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## The Importance of Predation and Competition in Organizing the Intertidal Epifaunal Communities of Barnegat Inlet, New Jersey\*

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**Summary.** Community organization was studied by experiment and observation from October 1972–October 1974 in the marine epifaunal assemblages at each end of Barnegat Inlet, New Jersey. The rock jetty at the wave-exposed eastern end of the inlet possesses an intertidal community with the following attributes: (1) a high intertidal zone dominated by the barnacle, *Balanus balanoides*, but also occupied by the blue mussel, *Mytilus edulis*, in rock crevices, (2) a mid and low intertidal zone with usually < 10% free space and extreme numerical dominance by *Mytilus edulis* (usually > 85% cover) during summer and fall, and (3) almost no intertidal predators or herbivores. The predatory seastar, *Asterias forbesi*, is abundant subtidally. Controlled removal experiments indicate that in the mid and low intertidal underlying barnacles perish as a consequence of the establishment of extensive secondary cover by *Mytilus*, probably because *Mytilus* outcompetes *Balanus* through suffocation or starvation. *Mytilus* transplants demonstrate that the mussels do not survive outside of crevices in the high intertidal, which thus may represent for *Balanus* a refuge from competition by *Mytilus*.

The pilings on docks at the protected western end of Barnegat Inlet possess an intertidal epifaunal community with the following characteristics: (1) a high intertidal zone that includes *Balanus balanoides*, a second barnacle, *Balanus eburneus*, and an herbivorous gastropod, *Littorina littorea*, (2) a mid and low intertidal zone with usually > 40% free space in the summer and fall and the remaining area covered by several abundant species with no extreme dominant, and (3) abundant predators, chiefly the oyster drill, *Urosalpinx cinerea*, the blue crab, *Callinectes sapidus*, and a mud crab, *Neopanope texana sayi*. *Asterias forbesi*, while abundant subtidally, is also occasionally present on intertidal surfaces. Controlled exclusion of predators by caging several replicate pilings at the western end of the inlet reveals that

\* This paper is dedicated to the memory of Robert H. MacArthur

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predation prevents monopolization of mid and low intertidal space by the apparent competitive dominant, *Mytilus*. Predation appears to be a direct cause of the relatively great temporal and spatial heterogeneity in the mid and low intertidal of these pilings.

Thus, although the Barnegat Inlet intertidal system appears to follow closely the patterns of community organization described for several other rocky intertidal coastlines, this organizational pattern is noteworthy because it is repeated here in a far more seasonal environment and with a new cast of interacting competitors and predators. That crabs play an important role as predators is novel for North America, but only perhaps because all previous North American studies have ignored the rocky intertidal zones of quiet, estuarine waters where in Europe predatory crabs are known to be extremely significant.

## Introduction

Probably the best understood communities in nature are those assemblages of plants and animals found on rocky intertidal shorelines. Numerous experimental analyses of organization in these systems have permitted the erection of a virtual paradigm to explain their structural dynamics. In particular, it appears that in the rocky intertidal communities of temperate-zones attachment space is a potential limiting resource for epifaunal plants and animals at all but the very highest levels of the shoreline (Connell, 1961a, b; 1972). The usual outcome of the competition for this limited space is extreme dominance by the single best competitor, which tends to exclude from the community all other potential occupiers of primary space. Disturbance in any of several forms has been shown capable of interrupting the competitive process and of preventing the monopolization of space by the competitive dominant. For instance, Paine (1966, 1971, 1974) in two historically divergent but analogously organized intertidal systems demonstrated that predation can act to lower densities of the epifauna, thus reducing the severity of interspecific interaction and preventing competitive exclusion. Not only predation, but also physical disturbances, can serve this function of opening up new intertidal space, which is then available for colonization by those species that would be reduced or even eliminated during any long period of uninterrupted competition (Dayton, 1971).

Although virtually all studies of rocky intertidal community organization have tended to confirm this organizational paradigm, most past work has been restricted to systems in fairly constant, maritime climates of temperate-zones such as the coasts of England (Southward, 1953), Ireland (Kitching et al., 1959; Kitching and Ebling, 1967), Scotland (Connell, 1961a, b), Japan (Hoshiai, 1965), the Pacific northwest (Paine, 1966, 1974; Paine and Vadas, 1969; Connell, 1970; Dayton, 1971; Menge, 1972; Menge and Menge, 1974) and New Zealand (Luckens, 1976; Paine, 1971). Only very recently have studies been initiated on the more seasonal east coast of North America (Sutherland, 1974; Menge, 1976; Menge and Sutherland, 1976; Osman, 1977).

In this paper, I present results of observations and manipulative experiments

from two intertidal communities in a very seasonal environment at Barnegat Inlet, New Jersey. In addition, because one of these communities exists on the open coastline in an area exposed to wave action while the second community is found in a very protected, almost estuarine area, my comparison of these two systems may provide a basis from which to understand some major differences in the results of North American studies, which are typically done on wave-beaten coasts, and European studies, which are more commonly done in very protected sites, often within estuaries or lagoons.

### Study Sites and General Methods

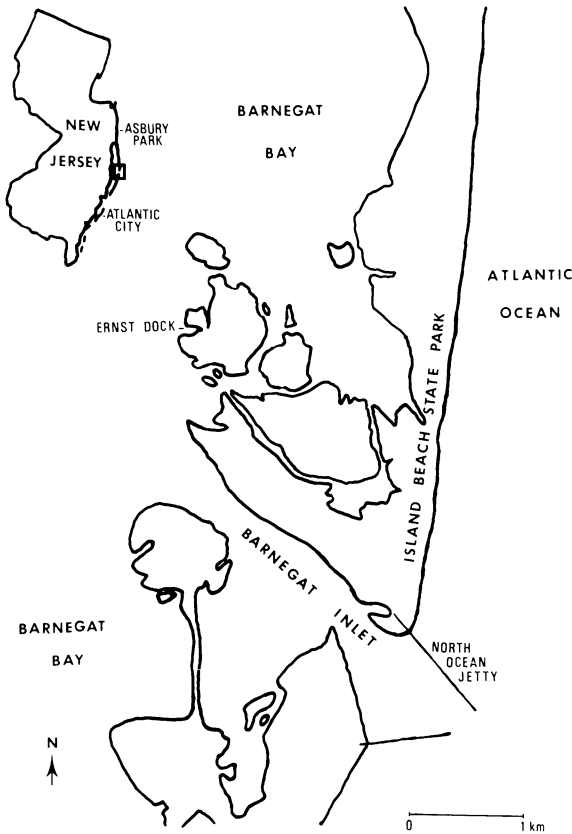
The two study sites are located at either end of Barnegat Inlet, New Jersey, USA. Barnegat Inlet, connecting Barnegat Bay with the Atlantic Ocean, separates Island Beach from Long Beach Island and is situated almost equidistant (~53 km) from the large New Jersey coastal cities of Atlantic City and Asbury Park (Fig. 1).

At the eastern end of the inlet two jetties, composed largely of granite boulders of up to about 4 m<sup>3</sup> in size, extend approximately 900 m out into the ocean. These jetties provide intertidal and subtidal surface for attachment by marine algae and epifauna. The north jetty, built out from Island Beach State Park, served as one study site (Fig. 1). All experiments and all permanent transects were located between about 300 and 600 m from shore where the effects of shifting sand were minimal and where human visitors were extremely rare. Although this jetty served as the only Atlantic Ocean study site, it resembles all other jetties and pilings that I have examined along the central New Jersey coast in possessing generally dense mussel cover in the mid and low intertidal and patchy barnacle cover in the high intertidal.

At the western end of Barnegat Inlet, several docks have been constructed on wooden pilings which provide both intertidal and subtidal surface for epifaunal attachment. One such dock (the "Ernst dock"), with each of its several wooden pilings serving as replicates, formed the second study site (Fig. 1). This dock is located at the north bank of a small cove about 170 m north of the flashing red coast guard buoy (labeled "26" on the 1968 U.S. Dept. of Commerce Nautical Chart 824-SC), marking the navigable channel of Barnegat Inlet. The wooden pilings of the Ernst dock were about 40 cm in circumference. Shoal waters nearby and the vigilant co-operation from the residents in the fishing cabin at Ernst dock helped to protect this study site from human interference. Although the Ernst dock was the only study site chosen at the west end of Barnegat Inlet, its intertidal community generally resembled that found on other docks in the vicinity: much free space usually was apparent, mussels were rare, and barnacles, bryozoans, crabs, and oyster drills appeared common on nearly all of the wooden pilings at the west end of Barnegat Inlet and of Manasquan Inlet, situated about 35 km to the north.

