect of overgrazing on community structure was facilitated by making comparisons within functional groups before and after urchin disturbance. Upright algae included foliose, filamentous, and sheet-like macroalgae. 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 at the time of sampling.
Monitored Mussel Beds

It was possible to determine the persistence of individual *Modiolus* beds at different depths by long-term photographic monitoring. Underwater epoxy was spread onto the rock substratum at 4 corners of a 0.25 m² plot around *Modiolus* beds in January, 1979. Four mussel beds were monitored at each of three depths (8, 18, and 30 m; n = 12 overall depths). The epoxy marks served as alignment guides for a fixed aluminum camera frame (quadrapod) specially designed for the photography of 0.25 m² quadrats. A Nikonos camera with a 15 mm wide angle lens and two electronic strobes were mounted on the frame. Marked mussel beds were photographed 3 to 6 times per year for 5 years. Mussels were easily counted from the photographs; individual mussels could be identified by specific patterns of crustose coralline algae encrusting the shells as well as by their spatial position within the bed. None of the mussels emigrated from the monitored beds. Each time that the beds were photographed (and on many other dives) notes were taken on the specific sources of mortality affecting mussels in the monitored beds. In conjunction with the photographs, these observations enabled three sources of mortality to be differentiated: (1) dislodgement of mussels following overgrowth by laminarian algae; (2) predation by *Asterias vulgaris*; and (3) shell crushing predation by crabs and lobsters. Ten percent of the 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. From the photographic record, adult mortality rates of *M. modiolus* were calculated. Recruitment of juvenile mussels to each monitored bed could be estimated by the appearance of small mussels.
Recruits could be recognized in the photographs only after they had attained a size of 5 to 10 mm shell length.
RESULTS

**Benthic Communities**

Cluster analysis separated the 80 dominant species of benthic invertebrates into three major groups (Fig. 2). The species composition of these three groups is listed in Appendix 1. Two way analysis of variance indicated that there was a significant effect of depth and habitat on the distribution of all species in groups A, B, and C (Appendix 1).

Group A consists of species that are most abundant at 30 m depth outside the mussel beds (Fig. 3). In terms of both number of species and number of individuals, Group A is dominated by gammarid amphipods. Most of the habitat structure in this community is created by the numerically dominant gammarid, *Photis macrocoxa*, which constructs a matrix of tubes on the rock surface. The most abundant encrusting invertebrates are a demosponge *Polymastia infrapilosa*, an octocoral *Clavularia modesta*, and the ascidians *Chelyosoma macleayanum* and *Polycarpa fibrosa*. The interaction of depth and habitat factors in 2-way ANOVA was significant for all but 8 species. The results of Student-Newman-Keuls tests on these 8 species indicated that they were significantly more abundant outside the mussel beds at 30 m (Appendix 1).

Group B contains the most ubiquitously distributed species which attain maximum densities outside the mussel bed at either 8 or 18 m depth. This is supported by SNK tests conducted on the 14 species where the interaction term in 2-way ANOVA was non-significant; these
species were significantly more abundant outside mussel beds (Appendix 1). Within this assemblage of 27 species, polychaetes and amphipods had high species richness (8 and 7 species, respectively). The three most abundant species in group B are the amphipods *Ischyrocerus anguipes* and *Pontogenia inermis*, and the herbivorous gastropod *Lacuna vineta*. All of these dominants inhabit macroscopic algae outside the mussel beds at 8 or 18 m (Fig. 3).

Members of group C are all most abundant within the mussel beds at either 8, 18, or 30 m depth (Appendix 1, Fig. 3). Consequently, group C is designated the *Modiolus* community. It is numerically dominated by the ophiuroid *Ophiopolis aculeata*, which lives between mussels at the base of the aggregation. Other numerically important fauna inhabiting the base of the mussel matrix include the polychaetes *Cistenides granulata*, *Nainereis quadracuspida*, *Amphitrite cirtata*, *Amphitrite johnstoni*, and the hiatellid bivalve *Hiatella arctica*. *S. droebachiensis* was abundant in the upper portion of the mussel matrix. 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 1). Although all 23 species in group C are most abundant in mussel bed habitats, the majority of these species (18) are eurytopic. The 5 species that occurred only inside *Modiolus* beds were the polychaetes *Cistenides granulata*, *Myticola 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 the mussel beds. Table 1 shows that there were
significantly higher densities of infauna in the mussel beds than on the substratum outside the beds at each depth.

**Predation Experiments**

Two characteristics of *Modiolus* community structure are: (1) an assemblage of 23 species is most abundant in the mussel beds and (2) overall densities of infaunal organisms are higher in *Modiolus* beds than elsewhere. Five predation experiments were carried out to search for the mechanisms maintaining these patterns of community structure. The hypothesis tested was that the mussel bed's structure acts as a buffer against the effects of biological disturbance by limiting the access of mobile predators to prey organisms residing in the mussel beds. If the mussel beds are a spatial refuge, then deaths from predation should be lower inside the beds.

**Hiatella arctica: Trial 1**

Predation on *H. arctica* outside the experimental mussel beds was dramatic (Fig. 4). Within an hour, three *Hiatella* outside the beds were consumed by predators. In twenty-nine hours mobile predators had consumed all *Hiatella* outside the mussel beds while only two *H. arctica* inside the mussel beds were eaten.

The predator guild consisted of two crabs *Cancer irroratus* and *Cancer borealis*, the lobster *Homarus americanus*, a neogastropod *Buccinum undatum*, and the sea star *Asterias vulgaris*. Most of the exposed *Hiatella* were eaten by *Cancer borealis* which foraged nocturnally as did *H. americanus* (Fig. 4). *B. undatum*, *A. vulgaris*, and *C. irroratus* fed on *Hiatella* during the day. *H. arctica* outside the mussel beds were devastated by nocturnal predation; between 7:00 pm
and 1:00 am, 21 exposed individuals were consumed. Ten of these deaths were witnessed during the 1 am dive. At this time, four large _C. borealis_ were seen eating a total of 9 _Hiatella_ and 1 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 were the trademark of crab or lobster predation since rock crabs and lobsters are known to crush bivalve and sea urchin prey (Elner, 1980) and both _A. vulgaris_ and _B. undatum_ left empty, intact shells which were still attached to the panels after the predation event. The only predator that penetrated the mussel aggregation was _A. vulgaris_ which consumed two _Hiatella_ (Fig. 4).

_Hiatella arctica_: Trial 2

Nineteen hours of the second _Hiatella_ trial was monitored by time lapse photography to follow the sequence of predation more directly. The camera was placed 2.5 m from the center of the experimental array so that the entire rack could be photographed at 10 minute 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.

Figure 4 shows that, as in trial 1, deaths from predation were greater outside the mussel beds. The camera ran out of film after 19 hours and 40 minutes. Consequently, the survivorship of the remaining prey had to be monitored by diving. Between 6:30 pm and 6:00 am, the last 10 _Hiatella_ outside the mussel beds were eaten. As before, crushed shells were left on the panels implicating crab and or lobster predation. None of the _Hiatella_ inside the mussel beds were consumed.
during the 32 hour 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 which were differentiated on the basis of total length (21, 17.5, 15 cm). C. borealis was also a significant predator, consuming 8 of the exposed Hiatella.

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

**S. drosbachiensis Trial**

Figure 5 shows that there was a striking difference in the survivorship of urchins inside and outside Modiolus beds. Within 44 hours, all exposed urchins were consumed by crabs, cunner, and a lobster. In contrast, no urchins were eaten inside the mussel beds or in the control cages.

There was some evidence of a temporal pattern to predation on exposed urchins. With the exception of 1 attack by C. irroratus during the day, crab predation was greatest at night because C. borealis preyed on urchins only at night. During the day, the cunner, T. adspersus was an important predator, consuming six urchins. The feeding behavior of cunner was observed on several occasions.
Typically, it consisted of an initial strike to damage the urchin test and expose the viscera which was 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 ($x^2 = 1.5$, 1 df, with Yates correction for sample size).

**Ophiopholis aculeata: Trial 1**

Although crabs and lobsters were present 65 minutes after the experiment began, no *Ophiopholis* were attacked until 3 hours later when a small lobster dragged away 4 tethered ophiuroids from outside the mussel beds (Fig. 6). Lobsters continued to prey on exposed ophiuroids throughout the night. By 2:15 am, all but 2 *O. aculeata* had been consumed by three different lobsters. None of the ophiuroids in the mussel beds were eaten throughout the 10.5 hour experiment.

**Ophiopholis aculeata: Trial 2**

A second trial was initiated during the day. In contrast to the night trial where lobsters accounted for all the predation on *Ophiopholis*, all of the daytime predation was by winter flounder, *Pseudopleuronectes americanus* (Fig. 6). Most of the predation was by a large flounder (35 cm total length) which continued to feed on exposed *Ophiopholis* for 70 minutes. The same flounder returned to ingest another ophiuroid before a different, smaller flounder (20 cm total length) consumed 7 ophiuroids tethered to two sinkers. As in the first trial, no ophiuroids in the *Modiolus* beds were consumed by predators.
The results of the experiment testing for artifacts associated with the method of tethering Ophiopolis are presented in Table 2. The result was the same for pierced and non-pierced individuals; all ophiuroids were eaten by morning. During the 11:30 pm dive, a C. borealis was seen feeding on pierced Ophiopolis and a H. americanus was caught with 4 non-pierced ophiuroids in its claw. These results falsify the hypothesis that the intensity of predation is higher on pierced O. aculeata.

Virtually all prey organisms placed in the experimental mussel beds escaped predation during the 5 refuge experiments, clearly supporting the hypothesis that the mussel beds are predation refuges for the dominant species of the Modiolus community.

**Predator abundance**

Table 3 shows diel and seasonal variation in the abundance of major predators in the vicinity of the experimental site at 8 m depth. The common fish predators were 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. With the exception of eelpout, all fish were seen only in the summer transects. Eelpout were present throughout the year. During the summer, both cunner and flounder were significantly more abundant during the day than at night (Table 3). 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. During the summer and winter all three crustacean predators, *C. irroratus*, *C. borealis*, and *H. americanus* were significantly more abundant at night than in the day (Table 3). *A. vulgaris* and *B. undatum* 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 performing cluster analysis on samples from the 8 m community before and after it was overgrazed by sea urchins. The analysis designated four major groups. Four *Modiolus* bed samples from before urchin disturbance clustered out together along with 1 pre-disturbance substratum sample in Group A. Group B represents a combination of 1 pre-disturbance and 4 post-disturbance *Modiolus* bed samples. In contrast to the *Modiolus* samples, samples from the community on the substratum outside the mussel beds separated into distinct pre-disturbance (Group C) and post-disturbance (Group D) clusters. Group C represents the invertebrate community associated with the laminarian algal bed before it was overgrazed by urchins. All samples from the urchin barrens clustered out in Group D which was characterized by the highest degree of internal similarity (samples linked at .30). This reflects the extreme change in community composition which was brought about by overgrazing. The inclusion of pre- and post disturbance 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.
Dominant Species

Rank analysis (Fager, 1957) was used to examine the effect of urchin disturbance on the species composition of 8 m communities in greater detail.

Outside Substratum Community. Table 4A lists the top ranked species before and after the disturbance. Before disturbance, multispecies assemblages associated with the kelp beds were dominated by the herbivorous gastropod *Lacuna vinca*. Of the top 10 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). *Pontogeneia 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. vinca*, *A. rubricata*, *L. phosphorea*) in the pre-disturbance community.

Intensive grazing by *S. droebachiensis* radically altered the rank order of dominance; none of the community dominants were ranked the same before and after the perturbation (Table 4A). The post-disturbance community was overwhelmingly dominated by the amphipod *Pontogeneia inermis*. *P. inermis* densities were not significantly different before and after urchin overgrazing ($f = 1.97$, 1.8 df, $p > .05$, 1-way ANOVA). The population densities of other dominant amphipods were, however, an order of magnitude lower after disturbance ($f = 8.2$; $p < .025$, *I. anguipes*; $f = 16$, $p < .005$, *S. bonelli*; $f = 28.7$, $p < .001$, *J. falcata*; $f = 21.8$, $p < .005$, *P. glaber*; $f = 16.8$, $p$...
Populations of tube-dwelling amphipods (A. rubricata, I. angipes, J. falcata, C. bonelli) were decimated because amphipod tube networks were grazed off the substratum by sea urchins. It is suggested that the ability of P. inermis to occupy pelagic habitats enabled it to escape the benthic-oriented disturbance. As expected, population densities of dominant herbivores were significantly lower after urchin disturbance ($f = 66.1$, $p < .001$, L. vincita; $f = 9.6$, $p < .025$, I. phosphorea; all comparisons by 1-way ANOVA with 1,8 df; A. rubricata as shown above). Other herbivores that incurred significant density reductions as a result of overgrazing but not ranked as dominants were Margarites helicinus ($f = 18.7$, $p < .005$) and Idotea balthica ($f = 6.1$, $p < .05$; both comparisons 1-way ANOVA with 1,8 df). Such reductions in herbivore population densities is attributed to the loss of macrophyte food resources and to the destruction of algal habitats.

**Modiolus Bed Community.** In striking contrast to the outside substratum community, the rank order of dominant species in the mussel bed community was nearly the same before and after urchin disturbance. For example, the rank order of six of the top ten species was not changed by the perturbation (Table 4B). Ophiopholis aculeata dominated the Modiolus community before and after disturbance. Fully eight of the species listed as dominants in the pre-disturbance community remained among the top ten ranked species after the disturbance.

Densities of the dominant species were compared before and after disturbance by one-way ANOVA. Pre- and post-disturbance densities were not significantly different for 7 of the top 10 ranked species ($f = .87$, O. aculeata; $f = .3$, N. quadricuspida; $f = 1.1$, A. cirrata;
Densities of *S. droebachiensis* were significantly lower after the urchin front passed over the mussel beds (*f* = 41.8, 1,8 df, *p* < .001, 1-way ANOVA). As in the outside community, densities of *L. vinca* and *L. anguipes* were significantly lower in the post-disturbance mussel bed community (*f* = 6.46, *p* < .05, *L. vinca*; *f* = 7.89, *p* < .05, *L. anguipes*, 1-way ANOVA, 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 overgrazing for a majority of the dominant species inhabiting them.

**Species Richness**

Figure 8 indicates that for 3 of the 4 functional groups, the effect of urchin disturbance was the same inside and outside the mussel beds. 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* = 180, *p* < .001, inside; mobile fauna: *f* = 135, *p* < .001, outside; *f* = 52.6, *p* < .001, inside; all comparisons by 1-way ANOVA with 1,8 df). A major exception to this trend was demonstrated by the infauna. While infaunal species richness was significantly reduced outside the mussel beds (*f* = 109, 1,8 df, *p* < .001, 1-way ANOVA), there was no significant difference in the species
richness of mussel bed infauna before and after urchin disturbance ($f = .3, 1.8$ df, $p > .05$, 1-way ANOVA). This result suggests that the destructive effect of urchin 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 ($\bar{x} = 24.6; F = 38.4; 1.8$ df, $p < .001$, 1-way ANOVA).

Species Diversity and Evenness

Mean values of Shannon Weiner diversity ($H^\prime$) and evenness ($J^\prime$) were computed by functional groups and are graphed in 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).

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 was higher inside the mussel beds. This was due to the elimination of all epifauna attached to rock and crustose coralline algae outside the mussel beds.

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 urchin barrens community (Table 4A).

**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 overgrazed \( (U = 25, \ p < .01) \). Low mean evenness in the Modiolus infauna was due to the dominance of Ophiopolis 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).

Urchin grazing eliminated all upright macroalgae, a majority of the species inhabiting algal habitat structures, and most species of encrusting invertebrates. Local species diversity was significantly lower in the post-disturbance urchin barrens community than in the pre-disturbance kelp bed community. The urchin barrens community has low species richness with a high concentration of dominance among few species, consequently, it has a low \( H' \) and low evenness.
Resistance and Mortality of Modiolus

The predation experiment and the natural grazing experiment indicated that the Modiolus beds are refuges from biological disturbance. Why then, are the mussel beds such effective refuges? This question was addressed by monitoring mussel beds for 5 years.

All Modiolus beds persisted for 5 years, 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 (1 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 meters was impacted by the large scale urchin disturbance. Changes in the mussel beds were documented for two years after the urchin front passed over the monitored beds between December, 1981 and February, 1982. Figure 10 shows that the Modiolus beds remained intact after the disturbance. Since a disturbance force was applied and resisted, the Modiolus populations at 8 m are characterized by a high degree of resistance stability. The deeper mussel beds were not subjected to a major disturbance during the 5 year monitoring 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 5, 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, $x^2 = 24.5$, $p < .005$; 8 m > 30 m, $x^2 = 18.2$, $p < .005$; chi square analysis). For example, the mortality rate at 8 meters was 7 times
higher than at 18 m, and 45 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, accounting for 76% of the deaths at 8 m, 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 urchin overgrazing to 5.2% in the 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 vulgaris on M. modiolus was greatest at 8 m and decreased with depth (8 m > 18 m, \( x^2 = 4.2, p < .05 \); 8 m > 30 m, \( x^2 = 3.9, p < .05 \)) (Table 5). Deaths from shell-crushing predators (crabs and lobsters) was a minor source of mortality and did not vary with depth.
DISCUSSION

The results demonstrate the functional significance of *Modiolus* beds as spatial refuges from both types of biological disturbance, predation, and grazing (Dayton, 1971) which are 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 grazing disturbance by occupying structurally complex mussel beds where they attain population densities which are significantly higher than in exposed habitats.

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 which 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 overgrazing sea urchins is comparatively infrequent, large scale, and causes radical changes in community structure. For example, shallow subtidal communities were overgrazed only once in a 5-year 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 A. vulgaris (Hulbert, 1980) and other members of the predator guild at the Isles of Shoals (Harris, 1984) and Nahant, Massachusetts (Sebens, 1984b) suggests that these 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 5 trials). This result is a function of the nocturnal foraging behavior of crustacean predators, as C. borealis, C. irroratus, and H. americanus were significantly more abundant at night (Table 3). Moreover, all C. borealis and H. americanus enumerated during the 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 fish than fish predation (e.g., by the wolfish 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 occurred only during the day and gunner and flounder were present at the experimental site only during the day (Table 3). This result is consistent with the observations of Bernstein et al. (1981) that fish predation is most intense during the day.

