Rocky Intertidal Zonation and Habitat Ecology of Gammaridean Amphipods in Long Island Sound

1997 Report

Submitted to the
Harry O. Haakonsen Research Fellowship

By

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Abstract

Rocky intertidal organisms are distributed in zones characterized by a few dominant species of animals and plants. Physical and biological factors have effects on such a pattern of abundance. In addition, food selection and habitat complexity play an important role in distribution and abundance of marine invertebrates. Few studies have been published on the zonation pattern of rocky intertidal amphipods. The results of this study will contribute significantly to the knowledge of the zonation pattern, habitat ecology, and seasonal patterns of amphipods in the rocky intertidal.

In this study, gammaridean amphipods were collected from two rocky intertidal sites in Long Island Sound: Rocky Neck State Park, East Lyme, Connecticut, and Outer Island in Stony Creek, Connecticut, during low tide in the *Fucus vesiculosus* and *Chondrus crispus* zones. The collections were made from August to October 1996 and April to June 1997. The species and abundance of amphipods found in *Fucus vesiculosus* and *Chondrus crispus* in the two study sites were compared. In addition, seasonal changes in species, abundance, and size of amphipods were documented. A laboratory experiment was also conducted to determine habitat selection by amphipods on submerged seaweeds.

A total of 9,773 amphipods of eight species were collected from the two study sites. Five species were found at Rocky Neck State Park while seven species were found at Outer Island. My study demonstrates that rocky intertidal amphipods of

southern New England occur in zones associated with species of seaweed. Physical and biological factors, food selection and habitat architecture may play important roles in the amphipod zonation patterns. In addition, seasonal changes have effects on species abundance and population biology of amphipods.

Very little is known about ecology of amphipods in the rocky intertidal zone in New England. Further investigation is needed to understand factors causing zonation, life history, and seasonal changes of amphipod species and abundance.

Acknowledgments

I would like to thank the Harry O. Haakonsen Research Fellowship for providing funding for this research.

I also would like to thank my advisor, Dr. Kim A. Wilson for her support, encouragement, and endless patience through this project. I thank Dr. Clayton A. Penniman and Dr. Barbara J. Nicholson for their useful comments and encouragement. I also would like to thank all faculty, staff, and graduate students in the department of Biological Sciences for their support. I am grateful to Adam J. Baldinger for the comments and the useful information on amphipods. I thank Captain Bob Milne for providing the ferry to the Outer Island. This work was also supported by Graduate Student Association thesis/research grant and CCSU Faculty/Student research grant.

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Introduction

On rocky shores, intertidal organisms are distributed in zones characterized by a few dominant species of animals and plants (Lewis, 1964). Based on schemes designed by Lewis (1964) and Stephenson and Stephenson (1972), the intertidal zone is divided into three major zones moving from the highest to the lowest elevation: the supralittoral fringe or littoral fringe, which is exposed to the air during low tide for the longest period, the eulittoral zone or midlittoral zone, and the sublittoral fringe or infralittoral fringe, which is only exposed to the air during extreme low water of spring tides. The eulittoral zone can be further subdivided into barnacle, brown algal, and red algal subzones. The brown algal subzone begins below the barnacles and covers most of the eulittoral zone. On wave exposed shores, *Fucus vesiculosus* tends to become dominant while *Ascophyllum nodosum* is more common on sheltered shores (Lewis, 1964). The red algal subzone, including *Chondrus crispus*, indicates the lowest part of the eulittoral zone. *Chondrus crispus* can also be found in the sublittoral fringe and subtidally.

Zonation patterns result from the interaction of physical and biological factors affecting the survival and growth of the organisms. Physical factors include desiccation, temperature, salinity, and wave action (Kennedy, 1976; Schonbeck and Norton, 1978). Schonbeck and Norton (1978) showed that desiccation and over-heating affected the zonation of littoral fucoids on a shore on the west coast of Scotland where there were five species of fucoid algae, each forming a well-marked zone. They found that the upper limits of the highest zone on the shore, dominated by *Pelvetia canaliculata*, *Fucus spiralis*, and *Ascophyllum nodosum*, suffered and died during the hot summer. The uppermost seaweeds of each species showed signs of tissue damage causing death after a period of drying conditions and high temperatures. None was damaged during cool weather in summer or winter.