The major difference between the physical environments of the jetty and dock study sites is the degree of wave action. The Ernst dock is located in a very protected area, subjected only to the occasional wind-driven whitecaps of Barnegat Bay. The north ocean jetty, on the other hand, is exposed to the full impact of Atlantic Ocean surf. There is also an obvious difference between the substrates at the two sites, the rock surfaces on the ocean jetty and the wooden pilings at the Ernst dock. However, some wooden pilings can be found intermingled among the jetty rocks. From these few pilings, data were taken in order to evaluate the possible effects of varying substrate type.

Temperature and salinity regimes are similar at both sites. Mean monthly water temperature varies seasonally from a usual winter low of about 2° C to a summer high of around 25° C. Late summer water temperatures are often about 3° C higher at the Ernst dock site. For instance, on 30 July 1967 I recorded a water temperature of 20° C at the north jetty at 11 am. Two hours later at Ernst dock the water temperature was 23° C. On 5 other occasions from June-October 1967, I found the difference in temperature to range from 0-3° C. On those same 6 occasions, surface salinity, measured by titration of water samples, was high at both sites, usually around 34‰, although occasionally somewhat lower at Ernst dock (on one occasion 32‰). After heavy rains salinity may fall even lower around the bay pilings.



**Fig. 1.** Location of Barnegat Inlet, New Jersey, equidistant from Asbury Park and Atlantic City, and location of the two study sites at either end of Barnegat Inlet: the north ocean jetty and the bay pilings at Ernst dock

The tidal range between MLW and MHW is about 1.3 m at the north jetty and 1.0 at the Ernst dock. Wind and rainfall patterns appear to more greatly influence water levels at the Ernst dock than at the north jetty, where tidal heights follow the lunar cycle more predictably. The phenomenon of wind tides is a general feature of enclosed, relatively shallow sounds (e.g. Roelofs and Bumpus, 1953; Macmillan, 1966) and can have great biological significance. Wind tides often produce week-long (or longer) periods during which the predicted lows are never even approached. Consequently, essentially subtidal predators have an occasional opportunity to forage without interruption in the low and even mid intertidal zones, thus potentially increasing predation rates.

The specific procedures that I have used in this study are described with the respective data. My general approach conforms with that employed by virtually all other investigators working with the ecology of rocky shorelines (e.g. Connell, 1961a; Dayton, 1971; Paine, 1974). I focus upon those macroscopic plants and animals occupying "primary space" on intertidal hard substrates. I am particularly interested in the provision of free space in this system and how that space is then occupied and held by subsequent colonists. This approach can be justified, at least in part, by the demonstration that primary space is potentially limiting in intertidal systems (Connell, 1961b), such that in studying the utilization of primary space one is examining the functional process of how a set of organisms share a common resource. As discussed by Paine (1974), this approach ignores the contributions made by microorganisms of all types and by the infauna living

in the byssus of mussels and around the base of bryozoans. It also ignores the utilization of "secondary space", as is provided by the shell surfaces of barnacles and mussels.

The simplification of the natural system that is implicit in the choice to study only the occupiers of primary intertidal space permits a relatively efficient means of collecting data. In this study, like many others, the natural composition of the intertidal community at each site was estimated from transects extending from MLW to the top of the intertidal. On the ocean jetty an approximately 0.3 m wide strip comprised each transect. Transects were located at haphazard positions along the jetty. On the Ernst dock, an entire piling formed a transect with intertidal surface area approximately equal to that of a single jetty transect ( $\sim 0.40 \text{ m}^2$ ). Marked transects at each site were periodically photographed using a Nikon macrolense and 35 mm high-speed Ektachrome color slide film. Several (usually 8) overlapping photographs of each transect were necessary to include sufficient detail. Even at this magnification (each  $2 \times 2$  slide containing about  $0.05 \text{ m}^2$  of substrate on about half the negative), juvenile barnacles could occasionally be identified to the species level only after some in the cohort had matured on later slides. At this magnification, juvenile *Littorina* and other gastropods were easily counted and identified. The spatial cover of each species was then later determined by projecting the slide onto a field of random dots: the proportion of dots falling upon a species approximates the proportion of primary space covered by that species. Likewise the proportion of unoccupied intertidal space can be estimated. Separate estimates of proportionate cover were made for 1) the high intertidal zone and 2) the mid-low intertidal zone (pooled because of their similarity). This random dot technique is frequently used in marine intertidal studies (e.g. Connell, 1970; Dayton, 1971; Menge, 1976) and results in a standard error of about 3% for 300 points (the number used here).

Food web relationships involving the primary space occupiers and their predators were determined chiefly from field observations but also from reports in the literature and feeding responses in an aquarium. The aquarium used recirculated sea-water, which was totally renewed biweekly. Animals were used for up to 7 days, after which they were returned to the field.

## Community Characteristics of the Two Study Sites

### *Species Composition*

On 9–12 October 1972, I visited both the north ocean jetty and the Ernst dock study sites where haphazardly located transect and quadrat samples were used to estimate the densities of all resident species. For floral and faunal occupiers of primary space, Table 1 presents the average percent spatial cover ( $\pm 1$  S.E.), as determined from the transects, and for the mobile animals (predators, herbivores, etc.) the average numerical densities ( $\pm 1$  S.E.), as determined from the quadrats. Table 1 also presents for each study site a complete list of all plants and animals which appeared and were recognized during the entire sampling period of October 1972–October 1974.

Two of the October 1972 transects were taken from wooden ocean pilings and three from nearby jetty rocks in order to permit an evaluation of the possible effects of changing substrate types. The pattern of space utilization in the mid-low intertidal of the wooden pilings on the jetty did not differ substantially from that of the rocks that surrounded them (Table 1), suggesting that the substrate difference between sites is not a significant factor in determining the biological differences in these lower zones. The high intertidal zone of the rocks contained denser populations of virtually all species, but relative abundances were similar. There is, however, a suggestion in Table 1 that *Balanus eburneus* may prefer wood to rock substrate and that *Porphyra* and *Telmatogeton*

**Table 1.** A list for each study site of all species observed on at least one occasion during October 1972–October 1974. Average % cover is estimated from sampling several  $\sim 2.5 \text{ m}^2$  transects in October 1972: 5 transects on the bay pilings at Ernst dock, 3 on the ocean rocks at Barnegat Inlet's north jetty, and 2 on ocean pilings. Predator, herbivore, and scavenger abundances also come from direct counts in the abutting quadrats which comprised each transect. One standard error is given in parentheses for each mean value. So that this table can simultaneously present the species lists for all dates and the abundances for one date, a zero entry is used to indicate that the species was not present in the October 1972 samples, but that it did appear at that site on at least one subsequent occasion, while a dashed-line entry indicates that the species was never observed at that study site