Although not 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 and move offshore into deeper water during the winter (Bigelow and Schroeder, 1953). Winter reductions of fish population densities in the New England subtidal have also been documented by Sebens (1984b). Unlike fish, nearshore lobster populations in the Gulf of Maine do not migrate offshore in winter (Cooper et al., 1975). 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 3). 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; *Asterias vulgaris, Buccinum undatum*, crabs, and lobsters is high enough to restrict the distribution of *Modiolus* community species to mussel bed refuges even 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 that predation pressure may also cause selection for cryptic habitats in subarctic subtidal regions. The cod, *Gadhus morhua*, is another predator that prey heavily on *O. aculeata* in the New England subtidal. For instance, the stomachs of 10 *G. morhua* feeding on the benthos of upper rock surfaces at 33 m depth at Pigeon Hill (30 Km SE of Star Island) contained 453 *O. aculeata* (unpublished data). An analog to the inter-habitat differences in ophiuroid population densities documented here occurs on Caribbean coral reefs with three congeneric species of *Ophiothrix* (Hendler, 1984). The ophiuroids *Ophiothrix lineata, Ophiothrix angulata, and Ophiothrix suensonii*, are significantly more abundant inside sponges than elsewhere, and Hendler (1984) demonstrated that the sponges protect the ophiuroids from fish predation. In subtidal communities off the coast of Nova Scotia, Bernstein et al., 1981 attributed the tendency of *S. 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 *S. droebachiensis* to seek shelter among rocks in laboratory conditions. At Star Island, *Cancer borealis* and *Tautogolabrus adspersus* had the
greatest effect on *S. droebachiensis*. In a detailed examination of predator effects in subtidal communities off northern Massachusetts, Sebens (1984) also found that *C. borealis* was a major predator on *S. droebachiensis*. It is suggested that populations of *Riatella 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 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 overgrazing. Mussel bed communities changed the least because the mussel bed structure damped the impact of overgrazing on the associated fauna. Thus, infaunal assemblages within the mussel matrix were not radically altered by the disturbance.

Intense grazing by aggregated *Strongylocentrotus* denuded the substratum of all species of upright macroalgae and nearly all encrusting invertebrates leaving *Modiolus* beds and crustose coralline algae. 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 populations of the gastropods *Lacuna vinca*, *Margarites helicinus*, and *Acmaea testudinalis*, the amphipod *Amphitoe rubricata*, and isopods *Idotea phosphorea* and *Idotea balthica*. In addition to *Strongylocentrotus*, the major herbivores remaining in the urchin barrens 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 overgrazing urchins (Langer, 1978; Steneck, 1982). The abundance of invertebrates in the community outside the mussel beds declined from a mean density of 2164 individual/0.25 m² prior to overgrazing to a mean density of 453 individuals/0.25 m² after overgrazing. In the St. Lawrence Estuary, Himmelman et al. (1983) demonstrated that the removal of urchins from barren areas caused the re-establishment of macroalgae which led to significant increases in population densities of herbivorous molluscs: *Acmaea testudinals, Margarites helicinus, Lacuna vincita,* and *Littorina obtusata* (Himmelman et al., 1983).

In this study, sea urchin grazing represented a large non-selective 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 similarly affected. The urchin barrens community outside the mussel beds was characterized by low species diversity ($H^1 = 2.14$; all functional groups pooled) and low species richness ($S = 22$ species), which is typical of the species diversity of communities following a severe disturbance (Connell, 1978; Lubchenco, 1978; Fox, 1979). Depending on the selectivity and intensity of grazing, sea urchin grazing may enhance or reduce local species diversity. By grazing on the competitively superior alga *Padina sanctae-crucis,* *Diadema antillarum* slowed the process of competitive exclusion, thereby increasing the diversity of algae on St. Croix coral reefs (Sammarco et al., 1974). More commonly, however, sea urchins...
overgraze algal communities and severely reduce the species richness and/or diversity of macroalgae (Paine and Vadas, 1969; Dayton, 1975; Lawrence, 1975; Breen and Mann, 1976; Foremann, 1977; Duggins, 1980; Himmelmann, 1980; Sammarco, 1982; Hagen, 1983). Very few studies have evaluated the effect of intense urchin grazing on invertebrate species diversity. Vance (1979) demonstrated 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, Himmelmann *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 post-disturbance communities at the 8 m site. A unique aspect of this study was that the analysis of the effect of sea urchin grazing on community structure was based on the knowledge of the distribution and abundance patterns of all macrobenthic species in the community.

Levels of species richness in the pre- and post-urchin disturbance communities reported here were substantially higher than those recorded by Himmelmann *et al.* (1983). For example, the mean species richness of invertebrates in the pre-disturbance kelp forest community at Star Island was 56.2 outside the mussel beds and 50.2 inside the *Modiolus* beds, compared to a species richness of 7.1 to 10.2 in kelp forest
communities in the St. Lawrence estuary (Himmelmann et al., 1983).
Similarly, mean species richness of invertebrates in the Star Island urchin barrens community was 24.6 outside the mussel beds and 34.2 inside the mussel beds, compared to a species richness of 1.3 to 4.8 in the St. Lawrence urchin barrens. Such striking differences in species richness may be partly attributed to the omission of amphipod species from Himmelmann et al.'s (1983) calculation of species richness, but is more likely a reflection of a lower diversity species pool in the inner reaches of the St. Lawrence estuary than in the fully marine habitats at Star Island. Species richness is known to decrease along estuarine gradients from the open ocean to the inner estuary (Sanders, et al., 1965; Wilkinson, 1980; Hardwick-Witman and Mathieson, 1983).

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

**Ecological Roles of Mussel Beds**

As competitive dominants on marine rocky shores, mussels play major roles in community organization (Paine, 1966, 1969, 1974; Seed, 1969; Dayton, 1971, 1973; Suchanek, 1978, 1979, 1984). Mussel beds have both direct and indirect effects on community structure. Direct effects include the formation of new habitats and the provision of new resources. Less is known about indirect effects which may involve the modification of levels of predation, competition, or disturbance.
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, 1984) but has not been explicitly demonstrated. The ability of mussel beds to provide protection from predators may be especially important in subtidal environments where predator abundance and foraging activity is not affected by tidal emersion and predators have the potential to be in constant contact with their prey. It should also be an important factor influencing habitat selection for mussel bed refuges by subtidal benthic invertebrates. The protection that Modiolus beds provide increased local diversity following large scale urchin disturbance. It is undoubtedly an important reason why Modiolus beds are inhabited by high densities of infaunal organisms. The effect of the Modiolus predation refuge on species diversity is consistent with Menge and Sutherland's (1976) prediction that habitat structural complexity reduces predation intensity, thereby increasing species diversity.

A critically important function of mussel beds in space-limited hard substrate environments is the provision of a structural matrix for species to inhabit. Secondary space is increased by the mussel bed structure (Dayton, 1971) due to an increased surface area of mussel shells. Suchanek (1979) found that the surface area of a Mytilus californianus bed was 3 to 15 times greater than the flat rock substratum outside the beds. Mussel shells support a diverse assemblage of epizoans including bryozoans, tunicates, sponges, polychaetes, crustose coralline algae, and foliose algae (Suchanek, 1979, 1984; this study). By emplacing physical replicas of Mytilus
caifornianus beds in the intertidal zone, Suchanek (1979) demonstrated that the high diversity of the Mytilus californianus community is a result of the physical complexity of the mussel bed structure. After a colonization period of 1 year, the diversity of the artificial mussel bed community was comparable to that of living M. californianus beds, providing unequivocal evidence that structural complexity is a major determinant of diversity in the rocky intertidal zone. As a large matrix forming species, Modiolus 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 shores, and are solitary but form dense, structurally complex habitats which harbor diverse communities.

Resistance and Refuge Suitability

The impact of mussel bed refuges in New England rocky subtidal communities is linked to several life history features of Modiolus modiolus. The results of age and growth studies indicate that Modiolus is a slow growing, long-lived species with an average lifespan of 17 to 30 years (Wiborg, 1946; Rowell, 1967; Seed and Brown, 1975, 1978; Brown and Seed, 1977; Comely, 1978). Maximum lifespans of 36 and 65 years have been recorded 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 years. In deep subtidal habitats (18 and 30 m) where disturbance caused mortality is low (Table 5), 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 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 imported by kelp (Witman and Suchanek, 1984). Photographic monitoring revealed that the Modiolus bed framework was able to withstand a severe overgrazing disturbance, which 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 overgrazing by Strongylocentrotus is a major mortality source, Modiolus bed refuges play a large role in the distribution of species abundance and diversity in urchin barren communities. Since Modiolus beds are the only large, biogenic habitat providing shelter in urchin barrens, they may be an important nursery area for many species of marine invertebrates. Additionally, populations of invertebrates living in post-disturbance 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 urchin barren areas.

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. Spatial refuges may be particularly common in kelp beds which have not been subjected to high levels of Strongylocentrotus.
grazing. These include various elements of algal habitat structure such as kelp holdfasts and canopies, turfs of red algae (Chondrus, Phyllophora, Phycodrys) and Corallina officinalis mats at the 8 m site, tufts of the red alga Pilota 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 provide the assemblages of amphipods, polychaetes, and gastropods associated with them (Fig. 2, Appendix 1) protection from fish predation may be inferred from other studies. For instance, Young and Young (1977) and Heck and Thoman (1981) provided experimental evidence that dense stands of vegetation provided more protection for prey than unvegetated bottoms or areas with sparse stands of vegetation. 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. C. officinalis was an abundant component of the understory algae outside the mussel beds at the 8 m site, with a mean dry wt biomass of 25.3 g per 10.25 m² prior to urchin disturbance, and is presumed to be a predation refuge. Unlike Modiolus beds, Corallina mats were grazed off the substratum by intense urchin overgrazing, consequently they probably 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 a situation in which a population resists 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). To my knowledge, this is the first demonstration that the ability of a species to resist disturbance contributes towards its capability to serve as a refuge for the organisms associated with it.

In the New England rocky subtidal zone, the principal effects of biological disturbance are to (1) bring about radical changes in the system state of shallow subtidal communities which are accompanied by massive reductions in species richness, diversity, and population densities of marine invertebrates; (2) cause significant mortalities of benthic invertebrates outside mussel beds; and (3) 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.
CHAPTER II

COEXISTENCE IN THE SHALLOW SUBTIDAL ZONE: THE IMPORTANCE OF PHYSICAL DISTURBANCE, COMPETITION, AND MUTUALISM IN MAINTAINING THE DEPTH ZONATION OF KELP AND MUSSELS

INTRODUCTION

Early research on mechanisms facilitating the coexistence of species within natural communities advanced the view that coexistence was achieved under equilibrium conditions set by competition (MacArthur and Levins, 1967; MacArthur, 1970; Cody, 1974). This view was challenged by the notion that predation could maintain competitively dominant species below carrying capacity (Paine, 1966; Connell, 1975), by the viewpoint that the strength of competition was variable and not incessant (Wiens, 1977), and by the theory that many communities are maintained in a non-equilibrium state by disturbance (Dayton, 1971; Levin and Paine, 1974; Connell, 1978; Fox, 1979; Sousa, 1979; Paine and Levin, 1981).

Rocky intertidal and subtidal communities provide excellent opportunities for research on mechanisms of species coexistence and processes structuring communities in general because (1) patterns of zonation are conspicuous with dominant species coexisting in ecotones and (2) most of the species producing the zones are sessile and amenable to experimentation. A considerable amount of experimentation has led to generalizations about the relative importance of factors maintaining the abundance and distribution of species along
environmental gradients in the rocky intertidal zone: (1) upper limits of species distribution are primarily set by physical factors (Connell, 1972, 1975) and (2) lower limits are primarily set by biological factors (Connell, 1961b; Dayton, 1971; Paine, 1974). These generalizations have been questioned by Dayton (1979) and Underwood and Denley (1984) who argue that they should not be used to interpret species distribution patterns in other communities without rigorous analysis.

Despite extensive descriptions of patterns of subtidal zonation in temperate rocky bottom environments (Peres, 1967; Golikov and Scarlato, 1968; Edelstein et al., 1969; Mann, 1972; Velimirov et al., 1977; Hiscock and Mitchell, 1980) very little is known about the mechanisms producing the patterns. Two broad subtidal zones have been recognized in cold-temperate (<20°C) regions: a shallow subtidal zone dominated by kelp (large brown algae of the order Laminariales) that extends as deep as there is light available for photosynthesis (Luning, 1981), and a region below the kelp zone that is dominated by sessile invertebrates but with scattered erect algae. Hiscock and Mitchell (1980) termed the kelp zone the infralittoral zone and the invertebrate dominated zone the circalittoral zone. In one of the first experimental studies of the mechanisms responsible for subtidal zonation, Jones and Kain (1967) demonstrated that the lower depth limit of the kelp zone could be determined by sea urchin grazing, above the depth imposed by light extinction. Dayton (1975) demonstrated that interspecific competition among kelps and sea urchin grazing maintained subtidal zonation at Amchitka, Alaska. Subtidal zonation is defined here as the successive predominance of one species or assemblage of species occurring within a
specified depth range (Wellington, 1982).

In this chapter, I use an experimental approach to elucidate the physical and biological processes maintaining the subtidal zonation of kelp (*Laminaria saccharina, L. digitata*) and mussels (*Modiolus modiolus*) at exposed, offshore sites in the Gulf of Maine, USA. In particular, I focus on the zone of overlap between kelp and mussels and address the question: What limits the upper distribution of *Modiolus modiolus*? I show that chronic physical disturbance and interspecific competition reduces the abundance of *Modiolus* at shallow depths. The coexistence of kelp and mussel competitors is maintained by a mutualistic interaction between mussels and sea urchins (*Strongylocentrotus droebachiensis*). Patch recolonization experiments have enabled me to show that the competitive dominance of kelp is linked to their ability to recolonize disturbance produced patches faster than mussels.
METHODS

Study Areas

Field studies were conducted at Star Island (42°58'30"N: 70°37'W) and Murray Rock (43°04'15"N: 70°37'20"W) off the coast of New Hampshire and southern Maine, respectively, and at Sea Point, Maine (43°05'10"N: 70°40'40"W; Fig. 11). The Star Island research stations were located on a sloping granite shelf from a depth of 4 to 33 meters, and are described in Chapter 1. Murray Rock is the shallowest (2 m depth at MLW) of four subtidal pinnacles on the crest of an extremely exposed ledge 5 km offshore. A research station was established adjacent to Murray Rock on the flanks of a deeper (5 m depth at MLW) unnamed pinnacle 0.2 km southeast of Murray Rock, at a depth of 8 to 11 m. This site will be referred to as Murray Rock and abbreviated as MR, although it is actually adjacent to Murray Rock. The substratum at Murray Rock is composed of granitic gneiss. All research at Star Island (abbreviated as SI) and Murray Rock was conducted underwater using SCUBA. Sea Point is a rocky promontory bordered by beaches on the northern and southern sides of the point. Sea Point was selected to survey mussel strandings because it appeared likely that onshore currents would transport mussels dislodged at Murray Rock to Sea Point. This current pattern was verified when a plastic sponge, originally emplaced at Murray Rock for a mussel recruitment experiment, was dislodged and retrieved on the north beach at Sea Point.

Population Surveys

To document subtidal vertical zonation patterns, populations of
horse mussels (*Modiolus modiolus*), kelp (*Laminaria saccharina* and *L. digitata*), and sea urchins (*Strongylocentrotus droebachiensis*) were quantitatively surveyed at Star Island and Murray Rock. A photographic apparatus called a quadrapod was designed and built for *Modiolus* population surveys (see Chapter 1). The stratified random sampling procedure consisted of blindly dropping a 10 m transect line onto the bottom from high up in the water column. One end of the line was stretched out across the substratum along a pre-selected compass bearing taken from a random number table. A 0.25 m² quadrat photograph was taken with the quadrapod at eight random marks along the line. The procedure was repeated 4 times within each depth stratum at Star Island (4, 8, 12, 18, 24, and 32 m) and at Murray Rock (8, 11, 14, and 17 m). Surveys were conducted in July 1979 (SI) and June 1983 (MR), yielding a total sampling area of 48.0 m² (SI) and 36.0 m² (MR). The resulting quadrat photographs were projected to count all *M. modiolus* > 0.5 cm shell length. To determine the accuracy of the photographic censusing method, a pilot survey was conducted to compare photographic counts to field counts. At each of 25 randomly located (as above) *Modiolus* beds, the mussels with a 0.25 m² quadrat were counted (field counts) and the same quadrat was photographed with the quadrapod for subsequent photographic counts. Field and photographic *Modiolus* counts were related as:

\[ y = 1.76 + 0.922 x \]

where \( y = \) field counts, \( x = \) photo counts, \( r^2 = .95, p < .01 \) and \( n = 25 \). Consequently, the photographic method was an accurate way of censusing *Modiolus* populations.
Kelp (i.e. members of the order Laminariales) densities were assessed by quadrat sampling. Within each depth stratum (4, 8, 12 m, SI; 8, 11, 14, 17 m MR), a 1.0 m² quadrat was blindly tossed onto the bottom ten times. Population sampling of kelp was not conducted at the deeper Star Island sites because kelp was not generally present below 12 m depth. The 1.0 m² quadrat was subdivided into four 0.25 m² quadrats to facilitate counting of all Laminaria saccharina and L. digitata.

Large canopy forming plants were easily identified to species, however, it was difficult to differentiate L. saccharina and L. digitata when the sporophytes were < 5 cm height. Consequently, separate counts of juvenile sporophytes and canopy plants were made in each quadrat. This sampling method yielded a total sampling area of 30.0 m² at SI and 30.0 m² at MR. Sampling dates were as above. Sea urchins were counted in each quadrat along with kelp plants at Murray Rock and at the two shallowest depths (4, 8 m) at Star Island.

To estimate the population densities of sea urchins in urchin fronts at 11.5 m (MR) and 12 m (SI), separate photographic surveys were conducted with the quadrapod (using the same techniques and sample sizes as described above). Population densities of sea urchins at 18, 24, and 32 m at Star Island were estimated by counting from the same photoquadrats taken for Modiolus surveys. Because two different sampling techniques were used to assess S. droebachiensis populations, only within depth comparisons (inside or outside Modiolus beds) of sea urchin densities were made.

Effect of Physical Disturbance on M. modiolus

To evaluate the role of storm disturbance on Modiolus overgrown by
kelp, the number of dislodged mussels cast ashore at Sea Point (Fig. 11) was estimated by conducting surveys from September 1981 to October 1983. Strand lines occurring along a 409 m tract of north beach and a 335 m tract of south beach were surveyed bimonthly and up to several times per week after severe storms. All dislodged mussels were counted; notes were taken on the number of Laminaria saccharina, L. digitata, and Agarum cribosum plants attached to each mussel. To avoid counting the same dislodged mussel twice, the attached kelp was cut off the mussel as it was counted.