Kennedy (1976) determined that temperature and desiccation affected zonation of three species of rocky shore mussels in southern New Zealand. The result indicated that the positions of the three mussel species on the shore were correlated with their respective tolerance to temperature and desiccation. Connell (1961) also demonstrated that the upper limit of the barnacle *Semibalanus balanoides* was set by desiccation.

Biotic factors, such as competition, grazing, and predation, greatly affect the pattern of zonation. Competition is an important factor in populations of marine littoral organisms (Branch, 1984; Olson and Lubchenco, 1990). The presence of one species can prevent colonization or growth of another species (Connell, 1961). Connell (1961) examined barnacle zonation on the west coast of Scotland and found a zone of *Chthamalus stellatus* high on the rocky shore and a zone of *Semibalanus balanoides* on the lower shore. He concluded that *C. stellatus* could settle below their main zone if *S. balanoides* was absent, but because of interspecific competition, *S. balanoides* normally outcompeted *C. stellatus* at the lower zone.

Preferences for individual algal species by grazers can also enhance the zonation in the rocky intertidal. Dixon (1978) showed that zonation of four species of intertidal limpets in southern California was determined by algal food source. Buschmann (1990) also concluded that different amphipod species feeding on different algal species induced vertical distribution on the rocky shore in central Chile.

Predators also play an important role in the distribution pattern and abundance of prey in the rocky intertidal zone (Paine, 1969; Paine *et al.*, 1985; Menge *et al.*, 1994). Paine *et al.* (1985) showed that predation by the starfish, *Pisaster ochraceus*, *Stichaster australis*, and *Heliaster helianthus* played a major role in development of community patterns. They concluded that removal of starfish from rocky shores in Washington State, New Zealand, and Chile lead to an increase in the abundance of the mussel, *Mytilus californianus*, and the goose barnacle, *Pollicipes polymerus*, in Washington State, the abundance of the green mussel, *Perna canalicula*, in New Zealand, and the abundance of the mussel, *Perumytilus purpuratus*, in Chile.

In addition, Navarrete and Menge (1996) demonstrated the importance of predation on mussels, *Mytilus trossulus*, by the keystone predator; the seastar *Pisaster ochraceus* and other predators such as the whelks *Nucella emarginata* and *Nucella canaliculata* under different environmental conditions in the Oregon intertidal zone. They concluded that *Pisaster* had effects on community patterns, such as increasing species diversity. Other predators played minor roles in the prey community.

Amphipods are generally small to medium-sized crustaceans (4-22 mm) characterized by a laterally compressed body, uniramous thoracic walking legs, sessile eyes, and lack of a carapace. About 5,500 species of Amphipoda have been identified of which nearly 85 percent are Gammaridean, nine percent Hyperiidean, six percent Caprellidean, and less than one percent Ingolfiellidean (Bousfield, 1973).

Gammaridean amphipods are generally considered primitive and are not highly specialized morphologically. They are free-living benthic animals living in fresh water, estuarine, and marine habitats, from high tide to the deepest ocean trenches, and from the tropics to the high arctic (Kaartvedt *et al.*, 1994; Jazdzewski *et al.*, 1995). Their ecological roles vary from deposit feeders and detritivores to benthic herbivores and free-swimming carnivores.

Gammaridean amphipods are important food sources for numerous animals and their annual production can be high enough to support populations of fish and other predators (Smith and Coull, 1987; DeBlois and Leggett, 1993a). They also may play a key role as a direct link between primary production and higher trophic level predators (Highsmith and Coyle, 1991; Lawson *et al.*, 1993).