	Bay Pilings		Ocean Jetty		Ocean Pilings	
	High	Mid-low	High	Mid-low	High	Mid-low
a) Epifaunal occupiers of primary space (% cover)						
<i>Mytilus edulis</i>	0.0	7.0(8.5)	19.9(6.2)	91.8(2.0)	5.9(3.2)	98.0(1.8)
<i>Balanus balanoides</i>	8.2(10.1)	4.0(1.2)	27.5(6.5)	2.7(1.5)	13.4(8.3)	0.5(0.8)
<i>Balanus eburneus</i>	0.3(0.2)	10.8(2.6)	0.3(0.4)	1.1(1.2)	4.5(4.5)	0.0
<i>Haliplanella luciae</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Modiolus demissus</i>	0.0	0.0	—	—	—	—
<i>Molgula manhattensis</i>	0.0	0.0	—	—	—	—
<i>Schizoporella unicornis</i>	0.0	0.6(0.6)	—	—	—	—
<i>Hydroides dianthus</i>	0.0	18.2(6.1)	—	—	—	—
<i>Bugula sp. cf. flabellata</i>	0.0	0.0	—	—	—	—
b) Algae and other (% cover)						
<i>Ulva-Enteromorpha spp.</i>	13.8(5.9)	15.6(8.1)	25.2(7.5)	1.4(1.1)	19.2(1.0)	0.0
<i>Fucus sp.</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Gelidium sp.</i>	0.0	0.0	—	—	—	—
<i>Codium fragile</i>	0.0	0.0	—	—	—	—
<i>Bryopsis sp.</i>	—	—	0.0	0.0	0.0	0.0
<i>Cladophora sp.</i>	—	—	0.0	0.0	0.0	0.0
<i>Porphyra sp.</i>	—	—	12.1(7.5)	0.0	0.0	0.0
<i>Telmatogeton japonicus</i>	—	—	6.7(0.4)	0.0	0.0	0.0
c) Free primary space (% cover)						
	66.8(7.8)	51.0(5.2)	8.3(1.1)	3.0(0.6)	57.0(4.9)	1.5(0.4)
d) Predators (no. $\text{m}^{-2}$ )						
<i>Asterias forbesi</i>	0.0	3.2(0.7)	0.0	0.0	0.0	0.0
<i>Libinia emarginata</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Neopanope texana sayi</i>	0.0	7.6(1.5)	—	—	—	—
<i>Callinectes sapidus</i>	0.0	0.0	—	—	—	—
<i>Urosalpinx cinerea</i>	11.0(3.2)	31.2(4.1)	—	—	—	—
<i>Cancer irroratus</i>	—	—	0.0	0.0	0.0	0.0
<i>Carcinus maenas</i>	—	—	0.0	0.0	0.0	0.0
e) Herbivores and scavengers (no. $\text{m}^{-2}$ )						
<i>Littorina littorea</i>	73.8(10.7)	21.8(4.7)	14.2(2.4)	0.0	10.4(2.0)	0.0
<i>Idotea balthica</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Bittium alternatum</i>	0.0	0.0	—	—	—	—
<i>Pagurus longicarpus</i>	0.0	0.0	—	—	—	—
<i>Ilyanassa obsoleta</i>	0.0	4.6(1.5)	—	—	—	—
<i>Gammarus sp.</i>	—	—	0.0	12.2(4.1)	0.0	8.6(2.0)

may prefer the rock substrate. Although no subsequent data were collected to compare these substrates, the pilings on the jetty generally resembled the surrounding rocks on all visits made during the two-year study period.

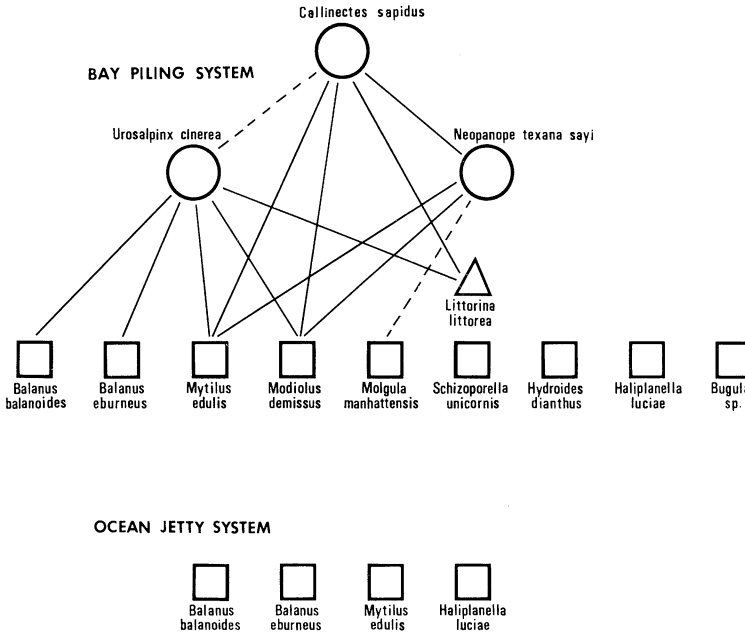
The intertidal communities at both sites were composed of only a few numerically important species (Table 1). Two species dominated the ocean jetty: the blue mussel, *Mytilus edulis*, and the rock barnacle, *Balanus balanoides*. The leafy green alga, *Ulva* sp. was often abundant. No intertidal predators were abundant, although the seastar, *Asterias forbesi*, was very common subtidally. Periwinkles, *Littorina littorea*, were occasionally found among the barnacles in the high intertidal zone of the jetty. Among the byssal threads of its mussels were abundant gammarid amphipods.

On the bay pilings *Balanus balanoides* and *Mytilus edulis* were much scarcer, although relatively important occupiers of primary space. They were joined by some other often common species: the acorn barnacle, *Balanus eburneus*, an annelid which constructs calcareous tubes, *Hydroides dianthus*, an encrusting bryozoan, *Schizoporella unicornis*, and a branching bryozoan, *Bugula* sp. Predators were abundant on the pilings, chiefly the oyster drill, *Urosalpinx cinerea*, and a xanthid mud crab, *Neopanope texana sayi*. The blue crab, *Callinectes sapidus*, is a very important and perhaps the dominant predator in this system; although its density appears low in Table 1, the blue crab's mobility makes estimation of density difficult. On 10 October 1972, I counted 18 *Callinectes* on approximately 36 m<sup>2</sup> of bottom surrounding Ernst dock. Although variable, the abundance of visible blue crabs remained at a similarly high level on subsequent visits. *Asterias forbesi* were found subtidally on the pilings and occasionally in intertidal areas during long periods of high tides. Periwinkles were more abundant at Ernst dock than on the ocean jetty.

The high intertidal zone was occupied in a similar fashion at both sites in October 1972 (Table 1). There was a great deal of free space. Barnacles, particularly *Balanus balanoides*, were the numerically dominant animals, although their densities were surprisingly low. Smaller barnacle populations in the high intertidal of the dock were probably a result of higher predation rates by *Urosalpinx*. *Ulva* sp. and *Enteromorpha* sp. were important space occupiers in the high intertidal of both sites. Data are pooled for these two taxa because of the difficulty in distinguishing between young plants. The red alga, *Porphyra* sp., occasionally attached to barnacles, was important in the high intertidal of the ocean jetty, although absent from the bay pilings. Also found exclusively on the ocean jetties were numerous midge larvae, *Telmatogeton japonicus*, encased in sand tubes and abundant only during late summer and autumn. Mussels were abundant in high intertidal rock crevices on the jetty, although they did not appear at all in the high intertidal at Ernst dock. In October 1972 nearly twice as much free space was available in the high intertidal of the bay pilings as in the high intertidal of the ocean jetty (Table 1).

Occupation of primary space in the mid and low intertidal zone was quite different at the two study sites in October 1972 (Table 1). There was much less free space on the ocean jetty (3% compared to 51%). Fewer macrofaunal species occupied primary space in these lower zones of the jetty (3 versus 5





**Fig. 2.** Food webs for the intertidal epifauna of the bay piling system and of the ocean jetty system. Diagrams include all sessile animals found occupying primary space (drawn as squares). Scavengers and primary producers are excluded. Only those intertidal predators (drawn as circles) which were observed to be abundant on at least one occasion appear in the diagram: consequently, the diagram for the ocean jetty system contains no consumers. The herbivore *Littorina* (drawn as a triangle) is placed above the level of the primary space occupiers because of its potential for clearing off recently recruited barnacles. Dotted lines indicate probable trophic links. Which of the trophic pathways are most important are indicated in the text

species on the bay pilings). One species, *Mytilus edulis*, spatially dominated this zone on the jetty, occupying 92% of the space in October 1972 while no such dominance was achieved by any of the species on the bay pilings. In addition, predators were far more abundant at the bay piling site (26.5/m<sup>2</sup> versus 0.0/m<sup>2</sup>).

### *Trophic Structure*

In Fig. 2 appear diagrammatic food webs for both the ocean jetty and bay piling community. These diagrams include all epifaunal occupiers of primary space but only those herbivores and predators which were abundant on at least one occasion during the study period. Since there were no abundant predators in the intertidal zone of the ocean jetty, none are included in Fig. 2. The ocean food web is probably completed by consumption that occurs only after the animals have been stripped from the rocks by occasional winter storms.