The sheer enormity of the strandings in October, 1982; August, 1983; and October, 1983 made it impossible to count all the dislodged mussels, thus it was necessary to subsample the bands of dislodged kelp and mussels washed up on the beach. This was accomplished by (1) measuring the area of the band of dislodged mussels as a series of rectangles and (2) making replicate counts in 1.0 m² quadrats randomly tossed onto the band of dislodged mussels. To count all mussels within the quadrat, I dug through layers of kelp with a pitchfork. Mean densities of dislodged mussels/1.0 m² were calculated and an estimate of the total density of mussels was obtained by multiplying the mean by the area of the stranding. This method probably underestimated the actual number of mussels dislodged because many mussels were buried by sand and cobble during severe storms. The size structure of random samples of dislodged mussels was determined by measuring the shell length of mussels in June, 1982 (summer) and February, 1983 (winter).

**Patch Surveys at Murray Rock**

Surveys were conducted in the kelp forest at 8-10 m soon after storms in April and October, 1982, and February and August, 1983 to
estimate the density and size of recently formed dislodgement patches. A three-sided 0.25 m$^2$ quadrat was blindly tossed onto the bottom and two types of patches were quantified: (1) patches in Modiolus beds created by the dislodgement of overgrown mussels and (2) kelp holdfast patches. The two types of patches were easy to differentiate because byssus threads were left in mussel dislodgement patches while holdfast patches were characterized by a large amount of bare rock and were bordered by newly fractured crustose coralline algae, not mussels. Patches were counted in ten replicate 0.25 m$^2$ quadrats on algal turf and in an equal number of quadrats on Modiolus beds during the quarterly sampling periods. Patches were photographed for subsequent measurement, which was accomplished by tracing the outline of the patch on a transparent plastic overlay (placed on the Model 260 Kodak Ektographic Projector). The area of the traced patch was measured on a Graphics Tablet connected to an Apple II plus computer.

**Effect of Kelp on Modiolus: Tagging Experiment**

A tagging experiment tested the null hypothesis that kelps have no effect on the ability of Modiolus to maintain space in the shallow subtidal zone (8 m) at Murray Rock. Permanent 1.0 m$^2$ quadrats were established around six mussel beds overgrown by kelp and six other mussel beds that were free of attached kelp (control) because they occurred within an urchin barrens area (Fig. 12). In November, 1981 a total of 50 kelp plants (35 L. saccharina and 15 L. digitata) attached to Modiolus within six permanent quadrats were tagged. I used nylon electrical ties with numbered plastic disc tags glued onto the ties for kelp tags. Tagged plants were surveyed monthly to determine mussel dislodgement rates. The null hypothesis would be rejected if the rate
of mussel dislodgement by kelp overgrowth was greater than the rate of mussel dislodgement (by shearing force of waves) in the kelp-free control quadrats. I repeated the experiment in November, 1982 by tagging 100 additional kelp plants (46 *L. saccharina* and 54 *L. digitata*). The tagging procedure was slightly modified by using Dymo labels superglued onto the nylon ties as a numbering system. Where possible, tags were attached to the haptera of the kelp.

An underwater drill was used to mark the permanent quadrats around the *Modiolus* beds. A Sears Craftsman Air Hammer (Model TM) was converted into an underwater pneumatic drill by machining a tapered drill chuck to fit into the "tool end". Holes were drilled into the granite bedrock at locations corresponding to the top 2 corners of the 1.0 m² plots in October, 1981. Brass screws (1/4 x 3 1/2 inch) were driven into plastic masonry sleeves which were previously inserted into the drill holes. Each permanent quadrat was numbered by fitting a numbered plastic Cow Ear Tag (Modern Farm Co., Cody, Wyoming) over one of the 2 brass screws, which served as alignment pins for 2 holes in the top corners of a 1.0 m² aluminum frame. This marking system was an effective way of relocating the same mussel bed each month, enabling accurate counts of the number of *Modiolus* remaining in treatment and control quadrats.

**Effect of Sea Urchins on M. modiolus: Urchin Removal Experiment**

The hypothesis that by grazing kelp off mussel shells, sea urchins increase *Modiolus* survivorship by decreasing the risk of dislodgement was tested by performing an urchin removal experiment. An additional set of six permanent 1.0 m² quadrats were set up around *Modiolus* beds in an urchin barrens area approximately 4 m horizontal distance from an
established kelp forest (Fig. 12). The quadrats were marked by the underwater drilling techniques described previously. All *S. droebachiensis* (x density = 107/m² ± 12.8 SD, n = 12) were manually removed from *Modiolus* beds within the six permanent 1.0 m² quadrats in October, 1981. At least 2 times/month for the next 25 months, all sea urchins in the vicinity of the removal plots were smashed (approximately 50.0 m² area). The six permanent quadrats around *Modiolus* beds in an unmanipulated urchin barrens area (described in previous section) served as controls for the effect of urchin removal on *Modiolus* survivorship. These mussel beds hereafter termed grazed control quadrats, were heavily grazed by *S. droebachiensis* which occurred in densities ranging from 75 to 180 urchins/1.0 m² throughout the two year experiment. If the hypothesis was correct, then the removal of *S. droebachiensis* from *Modiolus* beds should result in the settlement and growth of kelp on mussels, leading to greater mortality of *Modiolus* (via kelp induced dislodgement) than in grazed control plots.

To determine the mortality rates of mussels in urchin removal and grazed control plots, the mussel beds were censused each month. This was accomplished by fitting a 1.0 m² aluminum frame onto the alignment screws and taking four 0.25 m² quadrat photographs within the 1.0 m² frame with the quadrupod. The grazed control plots were photographically censused for the entire experimental period, however, by February, 1982 algae settling in the removal plots obscured the mussels so photographic censusing was abandoned. From February, 1982 on, the number of mussels remaining in the removal plots were counted in situ each month. Beginning in December, 1982 when juvenile kelp
first appeared in the urchin removal plots, the density of *L. saccharina*, *L. digitata*, and *A. cribosum* in the 1.0 m² removal quadrats were counted *in situ*. Despite frequent urchin smashing, an urchin front advanced into the edge of the urchin removal area between February and March, 1982 and eliminated the algae in one of the six removal quadrats. Consequently, this quadrat was dropped from the experiment, and the analysis of urchin removal effects was based on the remaining five 1.0 m² quadrats. Two other sources of *Modiolus* mortality (in addition to dislodgement) were: (1) predation by *Asterias vulgaris* and (2) predation by shell crushing predators (crabs and lobsters). Predation by *Asterias* was directly witnessed and noted in monthly censuses of mussel beds in grazed control and urchin removal quadrats. Predation by crabs and or lobsters was inferred from crushed *Modiolus* shells appearing in the monitored mussel beds.

**M. modiolus Gonad and Body Weight Analysis**

To test the hypothesis that kelp overgrowth decreases the gonad and or body weight of *Modiolus*, approximately 50 large (> 8.0 cm shell length) mussels with attached kelp and 50 large mussels without kelp were collected from the same habitat at 8 m depth at Murray Rock. Mussels were frozen at -20°C. Color of the gonad was used as a criterion for sex determination; females have bright orange red gonads and male gonads are yellowish white (Wiborg, 1946). Gonads were carefully dissected away from the mantle tissue, then gonads and body tissue (mantle and muscle) samples were dried for 24 hours at 65°C, and then weighed on a Mettler balance. Prior to dissection, the height, width, and length of each shell were measured with calipers.
Patch Recolonization Experiments

To examine the ability of kelp and Modiolus to recolonize patches of free space created by the dislodgement of overgrown mussels and kelp, I conducted two patch recolonization experiments beneath the kelp canopy at Murray Rock (8-9 m). Natural dislodgement disturbance was simulated by creating replicate clearings in Modiolus beds (mussel/bed patches) and in the turf of understory red algae (algae turf patches). The hypothesis tested was that kelps have a faster response to disturbance than Modiolus and are able to recolonize dislodgement patches more rapidly than Modiolus. Mussel bed patches were created by removing all Modiolus in a 115.0 cm² area (approximate size of natural patches — see below) on the bed. The underlying rock surface was scraped with a paint scraper to remove encrusting organisms. The procedure left a clearing dominated by bare rock, crustose coralline algae, and a mat of byssus threads, which was nearly identical to natural mussel dislodgement patches (Fig. 20). Patch sites were established by blindly throwing a 115 cm² quadrat onto mussel beds. Fifteen replicate patches were created at the end of October, 1982, shortly after a severe northeast storm. I chose this time to initiate the clearings because it was apparent from the beach surveys of dislodged mussels that storm disturbances were common during the fall, and the experiment was meant to simulate natural disturbance as closely as possible. The two top corners of each rectangular 115.0 cm² patch were marked with a blob of Sea-Goin Epoxy Putty. The epoxy marks served as alignment points for a 3:1 Subsea closeup framer attached to a Nikonos underwater camera. The patches were photographed on 16 monthly visits over a 20-month interval which enabled an assessment of
recolonization patterns.

An equal number of 115 cm² algal turf patches were created by scraping macroscopic algae off the rock surface with a paint scraper. Patch sites in the algal turf were located by blind 115 cm² quadrat tosses. This experiment simulated patches formed by the dislodgement of kelp plants at the holdfast base which occurred during severe storms. Holdfast dislodgement usually removes underlying crustose coralline algae adhering to the base of the holdfast, leaving a patch of bare rock corresponding to the same basal area as the holdfast. Natural holdfast patches ranged from 39.0 to 122.0 cm²; consequently, the 115.0 cm² patches were within the natural size range. Epoxy marks were placed at the top corners of each rectangular patch, and they were photographed (as above). The algal turf patches were rapidly recolonized by algae, which made it difficult to relocate the epoxy marks. Two of the 15 algal patches were lost. Therefore, the analysis of recolonization to algal patches was based on 13 replicate patches.

Densities of kelp sporophytes settling in both the mussel bed and algal patches were counted during monthly visits. Both mussel and algal patches were located below a kelp canopy and were open to grazing chitons, limpets, sea urchins, and gastropods. Along with the monthly kelp counts, grazer densities (*Tonicella marmorea, Acmaea testudinalis, Strongylocentrotus droebachiensis, Lacuna vinca*) were determined. In addition, monthly counts of the number of *Lacuna* egg masses and *Lacuna* grazing holes in the kelp colonies recolonizing the patches were made.

Recolonization patterns were reconstructed by analyzing the patch photographs. The color transparencies were projected onto the screen of a Kodak Ektographic Projector Model 260. A transparent plastic
sheet with 100 randomly placed 2 mm circles on it was overlayed on the projector screen. All organisms under each circle were identified to major taxon and counted, yielding an estimate of percent cover (modification of the methods of Dayton, 1971; and Sebens, 1984a). It was possible to identify organisms > 0.5 mm maximum dimension in the photographs. As the patches were colonized and dominated by kelp sporophytes, the kelp canopy obscured some of the understory organisms and it was clear that variation in their percent cover would be largely due to variation in the amount of kelp covering the substratum. Therefore, when the kelp canopy exceeded 15% cover in the patch, the percent cover of understory organisms was not quantified.

**Mussel Recruitment Study**

A critical part of the kelp-mussel interaction involves the ability of each species to recolonize disturbance produced patches which is a function of recruitment rates. A sampling program was initiated in October, 1982 to examine the rates of mussel recruitment to *Modiolus* beds and to the turf of red algae. On a monthly basis from October, 1982 to November, 1983, 5 replicate 0.0156 m² (1/64 m²) areas of *Modiolus* beds and 5 replicate 0.0156 m² areas of algal turf were sampled with an airlift. The sampling procedure consisted of blindly tossing the 0.0156 m² quadrat onto the bottom. If it landed on a *Modiolus* bed, the mussels within the quadrat were pulled out of the bed while simultaneously vacuuming with the airlift. The remaining fauna and debris were airlifted into a Nitex mesh bag (100 um mesh size) at the end of the airlift. If the quadrat landed on the red algal turf outside the mussel bed, the algae in the quadrat was scraped off the rock with a paint scraper. The algae was sucked up into the Nitex bag.
as it was removed. Both mussel bed and algal turf samples were collected from 8-9 m depth at Murray Rock.

Airlift samples were frozen at 20°C for several weeks until transferred to 8% buffered formalin. The samples were sorted under the microscope and all recently settled mussels (plantigrades) were counted. The size range of plantigrades was approximately 300 to 1000 um maximum dimension; most were approximately 500 um size. By 500 to 600 um size, the umbo was subterminal, which is a distinguishing characteristic of *M. modiolus* (Soot-Ryen 1955). Although some *Mytilus edulis* plantigrades were undoubtably included in the counts, my qualitative impression is that most of the plantigrades were *M. modiolus*. 

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RESULTS

Zonation Patterns

A distinct pattern of depth zonation between kelp (Laminaria digitata and L. saccharina) and the horse mussel (Modiolus modiolus) was evident at the two study sites (Fig. 13). Kelps were abundant at shallow depths (4-8 m), attained maximum mean densities at 8 m (6.8 ± 2.6 SDL. digitata and 5.3 ± 5.2 SDL. saccharina plants/0.25 m², n = 40), and declined sharply to 11-12 m depth. The mixed species stands of kelp formed a canopy 1-2 m above the rock substratum. The depth distribution of juvenile Laminaria sporophytes beneath the canopy (Table 6) mirrored the distribution of the larger canopy forming plants (Fig. 13).

Rock surfaces at intermediate depths (11 to 18 m) were characterized by high densities of M. modiolus, which formed beds ranging in size from 0.1 m² to 2.2 m². Modiolus densities were low at the shallowest depths sampled (8 m MR, 4 m SI), increased abruptly between 8 and 12 m to 17-18 m where peak densities of 39.4 ± 19.8 (SD, n = 36) and 11.6 ± 13.9 (SD, n = 32) mussels/0.25 m² occurred at MR and SI, respectively. The inverse relationship between the abundance of Laminaria spp. and M. modiolus is clearly evident in Fig. 13. As Laminaria density decreased, M. modiolus density increased sharply with depth below the Laminaria dominated zone, suggesting a negative interaction between Laminaria spp. and M. modiolus at shallow depths. Kelps and mussels coexist in ecotonal areas between 8-10 m depth at Murray Rock and 4-10 m depth at Star Island.

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High density aggregations or "fronts" of *Strongylocentrotus droebachiensis* at 11 m (MR) and 12 m (SI) were a characteristic feature of the transition between the shallow *Laminaria* zone and the deeper *Modiolus* zone (Fig. 14). The urchin front was present at Murray Rock for the duration of the three year study, and since 1977 at Star Island. With the exception of the urchin fronts, densities of sea urchins were significantly higher inside mussel beds than outside both at depths within the kelp zone and below the kelp zone at Murray Rock (Fig. 14; *F* = 31.0, 8 m; *F* = 59.5, 11 m; *F* = 55.6, 14 m; *F* = 50.5, 17 m; all *p* < .001, 1,38 df, 1-way ANOVA). Similarly, at Star Island sea urchins were significantly more abundant in *Modiolus* beds than outside (*F* = 15.1, *p* < .001, 1, 38 df, 4 m; *F* = 5.5, *p* < .05, 1,38 df, 8 m; *F* = 5.2, *p* < .05, 1,32 df, 18 m; *F* = 6.1, *p* < .05, 1,32 df, 24 m; *F* = 4.9, *p* < .05, 1,32 df, 32 m, 1-way ANOVA). The only exceptions occurred at 11 and 12 m where urchins formed fronts outside the mussel beds.

**Mussel Recruitment**

Figure 15 shows the density of recently settled mytilid plantigrades to *Modiolus* beds and algal turf habitats at 8-9 m depth. Murray Rock. With the exception of June, 1983, plantigrade densities were significantly higher in the red algal turf (primarily *Phyllophora* spp. and *Phycodrys rubens*) than in *M. modiolus* beds (*F* = 7.86, 1,7 df, *p* < .05 October; *F* = 15.25, 1,9 df, *p* < .005 February; *F* = 233.75, 1,8 df, *p* < .001 September; 1-way ANOVA). There was no significant difference in plantigrade densities between habitats in June, 1983 (*F* = 1.97, 1,8 df, *p* > .05, 1-way ANOVA). Differences in the density of recently settled plantigrades were particularly striking in October, 1982 and September, 1983 when mean densities were an order of magnitude
higher in algal turf during both months. There was significant
temporal variation in recruitment of mytilids to both habitats.

Highest post-settlement densities in algal turf occurred in October
1983, dropped to significantly lower densities in February and June
\(F = 10.55, 1,9 \text{ df}, p < .025\) February; \(F = 5.84, 1,8 \text{ df}, p < .05\) June;
1-way ANOVA), and increased sharply to September \(F = 34.0, 1,8 \text{ df},
p < .001, 1\)-way ANOVA). Plantigrade density was significantly higher
in fall 1983 than in fall 1982 \(F = 5.99, 1,8 \text{ df}, p < .05\). The
abundance of mytilid plantigrades in Modiolus beds decreased
significantly from a maximum mean density of \(208 \pm 83.2 \text{ SD/0.0156 m}^2\) in
October 1982 to \(38.8 \pm 9.8 \text{ SD/0.0156 m}^2\) in February 1983 \(F = 45.87,
1,7 \text{ df}, p < .001\) ANOVA). Densities of recently settled mytilids in
Modiolus beds increased between February and June \(F = 45.8, 1,8 \text{ df},
p < .001\) ANOVA), however, settlement densities were not significantly
different between June and September.

In summary, mussel settlement was high during both fall sampling
periods, and low in winter and early summer.

**Physical Disturbance**

**Mussel Dislodgement at Sea Point**

Figure 16 shows that large numbers of *M. modiolus* with attached
kelp were dislodged and cast ashore on the north and south beaches at
Sea Point between September, 1981 and October, 1983. Overgrown mussels
were dislodged every month, however, very few mussels (< 50) were
dislodged during the months of May, July (1982) and January (1983). A
total of 60,912 recently stranded *Modiolus* had kelp attached to their
shells; horse mussels lacking attached algae were never observed during
dislodgement surveys. There were massive strandings (> 2500 mussels

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dislodged) in April, June, August, and October. An extremely large stranding occurred in October, 1982 when 34,888 Modiolus were dislodged. After this disturbance, dislodged kelp and mussels formed a continuous layer approximately 1.0 to 1.5 m thick and 3-4 m wide along the north and south beaches (409 and 335 m long, respectively).