The bay food web was constructed from field observations, aquarium experiments, and published accounts (e.g. Carriker, 1955; Darnell, 1958; Tagatz,

1968; Wood, 1968; Hamilton, 1976; Menge, 1976). The observations noted below indicate which of these three sources was used for each trophic link. The blue crab, *Callinectes sapidus*, can often be seen eating both *Mytilus edulis* and the horse mussel, *Modiolus demissus*, in Barnegat Inlet. When offered in an aquarium every species from the bay community, *Callinectes* consumed only *Mytilus*, *Modiolus*, *Littorina littorea*, and *Neopanope texana sayi*. *Callinectes* broke the apertures of several *Urosalpinx cinerea* although it did not actually consume any. The blue crab also broke the arms off of several small *Asterias*. Of the various prey in its diet the *Callinectes* in Barnegat Inlet seem to consume *Mytilus* more often than any other species. This agrees well with Tagatz's (1968) and Darnell's (1958) observations of *Callinectes*' feeding behavior.

The mud crab, *Neopanope texana sayi*, was observed eating only *Mytilus edulis* at the bay piling site. The only other species *Neopanope* consumed in the aquarium was *Modiolus demissus*. The mud crabs also killed all of the tunicate, *Molgula manhattensis*, in the aquarium, although they did not appear to actually consume their victims.

The oyster drill, *Urosalpinx cinerea*, could be observed at Ernst dock in the process of feeding on *Mytilus edulis*, *Balanus balanoides*, and small *Balanus eburneus*. In the aquarium, *Urosalpinx* consumed *Balanus balanoides* and *Littorina littorea*, but no other species. Wood (1968) noted that *Urosalpinx* preys predominantly upon *Mytilus edulis* and several *Balanus* species in study sites ranging from Massachusetts to Florida. Carriker (1955) reported that *Urosalpinx* also preys upon *Modiolus* and encrusting bryozoans (perhaps *Schizoporella* although because of a lack of confirmation, I have not included this trophic link in Fig. 2). All reports seem to agree that the major components of the oyster drill's diet are *Mytilus edulis*, *Balanus* spp., and small oysters, when these prey are available.

Although the three predators, *Callinectes*, *Neopanope*, and *Urosalpinx*, were quite common on the bay pilings, predators were seldom seen in the intertidal zone of the ocean jetty, even at high tide. The seastar, *Asterias forbesi*, was an abundant subtidal predator at both sites. On those rare occasions, when *Asterias* was found intertidally on the ocean jetty, the animals appeared moribund. However, *Asterias* predation on *Mytilus* appeared to be quite heavy subtidally and is probably the cause of an abrupt lower boundary to the *Mytilus* distribution on the ocean jetty. Menge's (1976) observation that *Asterias* predation produces a sharp subtidal boundary to the *Mytilus* distribution on the rocks of the New England coast supports this suggestion.

Although *Asterias* was rarely found on exposed intertidal surfaces at Ernst dock, the starfish do forage upwards into the intertidal zone at high tide. During periods when tides never fall to low levels, these starfish appear to remain in the low intertidal for long periods of time. Such periods often last for weeks at the bay site when wind-driven tides have dominated the tidal flux and produced a long period for essentially uninterrupted feeding by basically subtidal predators. On the ocean jetty where tides follow a more predictable lunar pattern, *Asterias* and other subtidal predators do not have this opportunity to nearly the same degree.

Despite these periods when *Asterias* can and does prey intertidally on the

bay pilings, I have not included it in Fig. 2. Starfish are far more abundant subtidally and even when they appear in the intertidal they are greatly outnumbered by *Neopanope* and *Urosalpinx*. At Ernst dock, *Asterias* could be found preying primarily upon *Mytilus edulis* but also upon *Balanus eburneus*. In the aquarium, *Asterias* consumed both of these species, as well as *Ilyanassa obsoleta*. *Asterias* would not consume in the aquarium any other species from this community. The *Asterias forbesi* in the New England rocky intertidal appear to have their most significant impact on *Mytilus edulis* populations (Menge, 1976).

### *Spatial and Temporal Variability*

Although Table 1 reveals the patterns of utilization of primary space and the predator densities on only one occasion, most features of and differences between these two systems persisted from at least April–October of each year. Table 2 presents data on the utilization of primary space on several marked, permanent transects at both study sites. On seven occasions from June 1973 to October 1974, the permanent transects at each site were photographed and the slides later analyzed to produce estimates of percent cover for each species.

Coverage data in Table 2 reveal some distinct seasonal patterns. For instance, *Porphyra* and the midge larvae do not appear in the high intertidal of the ocean jetty until late summer or fall. At Ernst dock, *Schizoporella*, *Hydroides*, and *Bugula* also become much more abundant by late summer. At each study site both barnacle species tend to show declining abundance from early summer to fall. Despite these seasonal changes, certain patterns in space utilization of the mid-low intertidal zone persist. Specifically, *Mytilus edulis* dominates primary space in the mid-low intertidal of the north jetty, usually covering 80% or more of the primary space, while the Ernst dock has no consistent dominant. Also the large difference between sites in available free space is a consistent and significant feature. The difference between sites in the species richness of the mid-low intertidal appears to be largely dependent upon season: the late summer additions to the bay piling community increase its species richness, while the species richness of the mid-low intertidal of the ocean jetty does not increase and may even decline through the loss of one or both *Balanus* species (Table 2). The high intertidal is largely a barnacle-alga zone at Ernst dock, while at the ocean jetty mussels appear also. Both sites show an anomalously large amount of free space in the high intertidal.

Predators remained more abundant in the intertidal zones at Ernst dock than at the inlet jetty. Abundances were estimated by use of quadrats on three occasions, October 1972 (Table 1), June 1973, and July 1974. On no occasion was a living predator found in the quadrats placed in the intertidal zone of the ocean jetty. The relatively high predator density found at Ernst dock in October 1972 was confirmed by the subsequent counts. In June 1973, predator densities averaged over the entire intertidal zone were 25.7/m<sup>2</sup> for *Urosalpinx*, 4.1/m<sup>2</sup> for *Neopanope*, 0.5/m<sup>2</sup> for *Asterias*, and 0.2/m<sup>2</sup> for *Callinectes*. In July 1974, the respective predator densities were 16.3, 2.1, 0.4, and 0.0 per m<sup>2</sup> of intertidal surface.

**Table 2.** Average percent utilization of primary space taken mostly from permanent transects located in the high and mid-low intertidal zones of the Ernst dock and north jetty at Barnegat Inlet, June 1973–October 1974. One standard error is given in parentheses

Date	North Jetty (Ocean)						
	6/14/73	8/15/73	9/11/73	10/13/73	5/21/74	7/19/74	10/1/74
No. of samples	10	10	9	8	16	6	10
a) High intertidal zone							
Free space	42.0(4.2)	22.5(2.8)	32.2(2.8)	29.4(4.2)	15.0(2.8)	21.3(2.6)	23.5(4.7)
<i>Mytilus edulis</i>	3.0(1.3)	27.5(5.8)	17.8(4.9)	13.1(3.4)	16.3(2.8)	18.8(1.0)	19.0(5.1)
<i>Balanus balanoides</i>	29.7(4.4)	29.2(2.9)	28.3(6.2)	25.1(5.3)	22.1(2.8)	21.8(4.3)	22.0(2.4)
<i>Balanus eburneus</i>	0.3(0.1)	0.0	0.0	0.5(0.3)	0.4(0.2)	0.7(0.4)	0.0
<i>Ulva-Enteromorpha</i> spp.	24.0(5.4)	20.8(2.5)	17.8(5.4)	13.1(4.2)	46.9(4.0)	37.5(2.0)	20.0(2.4)
<i>Porphyra</i> sp.	0.0	0.0	0.0	6.9(2.1)	0.0	0.0	3.5(2.4)
<i>Telmatogeton japonicus</i>	0.0	0.0	3.9(2.3)	11.9(4.7)	0.0	0.0	12.0(4.2)
b) Mid-low intertidal zone							
Free space	14.5(3.4)	2.0(1.1)	13.3(3.1)	8.8(1.2)	0.9(0.5)	0.8(0.8)	0.5(0.5)
<i>Mytilus edulis</i>	47.0(9.0)	85.0(5.2)	76.7(4.8)	83.8(2.4)	95.9(1.5)	95.0(1.8)	96.5(1.5)
<i>Balanus balanoides</i>	15.8(6.2)	2.5(2.0)	0.0	2.7(2.5)	1.5(0.9)	0.0	0.0
<i>Balanus eburneus</i>	1.2(0.7)	0.0	0.0	0.4(0.2)	0.1(0.1)	0.0	0.0
<i>Ulva-Enteromorpha</i> spp.	20.5(4.1)	10.5(4.1)	10.0(2.6)	4.4(1.1)	1.6(0.8)	4.2(1.6)	3.0(1.3)
Date	Ernst Dock (Bay)						
	6/15/73	8/13/73	9/8/73	10/7/73	5/17/74	7/14/74	10/2/74
No. of samples	6	6	6	6	5	5	5
c) High intertidal zone							
Free space	72.5(5.7)	67.2(6.0)	91.2(2.6)	87.4(2.9)	68.7(2.9)	81.9(3.8)	83.1(3.2)
<i>Mytilus edulis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Balanus balanoides</i>	8.3(3.0)	1.5(0.7)	0.4(0.4)	0.1(0.1)	4.7(1.1)	2.3(0.6)	0.1(0.0)
<i>Balanus eburneus</i>	8.8(4.8)	1.5(0.7)	0.3(0.2)	0.0	16.1(3.6)	3.4(2.2)	2.2(0.5)
<i>Ulva-Enteromorpha</i> spp.	10.0(3.4)	27.7(4.7)	7.8(2.7)	12.3(2.8)	10.7(1.6)	11.9(3.6)	14.4(3.4)
d) Mid-low intertidal zone							
Free space	41.0(4.5)	45.9(9.3)	77.4(2.2)	67.7(4.2)	36.5(5.1)	41.9(6.6)	65.2(3.8)
<i>Mytilus edulis</i>	0.6(0.5)	1.5(1.4)	1.1(0.5)	0.8(0.5)	3.8(1.2)	9.9(2.5)	1.8(0.8)
<i>Balanus balanoides</i>	12.5(3.0)	2.6(0.5)	0.6(0.3)	2.3(0.9)	19.3(5.9)	15.1(8.3)	4.1(1.7)
<i>Balanus eburneus</i>	17.9(6.4)	3.9(1.1)	3.2(1.4)	0.6(0.2)	21.0(4.7)	3.4(1.3)	2.7(0.8)
<i>Ulva-Enteromorpha</i> spp.	27.9(9.4)	45.5(9.6)	17.7(2.4)	18.2(5.0)	19.5(5.8)	30.0(4.5)	17.6(6.3)
<i>Haliplanelle luciae</i>	0.0	0.1(0.1)	0.0	0.0	0.0	0.0	0.2(0.1)
<i>Schizoporella unicornis</i>	0.0	0.0	0.0	0.9(0.6)	0.0	0.0	2.7(1.1)
<i>Hydroides dianthus</i>	0.0	0.1(0.0)	0.2(0.2)	1.7(0.6)	0.0	0.0	1.5(0.6)
<i>Bugula</i> sp.	0.0	0.0	0.0	6.9(3.8)	0.0	0.0	4.1(2.8)

Some degree of both temporal and spatial variability in community composition can be observed in all natural systems even in apparently homogeneous habitats (e.g. Levin and Paine, 1974). Understanding the causes of such variability has been difficult and remains a major current goal in community ecology. Because I was working in two systems which appeared to differ substantially in their organization, I chose to measure both temporal and spatial heterogeneity in community composition to see whether any differences existed between these systems. Such differences, if consistent, may help to explain both how spatial and temporal patchiness is generated in natural systems and what forces tend to reduce it.

To estimate the spatial integrity and temporal persistence of each system, I used an index of percent similarity ( $I$ ), as proposed by Whittaker (1960) and subsequently used by several workers:

$$I = 100 \times (1.0 - 0.5 \sum_{i=1}^S |A_i - B_i|),$$

where  $I$  equals the percent similarity between two samples,  $A_i$  equals the relative abundance of species  $i$  in sample  $A$ ,  $B_i$  its relative abundance in sample  $B$ , and there are  $S$  total species. To calculate the spatial integrity in community structure, I computed the average percent similarity between all possible pairs of replicate samples at each sampling date. Free space was treated as a species category in this analysis, so as to give emphasis to similarity in absolute cover values rather than relative abundance. The average similarity values appear in Table 3.

In general, the Ernst dock possesses a high intertidal community with significantly greater spatial integrity (lower spatial variability in community structure) than the ocean jetty. Five of seven comparisons are significant. However, the mid-low intertidal community of the north ocean jetty reveals generally higher spatial integrity than its piling counterpart. Five of the seven comparisons reveal significantly higher values at the jetty site, while on one occasion the piling community had a significantly higher value. Like most similarity indices, this one is particularly sensitive to changes in the abundances of the most abundant species. Nevertheless, these calculations suggest that there is less spatial heterogeneity in the mid-low intertidal of the ocean jetty and in the high intertidal of the Ernst dock.

The high similarity among replicate samples in the mid-low intertidal of the ocean jetty is a result of the low variance in the abundance of *Mytilus*, the spatial dominant. A high correlation between the percent cover by *Mytilus* and the average similarity among samples in the mid-low intertidal of the jetty system ( $r=0.97$ ,  $n=7$ ,  $p<0.001$ ) demonstrates the significance of *Mytilus* to this overall community pattern. Even independent of site, percent mussel cover explains a large proportion of the variance in average spatial similarity in the mid-low intertidal ( $r=0.64$ ,  $n=14$ ,  $p<0.05$ ). The higher similarity values in the high intertidal of the Ernst dock are likewise a partial result of the relatively low variance in percent free space, which is the dominant category at that site ( $r=0.71$ ,  $n=14$ ,  $p<0.01$ ).

The percent similarity index ( $I$ ) was also used to determine the temporal

**Table 3.** Spatial integrity in community structure, as measured by the average percent similarity ( $\bar{I}$ ) between all possible pairs of replicate samples on each sampling date ( $\pm 1$  S.E.). See text for an explanation of the similarity index

	Sampling Dates						
<i>North jetty</i>	6/14/73	8/15/73	9/11/73	10/13/73	5/21/74	7/19/74	10/1/74
High intertidal zone	71.6 $\pm 2.2$	74.7 $\pm 1.9$	64.3 $\pm 1.8$	61.4 $\pm 2.6$	72.7 $\pm 1.3$	85.8 $\pm 1.7$	63.0 $\pm 2.0$
Mid-low intertidal zone	56.7 $\pm 2.7$	79.8* $\pm 2.0$	81.5 $\pm 1.7$	89.5** $\pm 1.3$	93.5** $\pm 0.6$	94.3** $\pm 0.8$	94.8** $\pm 0.7$
<i>Ernst dock</i>	6/15/73	8/13/73	9/8/73	10/7/73	5/17/74	7/14/74	10/2/74
High intertidal zone	76.7 $\pm 3.3$	83.2* $\pm 3.8$	84.3** $\pm 2.5$	91.3** $\pm 1.5$	87.0** $\pm 2.0$	86.6 $\pm 1.8$	85.0** $\pm 2.1$
Mid-low intertidal zone	66.3 $\pm 4.3$	67.3 $\pm 4.5$	90.5** $\pm 1.0$	76.0 $\pm 2.7$	72.7 $\pm 4.0$	68.9 $\pm 4.7$	71.1 $\pm 4.3$

\* mean similarity is significantly greater than corresponding value for that tidal height at the other site ( $p < 0.05$  on two-tailed  $t$ -test)

\*\* as above except  $p < 0.01$

**Table 4.** Temporal persistence in community structure, as measured by the average percent similarity ( $\bar{I}$ ) between all possible pairs of sampling dates ( $\pm 1$  S.E.). See text for an explanation of the similarity index

	$\bar{I}$ over four summer months 1973	$\bar{I}$ over three summer months 1974	$\bar{I}$ over three Octobers 1972-3-4
<i>North jetty</i>			
High intertidal zone	79 $\pm$ 3	82 $\pm$ 5	80 $\pm$ 4
Mid-low intertidal zone	78 $\pm$ 6	98 $\pm$ 0.4**	91 $\pm$ 2
<i>Ernst dock</i>			
High intertidal zone	82 $\pm$ 3	88 $\pm$ 4	85 $\pm$ 5
Mid-low intertidal zone	71 $\pm$ 4	70 $\pm$ 5	81 $\pm$ 6

\*\* difference between this figure and the corresponding mean for that tidal height at the other site is highly significant ( $p < 0.01$  on two-tailed  $t$ -test).

persistence of the community structure at each site. Three separate comparisons were drawn: 1) the average similarity between all dates in summer 1973, 2) the average similarity between all dates in summer 1974, and 3) the average similarity between the three October samplings (1972-3-4). Table 4 presents these mean similarity values. Again the ocean jetty possesses a mid-low intertidal community with greater temporal persistence than that of the Ernst dock: all three averages are consistently higher at the jetty site, although only one of the three is statistically significant. The average temporal similarity of the high

intertidal system is consistently greater at the Ernst dock site, but these differences are smaller and all are non-significant.