Size frequency distributions constructed from random samples of mussels dislodged in June, 1982 and February, 1983 indicated that the disturbances affected predominately large Modiolus (Fig. 17). In both summer (June) and winter (February) samples, the major mode was centered around the 8-9 cm (shell length) size class. The null hypothesis that mussels dislodged during the summer and winter had the same size frequency distribution was accepted (p > .05, Kolmogorov-Smirnov test). Since sexual maturity in M. modiolus is attained at a shell length of 3-4.5 cm (Brown and Seed, 1977), it can be inferred that the majority of dislodged mussels are sexually mature (Fig. 17).

Modiolus was dislodged following overgrowth by Laminaria digitata, L. saccharina, Agarum cribosum or any combination of these on the same mussel (Table 7). Dislodgement following overgrowth by Alaria esculenta was rarely observed. The majority of Modiolus cast ashore (> 50%) had L. digitata plants attached to the shells. Moreover, single mussels with 1 attached L. digitata plant were dislodged most frequently, usually comprising 40 to 60% of the total number of mussels stranded. Up to 11 mussels were dislodged as a single unit, however, such large mussel clumps were rarely encountered. Mussels were commonly dislodged in clumps of two (approximately 10% of the total monthly strandings).
**Storm Conditions**

Massive strandings of kelp overgrown *Modiolus* occurred when severe storms struck the coastline of New Hampshire and southern Maine. Marine weather data recorded from White Island, Isles of Shoals, indicated that 4 of the 5 largest strandings at Sea Point occurred during major northeast storms (northeasters; Table 8). Both of the two largest strandings were caused by northeast storms in October. They had an extremely destructive effect on *Modiolus* populations because they lasted for several days (Table 8). The most destructive storm began on October 12, 1982 and was stalled in the southern Gulf of Maine for eight days generating waves > 3.96 m high for the entire period. Wave heights breaking along the coast exceeded 5 m (National Weather Service, Portland, ME) and breakers > 6 m high impacted Murray Rock (personal observations).

Monthly maximum wave height at White Island was correlated with the number of *Modiolus* dislodged at Sea Point (r = .73, p < .05, n = 26). Five years of wave height data from the White Island station indicated that the largest waves (> 2 m) occurred between October and March (Fig. 18). Therefore, the sea conditions associated with mussel dislodgement are most likely to occur during fall (October) to late winter (March). Based on the frequency of storms generating wave heights > 2 m, January was the roughest month with 36% of such storms occurring in January (Table 9). December and October were ranked second roughest, with 18% of storms producing waves > 2 m. Table 9 shows that most of the large storms were generated by northeast winds (7 of 11). The extremely large waves produced during the October 1982 northeast storm are shown in Fig. 18. A disturbance of this magnitude
occurred only once in five years (Fig. 18, Table 9).

**Patch Formation at Murray Rock**

**Mussel Dislodgement Patches.** Table 10 lists the density and size of patches formed in *Modiolus* beds during storms. Patch densities within mussel beds ranged from a mean of 0.9/0.25 m\(^2\) in summer to 2.5/0.25 m\(^2\) in fall. The null hypothesis that the density of patches formed in different seasons was the same was rejected (H = 23.58, p < .005, Kruskal Wallis test). The highest density of patches occurred in the fall. The size of mussel bed patches ranged from 25.0 cm\(^2\) created by the dislodgement of a single mussel (Fig. 19) to 445 cm\(^2\). Figure 20 shows an average size (105 cm\(^2\)) patch generated by the dislodgement of overgrown *Modiolus*. Mean patch sizes ranged from 91.0 cm\(^2\) (fall) to 122.0 cm\(^2\) (winter). The null hypothesis that the size of patches created in different seasons was the same was accepted (H = 1.2, p > .05, Kruskal Wallis test). The percent of mussel bed removed was highest after the fall storm (9.11%) and lowest after the summer storm (3.49%).

**Kelp Holdfast Patches.** Table 11 gives the characteristics of patches formed when kelp plants (*L. digitata* and *L. saccharina*) were dislodged at the holdfast base. On the average, a minimum of 0.5 patches/0.25 m\(^2\) appeared after a summer storm, while a maximum of 1.3 patches/0.25 m\(^2\) appeared after a fall storm. The null hypothesis that characteristics of holdfast patches were the same for the seasons sampled was rejected for patch density (H = 10.87, p < .025), but accepted for patch size (H = 3.81, p > .05, Kruskal Wallis test). As in the mussel dislodgement patches, the maximum amount of patch space (4.88%) was generated during the October, 1982 northeaster.
Interactions Between Kelp, Sea Urchins, and Mussels

Effect of Kelp on Modiolus: Tagging Experiment

Survival curves of tagged mussels at Murray Rock indicate that mussels overgrown by kelp are regularly dislodged in the Laminaria dominated zone (Fig. 21), yet no Modiolus were dislodged in the control quadrats (Fig. 24). Thus, kelp overgrowth clearly has a negative effect on the survivorship of Modiolus in the Laminaria zone at Murray Rock. In 1981-82, 84% of the tagged mussels were dislodged in 11 months. During monthly tag censuses, sea urchins were observed grazing tagged kelp plants off mussels; the kelp attached to the remaining 16% of the 1981-82 tagged mussels were consumed by S. droebachiensis residing in the Modiolus beds. Dislodgement rates were higher in the 1982-83 tagging period, as 50% of the tagged mussels were dislodged in 4 months (Fig. 21). All overgrown and tagged mussels were lost within 9 months; 78% were dislodged and 22% were removed by S. droebachiensis chewing through the kelp stipes. There were no tag losses.

Kelp overgrown mussels that were dislodged from the shallow Modiolus beds (8-10 m) accumulated in a gully at 14 m (Fig. 21). Twenty-four of the 150 tagged overgrown mussels were found in the gully, indicating that at least 16% of dislodged Modiolus were transported deeper into the subtidal zone. The kelp plants that were swept into the gully were rapidly consumed by sea urchins which made it difficult to recover the tagged overgrown mussels. The gully floor was covered by extensive shell beds of articulated and disarticulated Modiolus shells. My observations suggest that the shell beds were formed by the dislodgement of mussels following kelp overgrowth in the shallow subtidal zone.
Sea Urchin Removal Experiment

The removal of sea urchins from mussel beds led to the rapid establishment of kelp (Fig. 23). One month after urchin removal, the mean density of kelp sporophytes was $1.0 \pm 3.5$ (SD)/1.0 m$^2$. Between November, 1981 and May, 1982 mean kelp densities increased exponentially in the urchin removal quadrats:

$$y = 0.48 e^{0.85x}$$

where $y =$ mean kelp density/1.0 m$^2$, $x =$ months, $r^2 = .99$, $n = 7$. By May, 1982 the urchin removal area was densely populated with kelp (167.4 ± 49.8 SD plants/1.0 m$^2$). On June 8, 1982 a northeast storm brought about a significant, 2.7 fold reduction in kelp densities ($F = 25.7$, 1,8 df, $p < .001$, 1-way ANOVA). Another significant reduction in kelp abundance in the urchin removal quadrats was caused by the severe northeaster on October 12, 1982 ($F = 5.32$, 1,8 df, $p < .05$, 1-way ANOVA). After 25 months of sea urchin removal mean kelp density was $46.6 \pm 18.95$ (SD) plants/1.0 m$^2$.

Continual grazing by Strongylocentrotus in the grazed control quadrats prevented kelp from overgrowing Modiolus beds. However, in March 1983 I observed 5 L. digitata plants and 1 Desmarestia viridis plant in the vicinity of the grazed control quadrats in the urchin barrens. Laminaria digitata plants achieved a temporary escape from urchin grazing; they were consumed within a month after they were noticed. Their occurrence suggests that the failure of kelps to become established in the control quadrats resulted from urchin grazing, not due to the limitations of Laminaria spore dispersal.

Within 7 months after removal of resident urchins from the mussel
beds, kelp overgrown Modiolus were dislodged (Fig. 24). Monthly rates of mussel dislodgement were highly variable, ranging from 1 to 43 mussels/5.0 m² after the October, 1982 northeaster. No Modiolus were dislodged from the grazed control quadrats where urchin grazing kept mussels free of kelp, validating the hypothesis that sea urchins increase Modiolus survivorship by reducing the risk of dislodgement following kelp overgrowth. Mussel dislodgement in the urchin removal quadrats at Murray Rock was significantly correlated with mussel dislodgement at Sea Point \( r = .85, p < .025, n = 24 \) indicating that wave generated disturbances were synchronous between coastal and offshore sites.

As a result of removing the sea urchin front, which was previously located at the site of the removal quadrats, the lower edge of the kelp zone extended deeper into the subtidal (Table 12). It stopped at 12.5 m depth where the gently sloping substratum dropped off sharply into a gully.

It is clearly evident from Figure 25 that of the three sources of mortality affecting adult Modiolus populations, kelp induced dislodgement is far more important than predation by the sea star Asterias vulgaris or by crabs and lobsters. Monthly mortality from kelp dislodgement exceeded 5% during three months and reached a maximum of 7% in October, 1982. In contrast, monthly mortality from Asterias predation was usually < 0.5%; a maximum of 1% mortality occurred in August, 1983. Shell crushing predators (crabs and lobsters) were comparatively unimportant. Due to the absence of kelp dislodgement mortality, percent mortality of Modiolus was 30 times lower in the grazed control quadrats than in the urchin removal quadrats.
Grazing Halos

Many *Modiolus* beds within the kelp dominated zone (4-8 m) had a band around the perimeter of the mussel bed that was devoid of upright macroalgae, which was caused by sea urchins foraging out from the mussel beds to feed on macroalgae (Fig. 26). Consequently, these areas are termed grazing halos (*sensu* Randall, 1965). A census of 41 randomly located *Modiolus* beds in April, 1983 revealed that 26 of these (63.4%) had grazing halos. The width of the halos ranged from 3 to 21 cm, with a mean halo width of 10.5 ± 2.5 cm (SD). Many of the mussel beds with grazing halos were conspicuously free of attached kelp, such as the *Modiolus* bed in Figure 26.

Effect of Kelp on Modiolus Gonad and Body Weights

Figure 27 shows differences in the mean dry weight of female gonads dissected from mussels with and without attached kelp collected from the same depth and habitat at Murray Rock. Mussels with attached kelp had significantly lower gonad weights than those without kelp (F = 51.3, 1,66 df, p < .001, 1-way ANOVA). Similarly, mussels with attached kelp had significantly lower dry body weights (remaining muscle and tissue) than those lacking kelp (\( \bar{x} \) body wt with kelp = 4.23 g ± 1.51 SD vs. \( \bar{x} \) body wt without kelp = 6.13 ± 1.12 SD, F = 35.26, 1,66 df, p < .001, 1-way ANOVA). There was no difference in the mean shell length of mussels in the two categories (\( \bar{x} \) length with kelp = 10.75 cm ± 1.34 SD vs. \( \bar{x} \) length without kelp = 10.58 cm ± 1.14 SD, F = 0.34, 1,66 df, p > .05, 1-way ANOVA). Therefore, the observed gonad and body weight differences were not a function of mussel size. For mussels without attached kelp, shell length and dry gonad weight were related as:
\[ y = -3.21 + 1.12x \]

where \( y \) = dry gonad wt, \( x \) = shell length, \( r^2 = .56 \), \( n = 38 \). The regression of equation for mussels with attached kelp was:

\[ y = -5.84 + 1.03x \]

with \( x \) and \( y \) same as above equation, \( r^2 = .43 \), \( n = 30 \).

**Patch Recolonization Experiments**

**Mussel Patches**

Patterns of recolonization to simulated dislodgement patches in *Modiolus* beds are shown in Fig. 28. Recently cleared patches were characterized by high percent covers of bare rock and byssal threads. Crustose coralline algae (primarily *Lithothamnium glaciale* and *Phymatolithon rugulosum*) covered, on the average, 14% of the space at the beginning of the experiment. The amount of free space (bare rock) available for colonization declined sharply between December and March as the patches were colonized by diatoms, red algae, and kelp. However, > 5% cover of bare rock remained at the end of experiment. Settlement and growth of crustose coralline algae also contributed to the decline of free space. For example, crustose coralline cover in one *Modiolus* patch increased from 0% to 54% in 20 months.

The colonial diatom *Licmophora* spp. recruited into the patches within 4 months after clearing and rapidly dominated patch space by February, 1983. In many patches, *Licmophora* first appeared on the residual tangle of byssal threads. The percent cover of the *Licmophora* mat declined sharply over the winter, partly as a result of grazing by limpets (*Acmaea testudinalis*) and sea urchins (*Strongylocentrotus*...
droebachiensis; personal observations). The red alga Antithamnion pylaisaei first appeared in the patches in January, 1983 (Table 13). The percent cover of Antithamnion increased gradually, reaching a peak of 7.4 percent cover at the end of the experiment.

Juvenile kelp sporophytes were visible 7 months after the patches were cleared in the Modiolus beds. The density of Laminaria spp. sporophytes (L. digitata and L. saccharina), and the kelp canopy cover increased sharply to July 1983 when the maximum mean density (21 plants/115 cm²) and the maximum mean percent cover (29.6%) occurred. There was a marked decline in kelp density and percent cover between September and November 1983.

At the end of the 20-month experiment, none of the 15 patches in Modiolus beds were closed by mussels, either from the encroachment of resident mussels surrounding the patch or from the settlement of mussel plantigrades. In contrast, kelps settled into all of the mussel patches dominating 7 of them (47% of total) after 20 months. This result clearly falsifies the null hypothesis of no difference in the ability of kelps and mussels to recolonize patches cleared by Modiolus dislodgement. Thus, kelps (especially L. saccharina) have a much more rapid response to dislodgement disturbance than Modiolus, and are able to recolonize patch space by recruitment.

There was, however, considerable among patch variation in kelp abundance. For example, 53% of the mussel bed patches were virtually free of kelp at the end of the experiment (Table 14). These patches were characterized by total grazer densities (Acmaea testudinalis, Tonicella marmorea, and Strongylocentrotus droebachiensis) that were significantly higher than the other 7 mussel patches that were kelp.
dominated (Table 14; \( W = 91.5, p < .0018 \), Mann Whitney U test). This suggests higher grazer pressure was responsible for preventing the dominance of kelp in 54% of the mussel patches.

The herbivorous snail, *Lacuna vincta*, appeared in 7 of the patches after they were dominated by *Laminaria* spp. (Table 13). *Lacuna* began laying egg masses on the kelp blades in August, 1983; heavy damage was evident in September and October when the mean number of *Lacuna* grazing holes was 2.1 and 3.4/plant during September and October, respectively. Grazing by *Lacuna* undoubtedly weakened the thallus, making kelps more susceptible to breakage during storm waves.

**Algal Turf Patches**

Figure 29 shows the patterns of recolonization into patches cleared in the red algal turf (simulated holdfast dislodgement). At the beginning of the experiment, most of the patch space was held by crustose coralline algae and fleshy red crusts (primarily *Peyssonnelia rosenvingii* and *Rhodophysema elegans*) which accounted for > 70% cover. Bare rock covered 25% initially, but declined rapidly as the patches were colonized by diatoms, red algae, encrusting bryozoans, and kelp. In contrast to patches in *Modiolus* beds, there was no free space (bare rock) in the algal turf patches after 5 months of colonization. The cover of coralline algae and fleshy red crusts declined over the winter of 1982–83 as they were overgrown by other sessile organisms. As in the mussel patches, a cover of the colonial diatom *Licmophora* spp. developed early in the colonization sequence in the algal turf patches, peaking in February, 1982.

There was a striking increase in the percent cover of the red alga *Phyllophora* spp. shortly after patch creation probably because of
vegetative regrowth from residual holdfast material. Upright blades sprouted between December and January. Two different Phyllophora blade shapes were observed; ovate blades (probably P. truncata) and elongate ones that forked into 2 blunt lobes at the distal end of the blade (probably P. pseudoceranoides). In several instances, Phyllophora clearly recruited into the patch.

Other upright red algae colonizing the patches were Phycodrys rubens, Chondrus crispus, and Antithamnion pylaisaei. Phycodrys first appeared in January and quickly attained a maximum mean cover of 23% in April. Chondrus uprights appeared two months after clearing. By following the photographic sequence, it was clear that early Chondrus uprights were produced by regrowth from crustose stages that survived the patch clearing process. Antithamnion cover was highest in April (Table 15).

The red algal turf was heavily epiphytized by bryozoans (primarily Electra pilosa) within 9 months. Bryozoans also encrusted the rock substratum beneath the red algal turf. The species of encrusting bryozoans were mainly Cryptosula pallasiana, Microporella ciliata, and Porella sp.

Strong dominance of the algal turf patches by kelp began 5 months after they were cleared. In April, the patches contained up to 50 L. saccharina juvenile sporophytes per patch. The maximum cover (56%) occurred in May, 1982. The distribution of kelp in the algal turf patches was much less variable than in the mussel patches; at the end of 20 months, all 13 algal turf patches were dominated by kelp. The cohorts of kelp in the algal turf patches were very conspicuous because they were surrounded by a turf of red algae. At the end of experiment,
L. saccharina was abundant while L. digitata occurred in low density (Fig. 28). None of the algal turf patches contained M. modiolus.

Lacuna vincta appeared in the patches 1 month after they were dominated by L. saccharina (Fig. 29). Lacuna density peaked in October when mean densities of 3.0 snails/115.0 cm² (SD = 2.1, n = 13) were recorded. I observed a total of 55 Lacuna egg masses laid on kelp between August and October. Periods of high Lacuna damage to L. saccharina occurred in August, October, and November when plants had an average of 2.0, 3.2, and 2.1 Lacuna grazing holes/plant (Table 15). Lacuna grazing invariably contributed to the decline of kelp between June and November.

Sessile invertebrates were more abundant in algal turf patches than in mussel dislodgement patches. For example, the colonial ascidian Apilidium pallidum occupied 3% cover after 20 months. Other ascidians present in low densities were Dendrodoa carneae and Molgula manhattensis (Table 15). It is suggested that the encrusting invertebrate community was better developed in the algal turf patches than the mussel patches because grazer disturbance was lower in the algal turf patches.
DISCUSSION

Maintenance of Zonation Patterns

This study suggests that the observed patterns of subtidal zonation result from the coupling of physical disturbance and biological processes. Dense populations of *Modiolus modiolus* dominated at intermediate depths (8-11 m) at exposed sites. The scarcity of *Modiolus* in the shallow kelp zone (4-8 m) results principally from kelp induced dislodgement, which caused extremely high *Modiolus* mortalities during storms. Dislodgement mortality was the most important source of mortality impacting *Modiolus* populations at Murray Rock (up to 7% mortality/month) and at Star Island (76% of total deaths/5 yrs). Moreover, it was the only agent of mortality solely restricted to shallow depths (Chapter 1: Table 5). Alternate hypotheses to kelp induced dislodgement setting the upper limit of *Modiolus* are (1) that it is set by predation and (2) that it is determined by the failure of *Modiolus* recruitment to shallow depths. Although these hypotheses have not been explicitly tested, the data available are not consistent with them. For example, rates of predation on adult *Modiolus* are extremely low, usually < 0.5% month; thus predator limitation does not seem likely. Moreover, the high densities of recently settled *Modiolus* plantigrades in algal turf and mussel beds between October, 1981 and October, 1982 indicate that there is substantial larval recruitment to shallow depths.

The experimental removal of the sea urchin front bordering the lower edge (9.1 to 10.5 m) of the kelp zone resulted in a downward
shift of the zone to 12.5 m depth, demonstrating that the lower limit of kelp (*L. saccharina* and *L. digitata*) was set by sea urchin grazing. This implies that the eradication of kelp by sea urchin fronts at 10-12 m depth releases *Modiolus* from severe dislodgement mortality, which is reflected in the striking increase in *Modiolus* population densities just below the kelp dominated zone (Fig. 13). Zonation patterns of kelp and sea urchins similar to those documented here occur in other temperate subtidal regions (Jones and Rain, 1967; Mann, 1972; Dayton, 1975; Choat and Schiel, 1982). By removing *Echinus esculentus*, Jones and Rain (1967) demonstrated that the lower limit of *Laminaria hyperborea* at the Isle of Man was regulated by sea urchin grazing. Dayton (1975) found that the lower limit of *Laminaria* spp. at 20 m depth coincided with high densities of *Strongylocentrotus* sp. He suggested that the lower limit of the *Laminaria* zone at Amchitka Island, Alaska was caused by grazing pressure and light limitation. In St. Margrets Bay, Nova Scotia, Mann (1972) showed that the typical depth range of mixed *Laminaria digitata*-*L. longicruris* stands was 3 to 13 m. At one transect where *S. droebachiensis* was abundant, the *Laminaria* zone ended abruptly at 5 m depth (Mann, 1972). Choat and Schiel (1982) showed that there was an abrupt transition between the shallow fucoid and laminarian algal zone and an intermediate zone dominated by sea urchins (*Evechinus chloroticus*) in northern New Zealand.

There are several types of field evidence indicating that the zone of overlap between *Modiolus* and *Laminaria* spp. distributions at 8-11 m (MR) and 4-12 m (SI) result from grazing by sea urchins residing in the mussel beds. Surveys revealed that *Modiolus* beds within the kelp
zone at MR and SI contained significantly higher densities of S. droebachiensis than outside the beds. In the tagging experiment, sea urchins in the Modiolus beds grazed tagged kelp off mussels, thereby reducing dislodgement mortality by 16-22%. Furthermore, the experimental removal of sea urchins from Modiolus beds demonstrated that mussels in beds without resident sea urchins incurred mortality rates (via kelp dislodgement) that were 30 times higher than those with resident sea urchins. Within the kelp zone, the occurrence of urchins in Modiolus beds was commonly indicated by the presence of a grazing halo around the mussel bed. Thus, by residing in mussel beds and grazing kelp off Modiolus, sea urchins facilitate the persistence of Modiolus beds in the shallow kelp zone where disturbance-caused mortality is highest (Chapter 1: Table 5).

The Disturbance Regime

The subtidal communities examined here were frequently impacted by storm generated disturbances which dislodged overgrown mussels. Different magnitudes of dislodgement disturbance were characterized by different frequencies of occurrence. Small disturbances, here taken to mean the dislodgement of < 2500 Modiolus/month (Sea Point), occurred on a monthly basis. Large disturbances (those dislodging > 2500 Modiolus/month) occurred three times in 1982 and twice in 1983. These large disturbances are disasters in the terminology of Harper (1977) because they recur within the generation time of the organism impacted (> 20 years for Modiolus). Although such disasters could occur during any time of the year, they were most common during the fall months. As indicated by the wave height data, an extremely large disaster (October, 1982 storm) occurs once in 5 years (Fig. 18). Additional
evidence is suggestive of a 5-yr period between extreme storms in the Gulf of Maine. The last extremely large storm occurred in February 1978 (National Weather Service, Portland, Maine) which was 4 years 8 months prior to the October, 1982 storm. Thus, there exists a high frequency of small disturbances, and a low frequency of large, intense disturbances, which is typical of physical disturbance regimes on shallow coral reefs (Connell 1978) and on temperate rocky intertidal shores (Sousa, 1979; Paine and Levin, 1981; Dethier, 1984).

The disturbance regime produced a mosaic of small sized patches in the shallow subtidal zone. On the average, the size of patches formed by the dislodgement of overgrown mussels was 102 cm$^2$ (SD = 58, n = 57, all months pooled). The size of patches did not differ between seasons, however, the greatest number of patches were formed in the fall. In contrast, Paine and Levin (1981) found that patches created by the dislodgement of *Mytilus californianus* were significantly larger in the winter than in summer. The rate of patch formation in *Modiolus* beds at Murray Rock is comparable to the rate of patch formation in *M. californianus* beds at Tatoosh Island, Washington (Paine and Levin, 1981), although the size of individual patches differed substantially. For example, 0.25 to 9.1% of *Modiolus* beds were removed per month at MR, compared to 0.4 to 5.4% of *M. californianus* removed per month at Tatoosh (Paine and Levin, 1981). Paine and Levin (1981) recorded a maximum patch size of 38.0 m$^2$; nothing like this was ever observed in *Modiolus* beds where the maximum patch size was 0.04 m$^2$. *Modiolus* beds are considerably smaller than *M. californianus* beds and are not as spatially continuous, consequently, patches > 2.2 m$^2$ (size of largest *Modiolus* bed) would not be expected in *Modiolus* beds.
In addition to causing extremely high mortality in *Modiolus* populations, storm generated waves were responsible for substantial mortality in populations of *Laminaria saccharina* and *L. digitata*. Kelps attached to mussels perished when they were cast ashore at Sea Point Beach. Kelps attached to dislodged mussels that were transported deeper into subtidal zone were rapidly consumed by urchins residing in gullies at Murray Rock. In the urchin removal area, large storms in June and October, 1982 caused significant reductions in kelp densities. As indicated by the patch survey, kelps were often dislodged at the holdfast base. Kelp holdfast patches were similar to mussel dislodgement patches in several ways: (1) they were approximately the same size with a mean of 89 cm$^2$, SD = 19, n = 29; all months pooled; (2) there was no significant temporal variation in patch area; and (3) densities of kelp holdfast patches were highest in fall. In contrast with mussel dislodgement patches, there was less variability in the size of kelp holdfast patches (coefficient of variation = 21.3% for holdfast patches vs. 56.8% for mussel dislodgement patches). This probably results from low variation in the basal area of the kelp holdfasts producing the patch. My observations suggest that the dislodgement of entire kelp plants may be facilitated by organisms boring into the crustose coralline pavement to which the holdfast adheres. Examination of coralline algae attached to holdfast of dislodged plants revealed that they were riddled with cirratulid polychaetes, especially *Dodecaceria concharum* which may weaken the underlying crust and make the plant more susceptible to dislodgement. Whole plant dislodgement was an important source of patch creation at Murray Rock, opening up 1.4 to 4.8% free space/month (of a 2.5 m$^2$ area
surveyed). Little attention has been given to the effects of storms on the regulation of kelp populations in the northwest Atlantic Ocean despite early reports that *Laminaria hyperborea* forests off the British Isles were devastated by storms (Kitching, 1937; Walker and Richardson, 1955). Clearly, more attention should be given to this topic.

**Recovery from Disturbance**

It was evident from the patch recolonization experiments that kelp (*Laminaria spp.*) and *Modiolus* differ substantially in their ability to respond to simulated dislodgement disturbance. After 7 months, kelp dominated 100% of the algal turf patches (simulated holdfast dislodgement) and 47% of the mussel patches (simulated mussel dislodgement). In striking contrast, none of the patches were dominated by *Modiolus*, despite heavy settlement of mussel larvae to the study area. Because of its failure to recover patch space, dislodgement severely reduces the ability of *Modiolus* to dominate space in the shallow subtidal zone. Kelps can bounce back from dislodgement disturbance and rapidly dominate patch space.

The recovery dynamics of *M. modiolus* are different than those of *Mytilus edulis* and *Mytilus californianus* (Menge, 1976; Suchanek, 1978; Paine and Levin, 1981). In the New England intertidal, Menge (1976) found that *M. edulis* could attain 90% cover within 7 months if the substratum was previously colonized by *Balanus (Semibalanus*) balanoides. On the west coast, *Mytilus edulis* rapidly colonizes disturbance-produced patches in beds of its competitively superior congener *M. californianus* (Suchanek, 1978). Paine and Levin (1981) found that small patches (< 100 cm²) that were approximately the same size as in this study (115 cm²) were closed in < 1 yr by *M.*
californianus leaning in from the border of the patch. Consequently, small patches in $M$. californianus beds had little effect on community dynamics (Paine and Levin, 1981). In contrast, none of the Modiolus patches closed by leaning or recruitment. The apparently unusual failure to recover from disturbance seen in Modiolus beds can be ascribed to a number of factors including (1) failure of larval replenishment to the patch; (2) high post-settlement mortality; and (3) lack of suitable substratum for attachment. From the recruitment study, it was clear that Modiolus settlement occurred in all seasons, moreover, the extremely high plantigrade densities in October, 1982 and September, 1983 suggested a late summer or fall spawning period. Therefore, there is an ample supply of mussel larvae available to settle in newly disturbed areas. Studies of the reproductive cycle of northeast Atlantic $M$. modiolus populations indicated both continual acyclic spawning (Seed and Brown, 1977; Wiborg, 1946), and pronounced spawning peaks in March-April (Wiborg, 1946). In this study, periods of high settlement coincided with temporal patterns of patch formation; plantigrade densities peaked in the fall when the greatest amount of patch space was cleared at Murray Rock (October). It is tempting to speculate that the timing of reproduction and settlement in Modiolus represents a response to take advantage of spatial resources made available by storm disturbance such has been documented for Mytilus edulis (Suchanek, 1978; 1981). However, more work is needed on the reproductive and larval ecology of Modiolus before this hypothesis can be evaluated. In particular, it is important to differentiate small (< 500 um) Mytilus edulis plantigrades in the samples from those of $M$. modiolus so that precise recruitment densities of Modiolus can be
determined. It can be inferred from the high densities of newly settled plantigrades (Fig. 15) and the absence of Modiolus cohorts in the mussel patches that high post settlement mortality is an important factor preventing the establishment of new mussel beds. Predation by Asterias vulgaris on mussel plantigrades may be important as 1-2 small A. vulgaris were generally present in the mussel patches, and Hulbert (1980) found that small A. vulgaris commonly prey on mussel spat at this depth. Until more is known about the feeding rates of A. vulgaris on newly settled mussels, it is difficult to invoke sea star predation as the primary cause of post-settlement mortality in the patches, for the 1-2 A. vulgaris present would have to consume > 3000 mussel plantigrades per patch to prevent mussel dominance. In addition to post-settlement mortality, the absence of suitable substrata for settlement might contribute to the observed lack of juvenile mussels in the patches. In rocky intertidal communities, mussel pediveligers settle primarily on filamentous algae (Bayne, 1964; Seed, 1969; Suchanek, 1979; Petersen, 1984) and byssus threads (Bayne, 1976; Suchanek, 1979; 1981). Petersen (1984) found that Mytilus Californianus plantigrades occurred on all elements of intertidal habitat structure except bare rock, which suggests that the large amounts of bare rock initially present in the mussel patches at Murray Rock (Fig. 28) were unsuitable for settlement. However, there were residual byssus threads in the patches which should have provided suitable substrata for Modiolus settlement. There is a need for experimental work integrating larval settlement with post-settlement mortality to understand mechanisms preventing the reestablishment of mussel beds in patches.
In situ observations suggested that grazing pressure reduced or prevented the establishment of kelp in a majority of the mussel dislodgement patches. In mussel patches where moderately high densities of chitons (Tonicella marmorea), limpets (Acmaea testudinalis), and sea urchins (Strongylocentrotus droebachiensis) were present, kelp settled but was consumed by these grazers (personal observations). Mussel patches with lower total densities of grazers were dominated by kelp (Table 14). The dominance of kelp in 47% of the mussel patches was unexpected given that all the mussel beds where experimental patches were created contained sea urchins and given that the patches were small enough to be contained within the grazing halo (10.5 cm mean width). Thus, it appears that grazer pressure was highly variable, and was not a totally effective defense against kelp dominance of mussel bed patches. I suggest that the variation of grazer pressure is an important key to understanding the complexities of the kelp-Modiolus interaction; it may explain why mussels are overgrown and dislodged by kelp despite the prevalence of grazing halos (63% of mussel beds) and the presence of high densities of sea urchins in the beds. It is likely that Modiolus beds are saturated by kelp spores in densities exceeding the ability of resident grazers to remove them from the mussel shells. For example, Chapman (1984) found that L. digitata recruitment was extremely high (0.98 x 10^6 recruits per 1.0 m^2 per year). Grazers maintain bare zones or grazing halos around their habitats in several benthic communities including Caribbean patch reefs (Randall, 1965; Ogden et al., 1973), rock crevice habitats off California (Nelson and Vance, 1979), and intertidal Mytilus californianus beds in the Pacific Northwest (Dayton, 1971; Stimson,
1973; Suchanek, 1978). Paine and Levin (1981) demonstrated that small patches in M. californianus beds (< 700 cm²) were not recolonized by other sessile organisms because the patches were small enough to be incorporated into the grazing halo. There was no evidence of the within patch variation in grazer pressure observed in subtidal Modiolus beds.

The herbivorous snail Lacuna vincta had a qualitatively different effect on the kelp colonists than grazing chitons, limpets, and urchins; it cropped the blades of small sporophytes. This was particularly evident in algal turf patches where a majority of sporophytes had 2-3 Lacuna holes on each kelp blade during fall 1983. The complete destruction of algal stands by Lacuna described in Fralick et al. (1974) was not witnessed at Murray Rock. It is suggested that L. vincta grazing increases the vulnerability of kelp to storm defoliation; more attention should be given to this interaction.

One of the similarities in the recolonization sequence of mussel patches and algal turf patches was the early arrival of the diatom Lichmophora sp. which dominated patch space by February, 1982. Heavy diatom cover preceeded kelp dominance in a majority of the patches. Similarly, Sousa (1979) and Dethier (1984) found that diatoms were the initial colonizers of experimentally cleared areas in the rocky intertidal zone. In this study, the red alga Phyllophora spp. recovered quickly. Within 4 months of patch formation, Phyllophora spp. covered, on the average, 25% of patch space. Such fast recovery time was primarily due to vegetative regrowth from residual portions of holdfasts that survived the disturbance (i.e. Phyllophora is a pseudoperennial sensu Knight and Parke, 1931).
Simulated holdfast patches were densely recolonized by *Laminaria* juveniles. In addition, many natural holdfast patches containing cohorts of juvenile *Laminaria* sporophytes were observed at Murray Rock. They were easily recognized as aggregations of sporophytes totally contained within the patch and surrounded by red algal turf. Such experimental results and observations suggest a negative interaction between *Laminaria* and the understory red algal turf (*Phyllophora*, *Phycodrys*, and *Chondrus*). A logical hypothesis is that the algal turf inhibits the competitive dominance of canopy forming kelps as demonstrated in California kelp communities (Dayton *et al.*, 1984). The implication of rapid recolonization ability in *Laminaria* is that it enables it to rapidly recover patch space created by the dislodgement of its own species or congener at the holdfast base. Importantly, Chapman (1984) showed that in Nova Scotia the recruitment of *L. longicuris* and *L. digitata* sporophytes increased 10-fold by clearing of 0.25 m² areas in red algal turf. However, the ecological significance of this finding was not elucidated.

**Modiolus-Strongylocentrotus Mutualism**

Predation experiments demonstrated that small *Strongylocentrotus droebachiensis* benefit from living in *Modiolus* beds because they are protected from predation by fish (*Tautogolabus adspersus*), crabs (*Cancer borealis* and *Cancer irroratus*), and lobster (*Homarus americanus*) while in the mussel beds (Chapter 1). In turn, *S. droebachiensis* grazes kelp off *Modiolus* shells, reducing dislodgement mortality. This was demonstrated in urchin removal experiments where mussels in beds without sea urchins suffered mortality rates (from kelp-induced dislodgement) that were 30 times greater than in beds
where sea urchin grazing kept the mussels free of kelp. Therefore, the
Modiolus-Strongylocentrotus interaction is a type of mutualism, defined
as an interaction between species that is beneficial to both (Boucher
et al., 1982). The mutualistic association is facultative, not obligate
(sensu Boucher et al., 1982) because Strongylocentrotus occurs in other
benthic habitats besides Modiolus beds.

These experimental results suggest that facultative mutualism
plays a large role in determining the upper limit of M. modiolus. With
sea urchin mutualists, Modiolus can coexist with kelp competitors in
the shallow subtidal zone.

An increasing amount of empirical evidence indicates that the
occurrence of mutualism in marine benthic communities is more prevalent
than previously suspected (reviewed in Vermeij, 1983; Orians and Paine,
1983). Of particular relevance here are mutualistic interactions which
enable interacting species to extend their distribution. In an
analogous situation to Modiolus-Strongylocentrotus mutualism, Osman and
Haugness (1981) showed that the hydroid Zanclea reduced predation on
the bryozoan Celleporaria which enhanced the ability of Celleporaria to
dominate space. Glynn (1976) found that xanthid crab mutualists
protected pocillopoid corals from predation by the sea star
Acanthaster planci. Importantly, Suchanek (1984) found that the
facultative association between grazers and Mytilus californianus is
mutualistic. Mytilus imparted benefits to resident grazers by
providing protection from desiccation stress, while grazers enhanced
the rate of patch closure in the mussel bed. M. californianus
recovered space lost by disturbance nearly 8 times faster with grazers
than without, although the exact mechanism of grazer facilitated
recovery was unclear (Suchanek, 1984). Thus, it appears that subtidal mussel beds (M. modiolus) and intertidal mussel beds (M. californianus) have several convergent ecological characteristics including (1) an associated fauna of mutualistic grazers that reduce dislodgement following overgrowth by kelp (M. modiolus) and speed recovery from disturbance (M. californianus) and (2) bare zones (grazing halos or browse zones) around the mussel beds maintained by grazers.