Predation is a major cause of the relatively high temporal variability in community composition in the mid-low intertidal at Ernst dock. Each year barnacle densities declined greatly during the summer, while partly as a consequence more free space became available (Table 2). Much of this added free space was in the form of empty tests of dead barnacles. This barnacle mortality occurred in the presence of large populations of *Urosalpinx* and was prevented by caging off these predators in an experiment described below. Predation also appears to cause the decline in mussel cover throughout the summer at Ernst dock and thereby adds to the temporal heterogeneity.

### **Manipulative Experiments on Barnegat Inlet's North Jetty**

#### *The Lower Limit of *Balanus**

The distinct zonation incorporating a sharp boundary between the *Balanus balanoides* distribution in the high intertidal and the *Mytilus edulis* distribution in the mid-low intertidal zone of the jetty suggests that competition may well be involved in determining some aspects of this pattern. Little free space is available and mussels show tremendous spatial dominance in this mid-low zone (Tables 1, 2). In addition, when clumps of mussels are pried from the rocks in the mid intertidal of the north jetty, the tests of dead *Balanus balanoides* can be found covering a large fraction of the area. For instance, on 1 October 1974 I removed mussels from 10 approximately 1 m<sup>2</sup> patches from near the top margin of the *Mytilus* distribution and discovered an average of 27% (S.E. = 4.7) of the area covered by dead *Balanus*.

Since *Mytilus* can and perhaps preferentially does attach its byssus to living barnacles, it seemed a reasonable hypothesis that the typically dense sheets of blue mussels smother any underlying barnacles and that this intense competition for space is responsible for preventing *Balanus* from maintaining high densities on the primary space of the mid and low intertidal zones of the ocean jetty. To test this hypothesis, I examined the fate of barnacles on two mid intertidal rocks, one where *Mytilus* was allowed to settle and one kept free of mussels.

For this experiment I chose two adjacent ~3 m<sup>3</sup> boulders, located in the mid intertidal zone and containing unusually few mussels and unusually large barnacle populations. From one of these rocks I removed all mussels on 8 May 1973 by pulling them away from the substrate until their byssal connections were severed. From 8 May–12 October 1973, I kept that one boulder free of mussels by removing all new mussel recruits on repeated visits at one month intervals. Natural settlement and growth of mussels and all other species were permitted to proceed on the adjacent control rock.

By 12 October 1973 *Mytilus* cover had increased greatly on the control rock, forming a nearly continuous sheet of animals over about two-thirds of

the rocks's surface (Table 5). On 12 October 1973, all these *Mytilus* were carefully removed in order to determine the fate of those barnacles that had been overgrown. A complete count revealed that over 80% of the barnacles that still remained attached to the rock were dead. In contrast, *Balanus* cover doubled on the removal rock and only about 4% were found dead at the end of the experiment (Table 5). Although this experiment was not replicated, the results suggest that competition from *Mytilus edulis* determines the lower limit to the *Balanus balanoides* distribution both by growing over and smothering any already settled barnacles and also by occupying primary space which then becomes unavailable for recruitment by *Balanus* or any other species. Although barnacles can settle on the shells of mussels, they seldom are found occupying this type of secondary space on the north jetty of Barnegat Inlet, perhaps because the mussels never grow old and large, but also because *Mytilus edulis* has the ability to polish its shell with its long foot and thereby prevent fouling. While increased predation on barnacles under the protection of a mussel cover by such predators as small gastropods, nemerteans, or flatworms might also explain these results, no such predators were ever observed in this system, even after prying off overlying mussel cover.

### *The Upper Limit of Mytilus*

The high intertidal zone of the ocean jetty is largely a *Balanus balanoides* zone (Tables 1, 2). *Mytilus* is also abundant in this zone, but the mussels there are found almost exclusively in crevices and under rock overhangs. Even in those places where the mussel distribution does extend upward into the high intertidal zone, a zone of barnacles can be found higher up on the intertidal surfaces above the mussels. This distribution pattern suggests that *Mytilus* may well be limited in its upward distribution by the more harsh physical conditions of the high intertidal zone. Such a physical limitation may be imposed upon the larvae at the time of settlement or, because *Mytilus* can move and reattach its byssus, it may operate later to prevent upward migration of larger mussels.

To test the hypothesis that the upper limit of the *Mytilus* distribution is set by physical conditions and to help to determine whether these factors operate upon the larvae or upon older mussels, I transplanted several older *Mytilus* to the high intertidal and compared their survival to controls placed in the mid intertidal zone. I initially removed four clumps of mussels from low intertidal rocks. Each clump was closely inspected to remove all dead shells and to cull it down to a size of about 200 living animals. I then used burlap bags and stainless steel wire to tie the clumps onto a piling in the midst of the rock jetty. Two clumps were placed in the middle of the high intertidal zone, while the other two were secured, as controls, in the mid intertidal zone. These clumps remained attached to the piling from 14 May–14 July 1974, when the experiment was terminated and survivorship of all mussels was determined.

Over these two months survivorship of mussels in the mid intertidal was high: picking apart these control mussel clumps revealed 5 dead and 173 alive in one clump and 0 dead, 187 alive in the other. In contrast, all *Mytilus* transplanted



**Table 5.** Survival of *Balanus balanoides* on two mid intertidal rocks from 8 May–12 October 1973. *Mytilus* was allowed to recruit and grow naturally on one rock (control) while on the other rock all *Mytilus* were continually removed. The standard error of the estimates of percentage cover is approximately  $\pm 3\%$ . Final *Balanus* cover was measured after removing all *Mytilus* and includes both live and dead *Balanus*

	% <i>Mytilus</i> cover		% <i>Balanus</i> cover		Final ratio of dead/live <i>Balanus</i>
	Initial	Final	Initial	Final	
Removal Rock	41	0	19	38	18/483
Control Rock	34	67	27	23	248/44

to the high intertidal died: 218 gaping, dead animals in one clump and 194 in the other replicate.

The two most likely causes of the observed mussel mortality in the high intertidal are starvation due to insufficient time for feeding and over-heating and desiccation resulting from long exposures in the sun and in the warm winds. The summer months are characterized by high air temperatures with many days on which the maximum exceeds  $33^{\circ}\text{C}$ . Winds tend to be strong from the south and the summer days tend to be clear and sunny. In addition, shading from the burlap bags, used initially to secure the mussel clumps, was probably only significant during the first 30 days of the experiment, because after that time the bags were torn and shredded. *Mytilus* attachment persisted only because all the animals had reattached their own byssus to the piling.

I suspect that desiccation is the more likely of the two possible causes of high intertidal *Mytilus* mortality in this experiment. Those mussels which are found naturally in the high intertidal rock crevices are frequently wetted by wave surge even at low tides. During these brief inundations, the mussels do not appear to open their shells and to feed. However, they are certainly cooled by this wetting process more often than are animals that live on the open rock faces where wave surge has no effect during low tides. I also suspect that the adult mortality illustrated in this experiment is the process that produces the upper limit to the *Mytilus* distribution, at least during the warm months of the year. I choose not to seek an explanation in larval behavior and mortality patterns because *Mytilus edulis* can and does, well after settlement, move by breaking its byssal attachment and reestablishing it in a new site (Harger, 1972). In addition, this experiment confirmed that the adults themselves are incapable of surviving at higher levels on the shoreline.