Evidence for Competition Between Laminaria and Modiolus

According to Emlen (1972) interspecific competition occurs when two or more species experience depressed fitness due to their mutual presence in an area. Several predictions follow from the hypothesis that interspecific competition for attachment space with kelp is the mechanism limiting the upper distribution of Modiolus:

1) The limiting resource, attachment space, should be in short supply.

2) Kelp should have a negative effect on individual fitness of Modiolus.

3) Modiolus should have a negative effect on the fitness of individual kelps.

Prediction 1.

Patch surveys conducted in the zone of overlap between kelp and mussels (8-10 m, MR) indicated that 95.1% (fall) to 98.5% (summer) of the substratum was covered by sessile organisms. It is clear that the amount of free primary space (sensu Dayton, 1971) available for attachment was in short supply, although less suitable secondary substrata (algae, sessile invertebrates) were available.
Prediction 2.

Two negative effects of kelp overgrowth on female mussels were: significantly reduced gonad weights and significantly reduced body weights. Because of reduced gonad weights, it is evident that mussels overgrown by kelp will have a lower reproductive output than mussels lacking kelp.

In addition, kelp overgrowth led to extremely high mortalities in Modiolus populations during storms. Since the majority of the stranded Modiolus were beyond the size at which sexual maturity is attained, these disasters must cause an enormous loss of reproductive potential in Modiolus populations.

The data are consistent with the prediction that kelp reduces reproductive output, a correlate of mussel fitness. There are, however, several unanswered questions. How does kelp overgrowth reduce the gonad and body weight of Modiolus? Two hypotheses are advanced for further evaluation. One hypothesis is that the effect is caused by increased drag from attached kelp (Witman and Suchanek, 1984) which rocks the mussel back and forth with wave surge. Sustained or violent agitation may cause the byssus threads to break and initiate the formation of new byssus threads. The energetic expense required for constant byssus thread production may represent a substantial energetic drain which is reflected in lower gonad and body weights. A second hypothesis is related to the occlusion of the incumbent siphon by the kelp holdfast, which may impair the filtration efficiency of the underlying mussel. In this situation, overgrown mussels simply wouldn't receive as much food as mussels without kelp, which would be reflected in reduced gonad and body weights of overgrown mussels.
Importantly, there is some evidence that *Mytilus californianus* overgrown by epifauna (sponges, ascidians) have lower body weights than non-overgrown mussels (Paine, 1976). These data suggest that epizoans may generally have a negative effect on mussels.

**Prediction 3.**

Kelps perished, as did the underlying mussel, when they were dislodged and cast ashore or swept into subtidal gullies. The interaction is detrimental to kelp because mussels represent an unstable substratum for attachment. Such massive mortality represents a substantial loss of kelp fitness.

The kelp-mussel interaction can be examined in light of Connell's (1983) operational definition for deciding whether a species was being affected by interspecific competition. "Following an experimental change in abundance of a potential competitor, if there was a statistically significant response in the opposite direction in the species being studied, interspecific competition was judged to be occurring" (Connell, 1983). In this example, the experimental addition of kelp (by urchin removal) caused a 30-fold reduction in *Modiolus* abundance relative to control quadrats. In summary, the data are consistent with several predictions of competition theory and meet Connell's (1983) criterion for demonstrating the existence of interspecific competition in field experiments.

The potential for spatial competition between plants and animals in marine hard substratum environments is great because many marine benthic plants and sessile invertebrates use space in similar ways, and because attachment space is often limiting in such environments (Jackson, 1977). Indeed, spatial competition between plants and
animals may be a unique feature of marine as opposed to terrestrial ecosystems. The interactions described here are remarkably similar to interactions between Patella, Balanus, and Fucus in Scotland (Burrows and Lodge, 1950) and Postelsia and Mytilus on the coast of Washington State (Dayton, 1973; Paine, 1979). In Scotland, Fucus and Balanus compete for attachment space on exposed rocky intertidal shores. Fucus germlings settle on Balanus, grow large to eventually smother and dislodge Balanus, creating a patch of bare rock (Burrows and Lodge, 1950). The interaction is mediated by limpet grazing (Patella) which removes Fucus from Balanus plates. Patch space created by barnacle dislodgement was apparently recolonized and dominated by barnacle cyprids, starting the process over again (Burrows and Lodge, 1950). In spatial competition between Mytilus californianus and Postelsia palmaeformis, barnacles, mussels and other sessile organisms are dislodged by Postelsia overgrowth. Patches cleared by dislodgement were rapidly saturated by Postelsia spores which grew to dominate the clearing (Dayton, 1973; Paine, 1979). On shallow coral reefs, disturbance-produced patches on living coral and invertebrate surfaces are rapidly colonized by filamentous and turfing algae which may determine the outcome of competition for space between stony corals, soft corals, and benthic algae (Benayahu and Loya, 1977; Bak et al., 1977). Sebens (1984a) showed that competitive interactions between crustose algae and encrusting invertebrates determine much of the spatial pattern on subtidal rock walls in New England. A common feature of overgrowth competition on subtidal rock walls (Sebens, 1984a) and on upper rock surfaces (this study) is that overgrown species do not die immediately, but they will if overgrowth persists.
Consequently, grazers can mediate the outcome of competition by grazing the superior competitor off the underlying species. An important difference between overgrowth competition among sessile invertebrates and upright algae (Burrows and Lodge, 1950; Dayton, 1973; this study) and overgrowth competition between sessile invertebrates and crustose algae (Sebens 1984a) is that the former competitive interaction is more likely to be mediated by physical disturbance processes because upright algae make the underlying competitor more vulnerable to physical disturbance (Witman and Suchanek, 1984).

**Conceptual Model**

Interactions among kelp, sea urchins, and *Modiolus* are summarized in a conceptual model (Fig. 30). The three endpoints of the interactions: Modiolus dominance, kelp dominance, and coexistence (corresponding to zonation patterns in Fig. 13) are influenced by the intensity of storm disturbance, sea urchin grazing, and the rate of recovery from disturbance. As demonstrated in the urchin removal experiment, sea urchin grazing has a negative effect on kelp (step 1) by regulating the lower depth limit of the kelp zone and restricting the local distribution of kelp (grazing halo observations). Sea urchin grazing has a positive effect on *Modiolus* (step 2) because it reduces dislodgement mortality (urchin removal experiment and tagging experiment). There is a positive feedback between *Modiolus* and urchins (step 3) as *Modiolus* beds provide a refuge from predation for resident sea urchins (predation experiment), indicating that the urchin-*Modiolus* relationship is mutualistic. As demonstrated in the patch recolonization experiments (step 4), fast recovery from disturbance enables kelp to monopolize patch space. The failure of *Modiolus* to
fill patches created by dislodgement indicates that, depending on the strength of grazing pressure, *Modiolus* will lose space to rapidly colonizing kelp. The coexistence of kelp and mussel competitors is facilitated by mutualism.
LIST OF REFERENCES


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Suchanek, T. H. 1984. The dynamics of a species-rich community associated with the mussel Mytilus californianus. (ms)


Table 1. Mean densities (± standard error) of infauna per 0.25 m² inside and outside *Modiolus* beds. Results of one way analysis of variance reported as follows; n = sample size; F = F ratio; P = significance level.

<table>
<thead>
<tr>
<th>Depth</th>
<th>Habitat</th>
<th>n</th>
<th>Mean Density</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>8 m</td>
<td><em>Modiolus</em> bed</td>
<td>5</td>
<td>374 (± 69.7)</td>
<td>10.2</td>
<td>.025</td>
</tr>
<tr>
<td></td>
<td>outside substratum</td>
<td>5</td>
<td>161 (± 25.5)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>18 m</td>
<td><em>Modiolus</em> bed</td>
<td>5</td>
<td>541 (± 77.8)</td>
<td>34.9</td>
<td>.001</td>
</tr>
<tr>
<td></td>
<td>outside substratum</td>
<td>5</td>
<td>65 (± 21)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>30 m</td>
<td><em>Modiolus</em> bed</td>
<td>5</td>
<td>308 (± 35.2)</td>
<td>7.7</td>
<td>.025</td>
</tr>
<tr>
<td></td>
<td>outside substratum</td>
<td>5</td>
<td>191 (± 27.5)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2. Experimental comparison of predation on *Ophiopholis aculeata* tethered by 2 different methods: ophiuroid disk pierced and sewn vs. monofilament double tied around disk (non-pierced). The number of *Ophiopholis* remaining on the substratum was determined by direct observation.

<table>
<thead>
<tr>
<th>Time</th>
<th>Pierced</th>
<th>Non-pierced</th>
</tr>
</thead>
<tbody>
<tr>
<td>7:00 p.m.</td>
<td>24</td>
<td>24</td>
</tr>
<tr>
<td>11:30 p.m.</td>
<td>19*</td>
<td>17**</td>
</tr>
<tr>
<td>7:00 a.m.</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

* *C. borealis* observed feeding on 4 tethered *Ophiopholis*

**H. americanus** observed feeding on 4 tethered *Ophiopholis*
Table 3. Mean 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. Data presented as mean density ± (standard deviation) per 25.0 m². Comparisons by Wilcoxon two-sample test, D = day, N = night, summer, S = summer, W = winter, P = significance level, ns = not significant.

<table>
<thead>
<tr>
<th>Fish:</th>
<th>Summertime</th>
<th>Wintertime</th>
<th>Summer vs Winter</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Day</td>
<td>Night</td>
<td>Comparison</td>
</tr>
<tr>
<td>Tautogolabrus adspersus</td>
<td>21.6</td>
<td>0.3</td>
<td>&gt;D</td>
</tr>
<tr>
<td>Pseudopleuronectes americanus</td>
<td>3.0</td>
<td>0</td>
<td>&gt;D</td>
</tr>
<tr>
<td>Gadhus morhua</td>
<td>0</td>
<td>1.6</td>
<td>ns</td>
</tr>
<tr>
<td>Pollachius virens</td>
<td>0</td>
<td>22.6</td>
<td>&gt;N</td>
</tr>
<tr>
<td>Macrozoaeracidae</td>
<td>0.3</td>
<td>0.6</td>
<td>ns</td>
</tr>
<tr>
<td>Americanus</td>
<td>(0.5)</td>
<td>(0.5)</td>
<td></td>
</tr>
</tbody>
</table>

| Invertebrates:     |                   |                   |                   |
|                    |                   |                   |                   |
| Asterias vulgaris  | 152.6  | 172    | ns          | 105.6  | 106.3 | ns          |                   |                   | ns              |
|                    | (23.7) | (8.2)  |             | (6.1)  | (11.8)|             |                   |                   |                 |
| Buccinum undatum   | 8.6    | 6.6    | ns          | 9.6    | 9.3   | ns          |                   |                   | ns              |
|                    | (2.5)  | (1.5)  |             | (1.5)  | (2.5)|             |                   |                   |                 |
| Cancer irroratus   | 2.6    | 6.3    | >N          | .05 | 0.3   | 3.6   | >N          | .05 | ns              |
|                    | (1.5)  | (1.5)  |             | (0.6)  | (0.6)|             |                   |                   |                 |
| Cancer borealis    | 6.0    | 15.3   | >N          | .05 | 3.0   | 8.3   | >N          | .05 | ns              |
|                    | (1.0)  | (2.5)  |             | (1.0)  | (1.5)|             |                   |                   |                 |
| Homarus americanus | 2.6    | 8      | >N          | .05 | 0.7   | 4.3   | >N          | .05 | ns              |
|                    | (0.6)  | (1)    |             | (0.6)  | (0.5)|             |                   |                   |                 |

* 6:00 p.m.; dark, but not late at night
TABLE 4A. Rank analysis of dominant species in samples collected outside mussel beds before and after urchin disturbance. Maximum score is 50. (P) = polychaete, (G) = gastropod, (B) = bivalve, (NU) = nudibranch, (CH) = chiton, (A) = amphipod, (C) = caprellid, (I) = isopod, (D) = decapod, (AS) = asteroid, (E) = echinoid, (O) = ophiuroid

BEFORE DISTURBANCE

<table>
<thead>
<tr>
<th>Species</th>
<th>Rank</th>
<th>Score</th>
<th>Mean Density (N/0.25 m²) and Standard Deviation (SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Lacuna vineta</em> (G)</td>
<td>1</td>
<td>45</td>
<td>255 (163)</td>
</tr>
<tr>
<td><em>Pontogeneia inermis</em> (A)</td>
<td>2</td>
<td>43</td>
<td>199 (82.4)</td>
</tr>
<tr>
<td><em>Lachyrocerus anguipes</em> (A)</td>
<td>3</td>
<td>34</td>
<td>386 (593)</td>
</tr>
<tr>
<td><em>Pleuromes glaber</em> (A)</td>
<td>4</td>
<td>32</td>
<td>120.4 (70.7)</td>
</tr>
<tr>
<td><em>Corophium bonelli</em> (A)</td>
<td>5</td>
<td>29</td>
<td>142.2 (122.8)</td>
</tr>
<tr>
<td><em>Amphipoe rubriceata</em> (A)</td>
<td>6</td>
<td>27</td>
<td>116.6 (97.4)</td>
</tr>
<tr>
<td><em>Jassa fulcata</em> (A)</td>
<td>7</td>
<td>24</td>
<td>188 (254)</td>
</tr>
<tr>
<td><em>Ophiopholis aculeata</em> (O)</td>
<td>8</td>
<td>15</td>
<td>61.2 (34.3)</td>
</tr>
<tr>
<td><em>Caprella linearis</em> (C)</td>
<td>9</td>
<td>8</td>
<td>64.2 (61.5)</td>
</tr>
<tr>
<td><em>Idotea phosphorea</em> (I)</td>
<td>10</td>
<td>7</td>
<td>38.2 (27.6)</td>
</tr>
</tbody>
</table>

AFTER DISTURBANCE

<table>
<thead>
<tr>
<th>Species</th>
<th>Rank</th>
<th>Score</th>
<th>Mean Density (N/0.25 m²) and Standard Deviation (SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Pontogeneia inermis</em> (A)</td>
<td>1</td>
<td>50</td>
<td>294 (126.8)</td>
</tr>
<tr>
<td><em>Ischyrocerus anguipes</em> (A)</td>
<td>2</td>
<td>37</td>
<td>19.2 (10.5)</td>
</tr>
<tr>
<td><em>Strongylocentrotus drobachiensis</em> (E)</td>
<td>3</td>
<td>36</td>
<td>15.6 (11.5)</td>
</tr>
<tr>
<td><em>Tonicella rubra</em> (CH)</td>
<td>4</td>
<td>30</td>
<td>16.6 (7.9)</td>
</tr>
<tr>
<td><em>Asterias vulgaris</em> (AS)</td>
<td>5</td>
<td>27</td>
<td>15.6 (7.4)</td>
</tr>
<tr>
<td><em>Pleurozetes glaber</em> (A)</td>
<td>6</td>
<td>24</td>
<td>14.4 (13.8)</td>
</tr>
<tr>
<td><em>Onchidoris moricata</em> (NU)</td>
<td>7</td>
<td>16</td>
<td>12.8 (21)</td>
</tr>
<tr>
<td><em>Corophium bonelli</em> (A)</td>
<td>8</td>
<td>13</td>
<td>9.8 (11.2)</td>
</tr>
<tr>
<td><em>Amphipoe rubriceata</em> (A)</td>
<td>9</td>
<td>12</td>
<td>9.8 (11.9)</td>
</tr>
<tr>
<td><em>Mereis pelagica</em> (P)</td>
<td>10</td>
<td>10</td>
<td>5.6 (3.8)</td>
</tr>
</tbody>
</table>

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TABLE 4B. Rank analysis of dominant species in *Modiolus* beds before and after urchin disturbance. Maximum score is 50. Taxonomic abbreviations as in Table 4A.

### BEFORE DISTURBANCE

<table>
<thead>
<tr>
<th>Species</th>
<th>Rank</th>
<th>Score</th>
<th>Mean Density (N/0.25 m²)</th>
<th>Standard Deviation (SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ophiopholis aculeata</em> (O)</td>
<td>1</td>
<td>50</td>
<td>273 (137.5)</td>
<td></td>
</tr>
<tr>
<td><em>Nainereia quadricuspida</em> (P)</td>
<td>2</td>
<td>40</td>
<td>59.8 (36.1)</td>
<td></td>
</tr>
<tr>
<td><em>Strongylocentrotus drobachiensis</em> (E)</td>
<td>3</td>
<td>38</td>
<td>54 (10)</td>
<td></td>
</tr>
<tr>
<td><em>Lacuna vinca</em> (G)</td>
<td>4</td>
<td>34</td>
<td>28.9 (723)</td>
<td></td>
</tr>
<tr>
<td><em>Amphitrite cirrata</em> (P)</td>
<td>5</td>
<td>31</td>
<td>20.4 (28.8)</td>
<td></td>
</tr>
<tr>
<td><em>Tonicella rubra</em> (CH)</td>
<td>6</td>
<td>28</td>
<td>15.2 (5.2)</td>
<td></td>
</tr>
<tr>
<td><em>Hiatella arctica</em> (B)</td>
<td>7</td>
<td>21</td>
<td>12.4 (9)</td>
<td></td>
</tr>
<tr>
<td><em>Ischyrocerus anguipes</em> (A)</td>
<td>8</td>
<td>20</td>
<td>10 (12.2)</td>
<td></td>
</tr>
<tr>
<td><em>Amphitrite johnstoni</em> (P)</td>
<td>9</td>
<td>19</td>
<td>8.8 (13.9)</td>
<td></td>
</tr>
<tr>
<td><em>Cistenides granulata</em> (P)</td>
<td>10</td>
<td>10</td>
<td>7.4 (3.4)</td>
<td></td>
</tr>
</tbody>
</table>

### AFTER DISTURBANCE

<table>
<thead>
<tr>
<th>Species</th>
<th>Rank</th>
<th>Score</th>
<th>Mean Density (N/0.25 m²)</th>
<th>Standard Deviation (SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ophiopholis aculeata</em> (O)</td>
<td>1</td>
<td>50</td>
<td>199 (140)</td>
<td></td>
</tr>
<tr>
<td><em>Nainereia quadricuspida</em> (P)</td>
<td>2</td>
<td>39</td>
<td>44.6 (21.5)</td>
<td></td>
</tr>
<tr>
<td><em>Strongylocentrotus drobachiensis</em> (E)</td>
<td>3</td>
<td>35</td>
<td>24.6 (4)</td>
<td></td>
</tr>
<tr>
<td><em>Tonicella rubra</em> (CH)</td>
<td>4</td>
<td>34</td>
<td>22.4 (14.8)</td>
<td></td>
</tr>
<tr>
<td><em>Amphitrite cirrata</em> (P)</td>
<td>5</td>
<td>30</td>
<td>18.6 (8.6)</td>
<td></td>
</tr>
<tr>
<td><em>Amphitrite johnstoni</em> (P)</td>
<td>6</td>
<td>24</td>
<td>14.6 (6.1)</td>
<td></td>
</tr>
<tr>
<td><em>Hiatella arctica</em> (B)</td>
<td>7</td>
<td>18.5</td>
<td>8.6 (6.8)</td>
<td></td>
</tr>
<tr>
<td><em>Eualus pusiolus</em> (D)</td>
<td>8</td>
<td>11</td>
<td>7 (3.4)</td>
<td></td>
</tr>
<tr>
<td><em>Nereis pelagica</em> (P)</td>
<td>9</td>
<td>7</td>
<td>5.8 (2.5)</td>
<td></td>
</tr>
<tr>
<td><em>Cistenides granulata</em> (P)</td>
<td>10</td>
<td>6</td>
<td>5.6 (1.8)</td>
<td></td>
</tr>
</tbody>
</table>
Table 5. Major sources of *Modiolus* mortality in monitored mussel beds as a function of depth. Data reported as number of mussels killed with percent mortality per 5 yrs in parentheses, based on photographic monitoring from January, 1979 to January, 1984. The total number of mussels in monitored beds at the beginning of the interval was 153 (8 m), 101 (18 m), and 98 (30 m).