### Experimental Removal of Predators at Ernst Dock

The abundance patterns in the mid and low intertidal zones of the Ernst dock, where neither *Mytilus* nor any other species consistently monopolized the primary space and where much free space was generally available (Tables 1, 2), suggest that some factor was operating to prevent *Mytilus* from dominating

this community in the same fashion as on the ocean jetty. Since predators, chiefly *Urosalpinx*, *Callinectes*, and *Neopanope*, were always much more abundant in the bay piling system, which is protected from all wave action, I proposed the hypothesis that higher rates of predation are responsible for the generally low epifaunal densities and for the failure of *Mytilus edulis* to monopolize mid and low intertidal space at Ernst dock.

To test this hypothesis, I used cages to exclude predators from several replicate pilings, while the predators retained free access to control pilings. The cages were cylindrical, made from sections of 6 mm ( $\frac{1}{4}$  inch) mesh hardware cloth and sewn together with stainless steel wire while in the field. Sections of four randomly chosen pilings were completely enclosed from about 10 cm below mean low water to the top of the intertidal zone. All predators, herbivores, and scavengers were removed from these pilings at the start of this experiment. These cages were periodically disassembled to remove any newly-recruited, juvenile predators.

Three types of controls were used in this predator exclusion experiment. Two replicate pilings were left untouched, as one sort of control. Around each of two other pilings, cage controls were constructed, consisting of a normal cage but lacking a bottom. Such a cage control permitted free access by predators and thus served to test for the effects of the cage itself. A third type of control, also built around two replicate pilings, comprised a full cage which included the usual complement of predators (except that no blue crabs were included) at a density equal to the average intertidal density found on the pilings in May–June 1973. Even though such inclusions of predators can produce unnatural, biased estimates of predation rates in part because the predators cannot emigrate when preferred prey are depleted, I present their results because they do not differ significantly from the other controls. Furthermore, escape into subtidal portions of the cage was possible for those predators which normally migrate vertically.

All caging material was cleaned by a scrub brush every 2–4 weeks from 2 June 1973, when their construction was completed, until 7 October 1973. In April 1974 the cages were revisited and again cleaned, although they did not become fouled over winter. From April 1974 until 14 July 1974 cleaning occurred at 2–4 week intervals. The intertidal piling surfaces under all exclusion cages and of all controls were photographed with high-speed Ektachrome using 8 overlapping shots on several occasions from 2 June 1973–14 July 1974. Community composition was estimated from the color slides by the random dot technique.

#### *Utilization of Primary Space in the Absence of Predation*

Table 6 gives the densities of mussels and barnacles (both *Balanus* species pooled) as well as the amount of free space available on experimental pilings and on control pilings at the beginning of this experiment and then at three subsequent dates. In the high intertidal, exclusion of predators had very little effect. Only

at the end of the experiment after  $13\frac{1}{2}$  months free from predation did a statistically significant difference appear between experimental and control pilings. Control pilings had significantly more free space (rank-order  $p=0.005$ ), but even then the difference was not great, 71% versus 47%. By this time mussel coverage and barnacle coverage in the high intertidal were only slightly higher on the exclusion pilings and neither of the differences was statistically significant.

In contrast, exclusion of predators caused major changes in the composition of the mid-low intertidal community (Table 6). The difference in amount of available free space between control and exclusion pilings was significant (rank-order  $p=0.014$ ) after 4 months and after  $13\frac{1}{2}$  months had increased even further. Specifically, in July 1974 control pilings contained an average of 43% free space in the mid-low intertidal zone, while exclusion pilings held only 6% free space (rank-order  $p=0.005$ ). Changes in both mussel and barnacle populations contributed to the differences between control and experimental pilings. In the absence of predation, barnacle populations failed to exhibit their typical summer decline, so that by 7 October 1973 barnacle cover averaged 22% on exclusion pilings, indistinguishable from the 20% level exhibited in June 1973. Over that same period barnacle cover on the control pilings dropped from 20 to 3%. Mussel cover increased over the summer on the exclusion pilings, while it declined on controls so that by 7 October 1973 the average mussel cover was 12% on pilings free from predation and 0% on controls.

After  $13\frac{1}{2}$  months the mussel cover on pilings free from predation had increased further to an average of 67% of the mid-low intertidal space, while average mussel cover on controls remained quite low at 5% (rank-order  $p=0.005$ ). However, by the same date there was no longer any difference in average barnacle cover between control pilings and the fully-caged pilings (Table 6). Mussels were found occupying space that in the summer of 1973 had been previously occupied by barnacles. This suggests that in the absence of predation both barnacles and mussels could increase relative to control levels until so little free space remained available (6%) that competition for space became a significant factor. At that point the mussels again began to exclude barnacles on the Ernst dock as they appear to do regularly on the ocean jetty. Although increased predation on barnacles from nemerteans or flatworms could provide a competing explanation for these results, no such predators were ever observed in this system.

The effect of *Mytilus* on the other species of the epifaunal community can be seen by examining how many epifaunal occupiers of primary space coexist with *Mytilus* on the experimental pilings compared to the species richness on control pilings where *Mytilus* is always rare or absent. The average number of epifaunal species (excluding *Mytilus*) occupying primary space on control pilings more than doubled from 2.0 (S.E.=0.0) in June to 4.3 (S.E.=0.4) in October 1973. On those pilings from which predators had been excluded, the increase was only 25%. In July 1974, control pilings again held more species (3.0, S.E.=0.4) than experimental pilings (2.0, S.E.=0.0). The difference between the average number of species present on experimental (with high *Mytilus* density) pilings was significant in both October 1973 ( $p<0.01$ ) and July 1974

**Table 6.** Effects of experimental exclusion of predators by caging four replicate pilings on the Ernst dock. Controls were of three types: two uncaged pilings, two cages which included predators, and two partial cages (cage controls). The experiment was initiated on 2 June 1973. Values given are means of the replicates

	Date			
	6/2/73	8/13/73	10/7/73	7/14/74
<i>High intertidal zone</i>				
a) % free space				
Predator exclusions	83	52	80	47**
Uncaged controls	77	52	91	84
Cage controls	72	24	63	70
Predator inclusions	77	26	80	60
	75	34	78	71
b) % mussel cover				
Predator exclusions	0	0	0	11
Uncaged controls	0	0	0	0
Cage controls	0	0	0	0
Predator inclusions	0	0	0	0
c) % barnacle cover				
Predator exclusions	4	2	2	7
Uncaged controls	4	7	0	3
Cage controls	6	3	0	1
Predator inclusions	8	4	2	1
	6	4	1	2
<i>Mid-low intertidal zone</i>				
d) % free space				
Predator exclusions	36	20	48*	6**
Uncaged controls	32	21	63	33
Cage controls	28	21	90	47
Predator inclusions	45	13	85	48
	35	18	79	43
e) % mussel cover				
Predator exclusions	0	8	12*	67**
Uncaged controls	3	0	0	7
Cage controls	0	0	0	8
Predator inclusions	0	0	0	1
	1	0	0	5
f) % barnacle cover				
Predator exclusions	20	17*	22*	15
Uncaged controls	36	7	5	30
Cage controls	14	3	1	6
Predator inclusions	10	4	2	9
	20	5	3	15

\*  $p < 0.05$  by rank-order probability  
\*\*  $p < 0.01$  by rank-order probability

( $p < 0.05$ ). Thus, there appears to be a reduction in species richness that occurs as space is monopolized by *Mytilus edulis* in the system. The absolute difference in species richness is not great, largely because the faunal richness of this area is not great. However, these experimental results help to explain the difference in species richness between the mid-low intertidal of the ocean jetty, where

mussels monopolize primary space, and the bay pilings, where mussels are generally scarce.