<table>
<thead>
<tr>
<th>Mortality Source</th>
<th>8 m</th>
<th>18 m</th>
<th>30 m</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dislodgement by kelp</td>
<td>43 (28%)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Asterias vulgaris</em> predation</td>
<td>10 (6.5%)</td>
<td>1 (0.9%)</td>
<td>1 (1.0%)</td>
</tr>
<tr>
<td>Crab and lobster predation</td>
<td>2 (1.3%)</td>
<td>1 (0.9%)</td>
<td>3 (3.0%)</td>
</tr>
<tr>
<td>Gaping mussels</td>
<td>1 (0.6%)</td>
<td>0</td>
<td>2 (2.0%)</td>
</tr>
<tr>
<td>Mussel disappearances</td>
<td>0</td>
<td>3 (2.9%)</td>
<td>2 (2.0%)</td>
</tr>
<tr>
<td><strong>Total mortality</strong></td>
<td>56 (36.4%)</td>
<td>5 (4.7%)</td>
<td>8 (8.0%)</td>
</tr>
</tbody>
</table>
Table 6. Densities of juvenile *Laminaria* spp. sporophytes (< 5 cm height).

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>Mean Density (0.25 m²)</th>
<th>Standard Deviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>MURRAY ROCK</td>
<td></td>
<td></td>
</tr>
<tr>
<td>8 m</td>
<td>18.74</td>
<td>25.96</td>
</tr>
<tr>
<td>11 m</td>
<td>8.7</td>
<td>14.38</td>
</tr>
<tr>
<td>14 m</td>
<td>2.37</td>
<td>2.48</td>
</tr>
<tr>
<td>17 m</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>STAR ISLAND</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4 m</td>
<td>6.57</td>
<td>8.13</td>
</tr>
<tr>
<td>8 m</td>
<td>12.37</td>
<td>19.17</td>
</tr>
<tr>
<td>12 m</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>18 m</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>24 m</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>32 m</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

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Table 7. Percent frequency of different species of brown algae attached to dislodged Modiolus at Sea Point. *L. digitata* (1:1) indicates 1 *L. digitata* on 1 *M. modiolus*. Abbreviations in combination column are *L. digitata* and *L. saccharina* on same mussel, A; *L. digitata* and *A. cribosum* on same mussel, B; *L. saccharina* and *A. cribosum* on same mussel, C.

<table>
<thead>
<tr>
<th>Month</th>
<th><em>L. digitata</em></th>
<th><em>L. digitata</em> (1:1)</th>
<th><em>L. saccharina</em></th>
<th><em>A. cribosum</em></th>
<th>Combination</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sept 81</td>
<td>46.0</td>
<td>(41.0)</td>
<td>50.0</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Oct 81</td>
<td>80.8</td>
<td>(77.7)</td>
<td>18.7</td>
<td>0.4</td>
<td>0</td>
</tr>
<tr>
<td>Nov 81</td>
<td>53.9</td>
<td>(39.5)</td>
<td>8.1</td>
<td>34.5</td>
<td>3.4 A</td>
</tr>
<tr>
<td>Dec 81</td>
<td>65.3</td>
<td>(56.0)</td>
<td>18.4</td>
<td>7.9</td>
<td>2.1 A</td>
</tr>
<tr>
<td>Jan 82</td>
<td>56.9</td>
<td>(45.5)</td>
<td>0.2</td>
<td>40.5</td>
<td>0</td>
</tr>
<tr>
<td>Feb 82</td>
<td>63.2</td>
<td>(44.2)</td>
<td>12.6</td>
<td>21.2</td>
<td>4.0 A</td>
</tr>
<tr>
<td>Mar 82</td>
<td>63.1</td>
<td>(55.0)</td>
<td>11.9</td>
<td>25.0</td>
<td>0</td>
</tr>
<tr>
<td>Apr 82</td>
<td>67.8</td>
<td>(46.7)</td>
<td>7.4</td>
<td>22.4</td>
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<td>(35.3)</td>
<td>35.2</td>
<td>5.8</td>
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<tr>
<td>June 82</td>
<td>62.3</td>
<td>(44.6)</td>
<td>12.2</td>
<td>20.2</td>
<td>0.4 B</td>
</tr>
<tr>
<td>July 82</td>
<td>45.4</td>
<td>(45.4)</td>
<td>27.2</td>
<td>36.3</td>
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</tr>
<tr>
<td>Aug 82</td>
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<td>(56.8)</td>
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</tr>
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<td>Sept 82</td>
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<td>(59.0)</td>
<td>25.0</td>
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</tr>
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</tr>
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<td>11.1</td>
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</tr>
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<td>6.1</td>
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<td>6.9 A</td>
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<td>69.2</td>
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<td>4.6</td>
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<td>(56.1)</td>
<td>19.0</td>
<td>10.0</td>
<td>7.0 A</td>
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<tr>
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<td>(59.3)</td>
<td>7.2</td>
<td>4.2</td>
<td>3.0 A</td>
</tr>
<tr>
<td>Jun 83</td>
<td>65.0</td>
<td>(55.0)</td>
<td>15.0</td>
<td>17.0</td>
<td>10.0 A</td>
</tr>
<tr>
<td>July 83</td>
<td>59.1</td>
<td>(54.0)</td>
<td>20.0</td>
<td>13.0</td>
<td>3.0 B</td>
</tr>
<tr>
<td>Aug 83</td>
<td>81.16</td>
<td>(56.4)</td>
<td>9.7</td>
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<tr>
<td>Sept 83</td>
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<tr>
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<td>78.57</td>
<td>(60.2)</td>
<td>7.1</td>
<td>5.1</td>
<td>3.6 A</td>
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Table 8. Marine weather conditions recorded at White Island, Isles of Shoals during storms that caused massive mussel dislodgement (> 2500 mussels dislodged) at Sea Point.

<table>
<thead>
<tr>
<th>Date</th>
<th>Wave Height (m)</th>
<th>Wave Period (sec)</th>
<th>Wind Speed (knots)</th>
<th>Wind Direction</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apr 3, 1982</td>
<td>1.83</td>
<td>6.0</td>
<td>20</td>
<td>SE</td>
</tr>
<tr>
<td>Jun 8, 1982</td>
<td>1.52</td>
<td>6.0</td>
<td>14</td>
<td>NNE</td>
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<tr>
<td>Oct 12-19, 1982</td>
<td>&gt; 3.96</td>
<td>unknown</td>
<td>45</td>
<td>NE</td>
</tr>
<tr>
<td>Aug 12, 1983</td>
<td>1.83</td>
<td>6.0</td>
<td>36</td>
<td>NE</td>
</tr>
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<td>Oct 23, 1983</td>
<td>1.22</td>
<td>6.0</td>
<td>7.0</td>
<td>WSW-NE</td>
</tr>
<tr>
<td>Oct 24, 1983</td>
<td>1.22</td>
<td>6.0</td>
<td>34</td>
<td>NE</td>
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<td>Oct 25, 1983</td>
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<td>5.0</td>
<td>26</td>
<td>NE</td>
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Table 9. Marine weather conditions recorded during months with wave heights > 2 m at White Island, Isles of Shoals.

<table>
<thead>
<tr>
<th>Date</th>
<th>Wave Height (m)</th>
<th>Wave Period (sec)</th>
<th>Wind Speed (knots)</th>
<th>Wind Direction</th>
</tr>
</thead>
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<td>Jan 25, 1979</td>
<td>3.04</td>
<td>3.0</td>
<td>45</td>
<td>NE</td>
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<td>Jan 6, 1980</td>
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<td>10.0</td>
<td>40</td>
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<tr>
<td>Jan 16, 1980</td>
<td>2.44</td>
<td>10.0</td>
<td>23</td>
<td>NNE</td>
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<tr>
<td>Mar 22, 1980</td>
<td>2.44</td>
<td>5.0</td>
<td>25</td>
<td>ENE</td>
</tr>
<tr>
<td>Oct 4, 1980</td>
<td>2.13</td>
<td>5.0</td>
<td>10</td>
<td>SW</td>
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<tr>
<td>Feb 2, 1981</td>
<td>2.44</td>
<td>8.0</td>
<td>33</td>
<td>SSE</td>
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<td>Dec 6, 1981</td>
<td>2.13</td>
<td>7.0</td>
<td>35</td>
<td>NW</td>
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<td>WSW</td>
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<td>unknown</td>
<td>45</td>
<td>NE</td>
</tr>
<tr>
<td>Nov 5, 1983</td>
<td>2.13</td>
<td>8.0</td>
<td>40</td>
<td>NE</td>
</tr>
<tr>
<td>Dec 5, 1983</td>
<td>3.04</td>
<td>5.0</td>
<td>15</td>
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Table 10. Characteristics of mussel dislodgement patches at 8-10 m depth, Murray Rock. Data reported in first two columns as means ± (standard deviation).

<table>
<thead>
<tr>
<th>Date</th>
<th>Mean density of patches per 0.25 m² mussel bed</th>
<th>Mean patch size (cm²)</th>
<th>Total patch area in cm² (per 25,000 cm²)</th>
<th>Percent Disturbed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring (Apr 82)</td>
<td>1.1 ± 0.31</td>
<td>107.51 ± 27.56</td>
<td>1,182.71</td>
<td>4.73</td>
</tr>
<tr>
<td>Fall (Oct 82)</td>
<td>2.5 ± 0.70</td>
<td>91.18 ± 48.41</td>
<td>2,279.60</td>
<td>9.11</td>
</tr>
<tr>
<td>Winter (Feb 83)</td>
<td>1.3 ± 0.40</td>
<td>122.56 ± 97.64</td>
<td>1,593.71</td>
<td>6.37</td>
</tr>
<tr>
<td>Summer (Aug 83)</td>
<td>0.9 ± 0.56</td>
<td>97.16 ± 16.87</td>
<td>874.50</td>
<td>3.49</td>
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</tbody>
</table>
Table 11. Characteristics of kelp holdfast patches at 8-10 m depth, Murray Rock. Data reported in first two columns as means ± (standard deviation).

<table>
<thead>
<tr>
<th>Date</th>
<th>Mean density of patches per 0.25 m²</th>
<th>Mean patch size cm²</th>
<th>Total patch area cm² (per 25,000 cm²)</th>
<th>Percent area cleared (2.5 m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring</td>
<td>0.6 ± 0.51</td>
<td>92.93 ± 23.1</td>
<td>557.58</td>
<td>2.23</td>
</tr>
<tr>
<td>(Apr 82)</td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>Fall</td>
<td>1.3 ± 0.48</td>
<td>93.94 ± 15.83</td>
<td>1,221.33</td>
<td>4.88</td>
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<tr>
<td>(Oct 82)</td>
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<td></td>
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</tr>
<tr>
<td>Winter</td>
<td>0.8 ± 0.42</td>
<td>88.24 ± 11.64</td>
<td>705.97</td>
<td>2.82</td>
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<tr>
<td>(Feb 83)</td>
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</tr>
<tr>
<td>Summer</td>
<td>0.5 ± 0.52</td>
<td>74.34 ± 27.97</td>
<td>371.74</td>
<td>1.487</td>
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<tr>
<td>(Aug 83)</td>
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</table>
Table 12. Lower limit of the kelp zone at Murray Rock before (Oct 1981) and 31 months after the removal of the sea urchin front at 9.1-10.5 m depth. Data reported as mean density ± (standard deviation).

<table>
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<th>Depth (m)</th>
<th>Mean algal density/0.25 m²</th>
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<tr>
<td></td>
<td>Before</td>
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<tr>
<td>10.0</td>
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<td></td>
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<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>12.5</td>
<td>0.65 ± 0.5 Agarum cribosum</td>
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</tbody>
</table>
Table 13. Abundance of algae and invertebrates in mussel patches that had low percent cover (< 10%) or density. Data reported as means with standard deviations in parentheses. Values for algae are percent cover; invertebrates are densities. Data on *Lacuna* are from the 7 kelp-dominated patches. Abundance of other grazers in mussel patches in Table 14. Densities reported per 115 cm².

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<tr>
<th></th>
<th>Oct</th>
<th>Nov</th>
<th>Dec</th>
<th>Jan</th>
<th>Feb</th>
<th>Mar</th>
<th>Apr</th>
<th>May</th>
<th>Jun</th>
<th>Jul</th>
<th>Aug</th>
<th>Sep</th>
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<th>Dec</th>
<th>Jan</th>
<th>Feb</th>
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<th>Apr</th>
<th>May</th>
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<tbody>
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<td>Fleasy red crusts</td>
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</tbody>
</table>
Table 14. Relationship between abundance of grazers observed in mussel patches and dominance of kelp in the patches. Total grazers are pooled densities of *Tonicella*, *Acmaea*, and *Strongylocentrotus* per 115 cm².

**PATCHES NOT DOMINATED BY KELP**

<table>
<thead>
<tr>
<th>Patch</th>
<th>Total Density of <em>Tonicella</em></th>
<th>Total Density of <em>Acmaea</em></th>
<th>Total Density of Sea Urchins</th>
<th>Total Grazers</th>
<th>Kelp Density at End of Expt.</th>
</tr>
</thead>
<tbody>
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<td>1</td>
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<td>3</td>
<td>2</td>
<td>5</td>
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**PATCHES DOMINATED BY KELP**

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| 11    | 0                           | 3                        | 0                           | 3             | 29                          |
| 12    | 0                           | 2                        | 0                           | 2             | 14                          |
| 13    | 0                           | 0                        | 0                           | 0             | 11                          |
| 14    | 0                           | 1                        | 0                           | 1             | 11                          |
| 15    | 1                           | 1                        | 0                           | 2             | 10                          |
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Table 15. Abundance of sessile organisms in algal turf patches that had < 10% cover or were present in low densities from October 1982 to May 1984. Data reported as means with standard deviation in parentheses; values for algae are percent cover, invertebrate values are densities unless denoted by (*) indicating percent cover. Months not sampled (-). Densities reported per 115 cm².

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FIGURES
Fig. 1. Map showing the location of study sites at 8, 18, and 30 meters depth off Star Island, Isles of Shoals. Depth contours in meters. Inset map shows location of Isles of Shoals in relation to New England coast.
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 Appendix 1. Group A represents a 30 meter outside substrate community, Group B an 8-18 meter outside substrate community, and Group C the *Modiolus* community.
Fig. 3. Photoquadrats (0.25 m²) of benthic habitats sampled. Increments at top and bottom of each quad 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 “turf” on substratum outside mussel beds at 8 m. Turf occurs under a canopy of kelp (Laminaria saccharina and Laminaria digitata) and is predominated by Chondrus crispus, Corallina officinalis, and Phyllophora membranifolia.
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 macroalgae 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 macroalgae 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.
Fig. 4. Results of predation experiments with 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 hours; 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.
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. 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.
Fig. 7. Dendrogram resulting from group average clustering of 20 samples collected at 8 m study site before and after sea urchin grazing. Group A consists of 4 pre-grazing Modiolus bed samples and 1 pre-grazing outside substratum sample; group B composed of pre- and post-grazing Modiolus bed samples; group C composed of pre-disturbance outside substratum samples (kelp forest community); and group D consists of post-grazing outside substratum samples (urchin barrens community).
EFFECT OF URCHIN GRAZING ON SE COMMUNITY STRUCTURE: SQ RT.PM CORREL. UPGMA
Fig. 8. Species richness of macrobenthic taxa within functional groups before and after sea urchins overgrazed the 8 m study site. Dark bars in front represent *Modiolus* bed samples; light bars in rear represent outside substrate samples. Species of upright algae listed in Appendix 3.
Fig. 9. Mean species diversity and mean evenness per quadrat of invertebrate functional groups before and after severe sea urchin grazing for *Modiolus* bed samples (dark bars in front) and outside substrate samples (light bars in rear).
Fig. 10. The number of *Modiolus modiolus* in 4 monitored mussel beds (0.25 m² area) at each of 3 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 given in parentheses.
Fig. 11. Map showing the location of study sites at Sea Point, Murray Rock, and Star Island. Inset map shows location of north and south beaches at Sea Point that were surveyed for dislodged mussels. Open circle designates location of wave height observations off White Island, Isles of Shoals.
Fig. 12. Diagram of experimental design at Murray Rock. Squares indicate permanent 1.0 m² quadrats established around *Modiolus* beds.
URCHIN BARRENS