On 14 July 1974, the exclusion experiment was terminated and cages were removed from three of the four exclusion pilings. After 13 days every mussel had disappeared from the pilings except for those inside the one remaining cage, where mussel density was not significantly altered. The cause of the disappearance was almost certainly predation by blue crabs. Piles of broken *Mytilus* valves could be seen at the base of all three pilings which had previously been caged. Several blue crabs were moving among the mussel debris feeding upon small clumps of unattached mussels. This experiment suggests that *Callinectes* are of major importance in structuring the bay piling community.

## Discussion

The major organizing forces in these New Jersey epifaunal communities seem to be competition for primary space at wave-beaten areas (such as on the north ocean jetty) and predation at protected sites (as on the dock pilings at the western end of Barnegat Inlet). In wave-beaten areas, predators are few, perhaps excluded by the violent wave action. Consequently, *Mytilus edulis*, the apparent competitive dominant, is able to realize its potential by monopolizing space in the mid and low intertidal zones. Such monopolization produces both a temporally persistent community and spatially homogeneous one. Only in the possible refuge of open rock faces in the high intertidal, where *Mytilus* is evidently incapable of surviving, do any barnacles persist in appreciable numbers. Even in this refuge, however, barnacle densities are paradoxically low. In contrast to the wave-beaten jetty, predator densities are high in protected areas like Ernst dock, where predation mainly by *Callinectes* and *Neopanope* prevents *Mytilus* from monopolizing space in the mid and low intertidal zones. Thus, predation on the competitive dominant serves to reduce the intensity of competition and to maintain a community of several abundant species. Consequently, predation can be considered the major organizing feature of the mid and low intertidal zones at protected sites. Such predation induces spatial patchiness in the community and also, by freeing space for different abundant larvae at different times, produces temporal variety in community structure. The high intertidal of protected sites is largely a *Balanus* zone. Interactions between the two common *Balanus* species may be important in the high intertidal community dynamics, but no such interactions were observed during this study, probably because barnacle densities remained low. Predation from *Urosalpinx* helps to explain the low barnacle densities in protected sites, but as in wave-beaten areas other unknown factors also seem to play a role.

Consequently, the Barnegat Inlet epifaunal communities of the mid-low intertidal zone appear to be organized in ways that are adequately described by the well-established paradigms of rocky intertidal community organization. The community is apparently simplified by intense competition for space unless a disturbance, such as predation, prevents the monopolization of space by the competitive dominant and thereby maintains diversity within the system.

Furthermore, the two most abundant species at the wave-beaten site, *Mytilus edulis* and *Balanus balanoides*, each tend to be limited in their upward distribution by physical factors and in the downward direction by biological factors, as predicted by Connell's (1972, 1975) inductive models. Nevertheless, I, like most of my predecessors (Paine, 1966, 1971, 1974; Dayton, 1971; Menge, 1976), fail to establish the exact mechanism by which the competitively dominant mussels outcompete the underlying barnacles. In addition, like the others, I fail to test whether the barnacles successfully reproduce in the high intertidal so as to demonstrate that this upper zone truly is a refuge from competition. These gaps in the paradigm remain unplugged.

Despite the substantial agreement between the predictions of the rocky intertidal paradigm and the data from the Barnegat Inlet system, these new data permit important elaboration of the rocky intertidal model. Specifically, they extend the general pattern into a new, more seasonally variable environment. Using the annual range in monthly mean water temperatures as a relative guide to the degree of seasonality, the Barnegat Inlet system with a range of about 2 to 25° C is substantially more seasonal than the Pacific northwest (about 7–11° C: Connell, 1970), the west coast of New Zealand (15–20° C: Paine, 1971), the coast of England and Scotland (7–13° C: Connell, 1961a), the northern coast of Japan (4–20° C: Hoshiai, 1965), and even the New England coastline (–1–14° C in Maine and 1–29° C in Massachusetts: Menge, 1976), where the previous studies have been carried out. Consequently, it appears that common mechanisms serve to organize marine epifaunal communities in quite different geographic areas. That these areas differ in the degree of environmental seasonality and possess different casts of competing space-occupiers and predators make the organizational similarities even more notable.

Only the fouling community studied by Sutherland (1974) and Sutherland and Karlson (1977) on ceramic tiles suspended from a dock at Beaufort, North Carolina exists in a more seasonal environment. However, the difference in seasonality between Barnegat Inlet and Beaufort is small. Mean monthly water temperature at Beaufort ranges from about 4–29° C (Sutherland and Karlson, 1977). As in other marine epifaunal systems, space appears to be limiting at Beaufort and, in the absence of urchin predation, competition is again an important determinant of community structure. However, the Beaufort system differs from the other epifaunal systems studied in that no single species appears to be the competitive dominant. Several species are capable of holding space for months at a time. One possible explanation for the Beaufort anomaly might be that a great degree of seasonality prevents the dense establishment and persistence of any long-lived competitive dominant. However, the data from Barnegat Inlet, where seasonality is very nearly as great, tend to refute this hypothesis.

Beaufort, like any other site south of Cape Hatteras lacks *Mytilus edulis*, the competitive dominant in Barnegat Inlet and in New England (Menge, 1976), probably because summer water temperatures limit the spread of *Mytilus* southward (Seed, 1976). In nearly all other marine epifaunal systems a mussel is simultaneously the competitive dominant and the preferred prey for the dominant predators: *Mytilus edulis* in Europe where it is prey for *Carcinus*, *Portunus*

and *Cancer* (Kitching and Ebling, 1967; Seed, 1969), in New England where it is prey for *Thais* and *Asterias* (Menge, 1976), in Barnegat Inlet where it is prey for *Callinectes*, *Neopanope*, and *Urosalpinx*; *Mytilus californianus* in the Pacific northwest where it is prey for *Pisaster* (Paine 1966, 1969) and *Thais* (Dayton, 1971); and *Perna canaliculus* in New Zealand where it is prey for *Stichaster* (Paine, 1971). That most of the data on which the rocky intertidal paradigm are based rely upon mussels playing a central role raises the suspicion that the paradigm is a type of taxonomic artifact such that the presence or absence of a mussel determines whether a given system will follow the predictions of the model. This would surely explain why the Barnegat Inlet and Beaufort systems are so different despite their similar degree of seasonality. However, that the rocky intertidal paradigm seems also to hold where various barnacle species and gastropod predators interact in the absence of mussels (Connell 1961a, b; 1970) suggests that the theory is robust to the loss of mussels from the system. Nevertheless, the issue of a taxonomic artifact requires further attention in light of Jackson's (1977) observations that epifaunal systems in cryptic tropical environments (which lack mussels) experience severe competition for space, yet retain high diversity and lack single competitive dominants.

In addition to extending the analysis of intertidal epifaunal systems into a highly seasonal environment, this study of Barnegat Inlet also provides data from a rather estuarine area that is protected from the wave action of the open coast. Such areas have commonly been studied along European coastlines in several locations at Lough Ine, Ireland (Ebling et al., 1964; Kitching and Ebling, 1967; Kitching et al., 1959), the coast of England (Seed, 1969), and other areas in northern Europe (Lewis, 1964), whereas in North America nearly all studies of intertidal epifaunal communities have been restricted to true oceanic coastlines. In these North American studies, mobile, "external" predators such as crabs and fishes assume no importance in the dynamics of the benthic communities (Paine, 1966, 1974; Dayton, 1971; Menge, 1972, 1976; Connell, 1970). This contrasts radically with the European work in quiet waters where crabs are common and significant predators. For example, in protected areas at Lough Ine (Kitching et al., 1959) crab predation, mainly by *Carcinus maenas* and *Portunus puber*, remove virtually all mussels from intertidal substrates. As in Barnegat Inlet, *Mytilus edulis* is abundant on the wave-exposed open coast of Lough Ine where crabs are absent. Since mobile predators such as crabs and other decapods seem quite likely to be readily eliminated from intertidal zones by wave action, this European pattern may actually prove to be an important one in North American systems also. Other recent experimental work on soft-substrate benthic communities (Young et al., 1976; Virnstein, 1977) has also demonstrated the importance of crabs and other unspecified mobile predators in estuarine and lagoonal sites along the east coast of North America. Perhaps, the benthic systems of highly protected areas will generally prove to differ from wave-exposed sites, where ecologically closed systems may be more prevalent, much in the fashion long suggested by European studies, but only now confirmed by North American examples.

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