KELP BED

TAGGED KELP-MUSSELS

INTERFACE

urchin removal

grazed control
Fig. 13. Depth zonation of kelp and mussels at Murray Rock and Star Island. Data are mean densities with 95% confidence intervals.
Fig. 14. Abundance of sea urchins (*S. droebachiensis*) inside and outside *Modiolus* beds at Murray Rock and Star Island. Error bars are 95% confidence intervals. Note high density aggregations of sea urchins outside mussel beds (urchin fronts) at 11 m (MR) and 12 m (SI).
Fig. 15. Mean densities of recently settled mussels in algal turf and Modiolus bed habitats at Murray Rock (8-9 m depth). Error bars represent 95% confidence intervals.
Fig. 16. Total number of *Modiolus* with attached kelp cast ashore at Sea Point (north and south beaches). Note log scale on y axis.
Fig. 17. Size frequency histograms of Modiolus with attached kelp cast ashore at Sea Point.
Fig. 18. Maximum wave heights recorded off White Island, Isles of Shoals. Data represent the height of waves in the open ocean, not the height of waves breaking on shore, which were higher.
Fig. 19. Photoquadrat (0.25 m²) showing a small patch created by the dislodgement of a *Modiolus* overgrown by kelp in the urchin removal quadrats. Patch area is 25 cm²; increments at top and bottom of quadrat are 2 cm.
Fig. 20. Photograph of an average size mussel dislodgement patch (105 cm²). Note tagged kelp on *Modiolus* in upper part of photograph. Algal turf habitat is shown in lower half of photograph. Black increments on ruler are 1 cm.
Fig. 21. Percent survival of tagged *Modiolus* overgrown by kelp at Murray Rock. Endpoints of 1981–82 (16%) and 1982–83 (22%) tagging represent the percent of tags removed by sea urchins chewing through kelp stipes.
PERCENT SURVIVAL OF TAGGED MUSSELS
Fig. 22. Schematic diagram of the study site at Murray Rock showing the tagging area, urchin removal area, and mussel shellbeds in a gully below the pinnacle.
Fig. 23. Mean densities of kelp in urchin removal and grazed control quadrats. Error bars represent 95% confidence intervals.
Fig. 24. Total number of *Modiolus* dislodged in urchin removal and grazed control quadrats.
Fig. 25. Major sources of adult *Modiolus* mortality in urchin removal and grazed control quadrats.
URCHIN REMOVAL

- Dislodgement by Kelp
- Asterias predation
- Crab/lobster predation

PERCENT MORTALITY

GRAZED CONTROL

1981 1982 1983
Fig. 26. Photograph of a grazing halo around a *Modiolus* bed at 9 m depth, Murray Rock. Note sea urchins consuming kelp around the mussel bed. Width of grazing halo ranges from 6 to 25 cm.
Fig. 27. Dry weight of *Modiolus modiolus* gonads with and without attached kelp. Error bars represent 95% confidence intervals.
Fig. 28. Recolonization of patches cleared in *Modiolus* beds at Murray Rock. Data are mean values with 95% confidence intervals.
Fig. 29. Recolonization of patches cleared in algal turf at Murray Rock. Data are mean values with 95% confidence intervals.
ALGAL TURF PATCHES

BARE ROCK

CORALLINE ALGAE

FLESHY RED CRUSTS

Licmophora MAT

Phyllophora

Phycodrys

BRYOZOAN EPISHYTES

ENCIRCRING BRYOZOANS

KELP

L. saccharina

L. digitata

Lacuna

1982 1983 1984

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Fig. 30. Conceptual model of interactions between kelps, sea urchins, and Modiolus. Begin at step 1 and follow arrows through diagram. The three endpoints of the interactions: Modiolus dominance, kelp dominance, and coexistence (corresponding to zonation patterns in Fig. 13) are influenced by the intensity of storm disturbance, sea urchin grazing, and the rate of recovery from disturbance. As demonstrated in the urchin removal experiment, sea urchin grazing has a negative effect on kelp (step 1) by regulating the lower depth limit of the kelp zone and restricting the local distribution of kelp (grazing halo observations). Sea urchin grazing has a positive effect on Modiolus (step 2) because it reduces dislodgement mortality (urchin removal experiment and tagging experiment). There is a positive feedback between Modiolus and urchins (step 3) as Modiolus beds provide a refuge from predation for resident sea urchins (predation experiment), indicating that the urchin-Modiolus relationship is mutualistic. As demonstrated in the patch recolonization experiments (step 4), fast recovery from disturbance enables kelp to monopolize patch space. The failure of Modiolus to fill patches created by dislodgement indicates that, depending on the strength of grazing pressure, Modiolus will lose space to rapidly colonizing kelp. The coexistence of kelp and mussel competitors is facilitated by mutualism.
REDUCED DISLODGEENT BY KELP

MODIOLUS : SLOW

DISLODGEENT

STORM DISTURBANCE

MODIOLUS DOMINANCE

REFUGE FROM PREDATORS

URCHIN POPULATIONS

COEXISTENCE

KELP DOMINANCE

FOOD

RECOVERY FROM DISTURBANCE

KELP: FAST

GRAZING

183
APPENDIX 1

Species groups identified by cluster analysis (depicted in Fig. 2).

Taxonomic abbreviations are as follows: (S) sponge, (OC) octocoral, (N) nemertean, (P) polychaete, (B) bivalve, (G) gastropod, (NU) nudibranch, (OP) ophistobranch, (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 dendrogram. Functional group categories are: epifauna (EPI), mobile fauna (MOB), infauna (INF). Mean densities with standard deviations in parentheses presented from samples inside Modiolus beds (IN) and on the substratum outside (OUT) at each depth.

Post-clustering analyses (2-way ANOVA and Student-Newman-Keuls test) identified the major distribution pattern shared among taxa in clusters A, B, and C in Fig. 2. The effect of depth (8, 18, 30 meters) and habitat (outside or inside Modiolus bed) on species density was tested by 2-way ANOVA. Statistical significance levels reported as * = p < .05, ** = p < .01, *** = p < .001. Where the interaction of depth and habitat were non-significant (NS); mean densities were compared by the Student-Newman-Keuls test (SNK), which indicated where the highest densities of each species occurred. All SNK results are significant at p < .05.
### MEAN DENSITY/0.25 m²

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<tr>
<th>TAXON</th>
<th>CODE</th>
<th>FUNCTIONAL GROUP</th>
<th>8 M</th>
<th>18 M</th>
<th>30 M</th>
<th>EFFECT OF DEPTH</th>
<th>EFFECT OF HABITAT</th>
<th>INTERACTION</th>
<th>DENSITY PATTERN</th>
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**GROUP A: 30 m COMMUNITY**
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<th>INTERACTION</th>
<th>DENSITY PATTERN</th>
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**Note:** The table above represents the ANOVA SNK for various taxa at different depths (8 M, 18 M, 30 M) with effects on depth, habitat, interaction, and density pattern.
<table>
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<tr>
<th>TAXON</th>
<th>CODE</th>
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<th>8 M</th>
<th>18 M</th>
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<th>INTERACTION</th>
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<td>Harmothoe labriforma (P)</td>
<td>HIMBR</td>
<td>MBG</td>
<td>3.8(2.8)</td>
<td>10.2(3.8)</td>
<td>2.0(1.8)</td>
<td>6.2(3.0)</td>
<td>0.8(1.1)</td>
<td>3.1(1.4)</td>
<td>***</td>
</tr>
<tr>
<td>Pleuveytia glaberrima (A)</td>
<td>PGLAB</td>
<td>MOB</td>
<td>28.8(21.4)</td>
<td>120.4(60.7)</td>
<td>58.0(30.2)</td>
<td>68.8(33.3)</td>
<td>1.4(1.7)</td>
<td>3.8(1.1)</td>
<td>***</td>
</tr>
<tr>
<td>Caprella septentrionalis (C)</td>
<td></td>
<td>CSEPT</td>
<td>7.8(6.1)</td>
<td>45.4(35.0)</td>
<td>21.0(22.7)</td>
<td>34.2(12.6)</td>
<td>0</td>
<td>1.7(1.4)</td>
<td>***</td>
</tr>
<tr>
<td>Pontogonalia lamarcki (A)</td>
<td>PINER</td>
<td>MOB</td>
<td>22.8(21.6)</td>
<td>199.0(82.4)</td>
<td>75.0(73.7)</td>
<td>162.2(114.5)</td>
<td>2.8(5.6)</td>
<td>11.6(6.5)</td>
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<td>GROUP</td>
<td>8 M IN</td>
<td>8 M OUT</td>
<td>18 M IN</td>
<td>18 M OUT</td>
<td>30 M IN</td>
<td>30 M OUT</td>
<td>EFFECT OF DEPTH</td>
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<tr>
<td>Corophium bonelli (A)</td>
<td>CBONE</td>
<td>M DB</td>
<td>11.6(19.9)</td>
<td>142.2(122.8)</td>
<td>9.4(8.3)</td>
<td>65.2(60.8)</td>
<td>0.8(1.3)</td>
<td>59.6(48.0)</td>
<td>*</td>
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<tr>
<td>Phylidocoecus maculatus (P)</td>
<td>PMAQU</td>
<td>M DB</td>
<td>4.4(6.2)</td>
<td>32.4(26.0)</td>
<td>0.6(0.9)</td>
<td>5.2(2.5)</td>
<td>5.4(6.5)</td>
<td>10.0(11.1)</td>
<td>**</td>
</tr>
<tr>
<td>Caprella linearis (C)</td>
<td>CLINE</td>
<td>M DB</td>
<td>10.8(4.7)</td>
<td>64.2(51.5)</td>
<td>5.8(6.2)</td>
<td>38.8(34.2)</td>
<td>0.6(0.9)</td>
<td>14.6(12.8)</td>
<td>**</td>
</tr>
<tr>
<td>Asterias vulgaris (AS)</td>
<td>AVULG</td>
<td>M DB</td>
<td>12.8(4.2)</td>
<td>25.8(6.9)</td>
<td>14.0(9.0)</td>
<td>34.4(21.7)</td>
<td>6.2(3.9)</td>
<td>15.8(7.7)</td>
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<td><strong>GROUP C: MODIOLUS COMMUNITY</strong></td>
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<td>Neanthes quadricuspida (P)</td>
<td>NQUAD</td>
<td>M DB</td>
<td>59.8(36.1)</td>
<td>24.6(18.4)</td>
<td>15.8(2.0)</td>
<td>0</td>
<td>4.4(2.5)</td>
<td>1.4(0.9)</td>
<td>***</td>
</tr>
<tr>
<td>Strongylocentrotus droebachiensis (E)</td>
<td>SOROB</td>
<td>M DB</td>
<td>54.0(10.4)</td>
<td>37.4(6.1)</td>
<td>28.0(3.0)</td>
<td>14.0(4.7)</td>
<td>14.8(11.0)</td>
<td>9.2(3.0)</td>
<td>***</td>
</tr>
<tr>
<td>Henricia sanguinolenta (AS)</td>
<td>HSANG</td>
<td>M DB</td>
<td>9.8(4.3)</td>
<td>5.4(2.6)</td>
<td>5.6(3.6)</td>
<td>1.0(1.7)</td>
<td>1.6(1.3)</td>
<td>0.6(0.7)</td>
<td>**</td>
</tr>
<tr>
<td>Amphiprion cirrata (P)</td>
<td>ACIRR</td>
<td>INF</td>
<td>20.4(28.8)</td>
<td>2.2(2.3)</td>
<td>41.6(20.3)</td>
<td>2.0(2.9)</td>
<td>6.8(3.0)</td>
<td>1.8(3.1)</td>
<td>**</td>
</tr>
<tr>
<td>Cistellina granulata (A)</td>
<td>CGRN</td>
<td>INF</td>
<td>7.4(3.4)</td>
<td>0</td>
<td>56.0(26.9)</td>
<td>0</td>
<td>26.8(14.3)</td>
<td>0</td>
<td>**</td>
</tr>
<tr>
<td>Ophiopholis aculeata (O)</td>
<td>OACUL</td>
<td>INF</td>
<td>273.0(137.5)</td>
<td>61.2(34.3)</td>
<td>357.2(119.0)</td>
<td>31.6(22.8)</td>
<td>148.8(62.1)</td>
<td>19.0(10.5)</td>
<td>**</td>
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<td>TAXON</td>
<td>CODE</td>
<td>GROUP</td>
<td>8 M IN</td>
<td>18 M IN</td>
<td>30 M IN</td>
<td>EFFECT OF DEPTH</td>
<td>EFFECT OF HABITAT</td>
<td>INTERACTION</td>
<td>DENSITY PATTERN</td>
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<tr>
<td>Histella arctica (B)</td>
<td>HARTI</td>
<td>INF</td>
<td>12.4(9.0)</td>
<td>4.0(3.3)</td>
<td>34.0(10.4)</td>
<td>0.0(1.6)</td>
<td>3.8(3.1)</td>
<td>4.2(5.4)</td>
<td>***</td>
</tr>
<tr>
<td>Amphitrite Johnstonei (P)</td>
<td>AJOH</td>
<td>INF</td>
<td>8.8(13.9)</td>
<td>0.2(0.4)</td>
<td>0.4(1.9)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>*</td>
</tr>
<tr>
<td>Acmea testudinalis (G)</td>
<td>ATEST</td>
<td>MOB</td>
<td>8.2(4.7)</td>
<td>0.2(0.9)</td>
<td>7.8(3.4)</td>
<td>3.0(1.4)</td>
<td>0.5(0.2)</td>
<td>0</td>
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<tr>
<td>Tonicaella rubra (G)</td>
<td>TRUBR</td>
<td>MOB</td>
<td>15.2(5.2)</td>
<td>4.0(6.0)</td>
<td>38.2(12.9)</td>
<td>20.0(15.6)</td>
<td>5.6(3.7)</td>
<td>3.0(2.6)</td>
<td>***</td>
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<tr>
<td>Cucumaria frondosa (H)</td>
<td>CFRON</td>
<td>INF</td>
<td>1.2(0.4)</td>
<td>0</td>
<td>4.8(2.5)</td>
<td>0</td>
<td>2.3(0.5)</td>
<td>0</td>
<td>**</td>
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<tr>
<td>Ischnochiton stilus (G)</td>
<td>IALBO</td>
<td>MOB</td>
<td>0.2(0.4)</td>
<td>0</td>
<td>0</td>
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<td>3.6(1.6)</td>
<td>0.2(0.4)</td>
<td>***</td>
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<tr>
<td>Amphiporus angulatus (H)</td>
<td>AANGU</td>
<td>MOB</td>
<td>7.2(6.9)</td>
<td>1.8(2.2)</td>
<td>5.0(6.4)</td>
<td>0.6(0.8)</td>
<td>0.8(1.3)</td>
<td>0</td>
<td>*</td>
</tr>
<tr>
<td>Eulalus gaudou (D)</td>
<td>EPOSI</td>
<td>MOB</td>
<td>7.0(7.6)</td>
<td>1.6(3.0)</td>
<td>16.2(8.9)</td>
<td>3.6(1.3)</td>
<td>12.6(11.5)</td>
<td>0.6(1.3)</td>
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<tr>
<td>Psolus fabricii (H)</td>
<td>PFABR</td>
<td>EPI</td>
<td>1.9(0.7)</td>
<td>0.2(0.4)</td>
<td>4.8(1.2)</td>
<td>0</td>
<td>1.0(0.7)</td>
<td>0.2(0.4)</td>
<td>*</td>
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<tr>
<td>Myxocola infaudiculum (P)</td>
<td>MINFU</td>
<td>INF</td>
<td>0</td>
<td>0</td>
<td>3.6(0.6)</td>
<td>0</td>
<td>5.2(1.1)</td>
<td>0</td>
<td>***</td>
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<tr>
<td>Flaballigera affinis (F)</td>
<td>FAFFI</td>
<td>INF</td>
<td>1.6(2.0)</td>
<td>0.2(0.4)</td>
<td>4.0(3.3)</td>
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<td>6.8(4.0)</td>
<td>1.0(1.2)</td>
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<td>TAXON</td>
<td>CODE</td>
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<td>8 M IN</td>
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<td>18 M IN</td>
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<td>30 M IN</td>
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<td>EFFECT OF DEPTH</td>
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<td>Turrilatopsis</td>
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<td>MGB</td>
<td>0</td>
<td>0.4(0.5)</td>
<td>7.2(6.9)</td>
<td>0</td>
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<td>acicula (G)</td>
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<tr>
<td>Opillura</td>
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<td>INF</td>
<td>2.6(1.2)</td>
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<td>25.2(19.3)</td>
<td>9.8(8.7)</td>
<td>38.2(20.4)</td>
<td>14.4(8.9)</td>
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<td>robusta (G)</td>
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<td>Bradea</td>
<td>BGRAN</td>
<td>INF</td>
<td>0</td>
<td>0</td>
<td>2.2(1.4)</td>
<td>0</td>
<td>5.8(7.5)</td>
<td>0</td>
<td>***</td>
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<tr>
<td>granosa (P)</td>
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<tr>
<td>Eucriama</td>
<td>ECOLL</td>
<td>INF</td>
<td>0.6(1.3)</td>
<td>0</td>
<td>0.6(0.8)</td>
<td>0</td>
<td>20.8(10.6)</td>
<td>1.8(3.4)</td>
<td>***</td>
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<tr>
<td>collaris (P)</td>
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<tr>
<td>Chirodota</td>
<td>CHIRO</td>
<td>INF</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3.8(0.8)</td>
<td>0</td>
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<tr>
<td>laevis (H)</td>
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<tr>
<td>Colus</td>
<td>CPRII</td>
<td>MGB</td>
<td>0</td>
<td>0</td>
<td>1.8(1.3)</td>
<td>0</td>
<td>19.4(4.4)</td>
<td>8.0(1.4)</td>
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<td>pygmaeus (G)</td>
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</table>
APPENDIX 2

Size structure of *Modiolus modiolus* and dominant members of the *Modiolus* community (*Ophiopholis aculeata*, pg. 196; *Hiatella arctica*, pg. 197; and *Strongylocentrotus droebachiensis*, pg. 198) inside and outside mussel beds at Star Island study sites (8, 18, 30 m depth).
SIZE DISTRIBUTION OF M. MODIOCLUS
ISLES OF SHOALS RESEARCH SITE
**Hiatella Outside Modiolus Bed**

- Sample size: $n = 35$

**Hiatella In Modiolus Bed**

- Sample size: $n = 252$

**Shells Length (mm)**

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APPENDIX 3

Species of upright algae used for determination of species richness in Fig. 8. All 23 species were present in the outside substratum samples and *Modiolus* bed samples from 8 m depth prior to sea urchin overgrazing.

PHAEODHYTA:

- Laminaria digitata
- Laminaria saccharina
- Agarum cibosum
- Alaria esculenta

RHODODYTA:

- Chondrus crispus
- Phyllophora pseudoceranoides
- Phyllophora truncata
- Phycodrys rubens
- Plumaria elegans
- Porphyra miniata
- Porphyra umbilicalis
- Ptilota serrata
- Callithamnion tetragonum
- Cystoclonium purpureum var. cirrhosum
- Ceramium rubrum
- Callophyllis cristata
- Palmaria palmata
- Membranoptera alata
- Antithamnion rylaissae
- Antithamnionella floccosum

CHLOROPHYTA:

- Chaetomorpha melagonium
- Ulva lactuca
- Cladophora sericea