Food selection of animals is influenced by food quality and environmental conditions, such as predation and competition (Raffaelli and Hawkins, 1996). Predation has an important influence on foraging and habitat utilization by foragers. Foragers tend to choose lower quality of food in order to avoid predators (Holomuzki and Short, 1988; Duffy and Hay, 1991). Duffy and Hay (1991) showed that the abundance of the marine amphipod, *Ampithoe longimana,* on five different species of seaweeds was more related to the algal preference of a fish predator than to feeding rates of the amphipods. *A. longimana* was more abundant on *Dictyota* and *Sargassum* which are unpalatable to fish, than on the palatable algae, *Hypnea*, *Chondria*, and *Calonitophyllum*.

Chemical defenses of seaweeds against different types of marine fish herbivores also play an important role in selection of seaweed by amphipods (Paul and Hay, 1986; Hay *et al.*, 1990). Hay *et al.* (1990) demonstrated that the amphipod *Pseudamphithoides incurvaria* builds and lives in a domicile that is constructed from the chemically defended brown alga *Dictyota bartayresii* which produced dictyol-class diterpenes which deter feeding by reef fishes. He also concluded that other brown algae in the family Dictyotaceae, that did not produce this deterrent, were avoided by the amphipods.

Vegetated aquatic habitats are recognized for their important biological, geological, and physico-chemical contributions to marine environments. Most amphipods live on seaweeds or other macrophytes. These habitats serve as sources of food, shelter, and refuge from predation (Leber, 1985). Macrophytes also play an important part as nursery habitat for many marine organisms (Herrnkind and Butler, 1986; Wilson *et al.*, 1990; Covi and Kneib, 1995). Vegetated habitat complexity, such as shape, structure, texture, and architecture affects distribution and abundance of motile marine invertebrates (Heck and Wetstone, 1977; Hicks, 1986; Hacker and Steneck, 1990; Edgar and Robertson, 1992). Edgar and Robertson (1992) demonstrated that the abundance of epifauna inhabiting the seagrasses *Amphibolis* *antarctica* and *Amphibolis griffithii* was changed when the seagrass was manipulated in three ways: the removal of epiphytes, the removal of leaves, and changing seagrass density. They concluded that epifauna tended to select dense seagrass habitats in order to avoid predation and excessive solar radiation. Hacker and Steneck (1990) also showed that different habitat architecture of benthic algae such as arrangement of habitat spaces and structures affected the habitat selection of *Gammarellus angulosus*. They reported significantly higher amphipod densities in branched and filamentous algae than algae with foliose and leathery macrophyte morphologies and that this may be due to differences in the spatial components of the algae.

The purpose of this study was to examine the distribution, habitat use, and seasonal abundance of gammaridean amphipods that live in the rocky intertidal zone in New England. Few studies have been published on the zonation pattern of rocky intertidal amphipods (Tararam *et al.*, 1986; Buschmann, 1990; Krapp-Schickel, 1993; Baldinger and Gable, 1995). The results of this study will contribute significantly to the knowledge of the zonation pattern, habitat ecology, and seasonal patterns of amphipods in the rocky intertidal. More specifically, the results will allow me to 1) compare the species and abundance of amphipods that live on *Fucus vesiculosus* and *Chondrus crispus*; 2) compare the amphipods and habitat characteristics collected from two different locations in Long Island Sound; 3) examine seasonal changes in the species, abundance, and sizes of amphipods that live in the two seaweeds. The results of this study confirm findings from other studies that organisms in the rocky intertidal occur in zones and are affected by several factors including habitat selection and seasonal changes that influence the abundance of amphipods in Long Island Sound. This study will also provide baseline information for further study of rocky intertidal amphipods.

Methods

Study Sites

Gammaridean amphipods were collected from two rocky intertidal sites in Long Island Sound: Rocky Neck State Park, East Lyme, Connecticut, and Outer Island in Stony Creek, Connecticut during low tide. Rocky Neck State Park is located near the Four Mile River which drains into Long Island Sound (Fig. 1). Outer Island is one island of the archipelago known as the Thimble Islands and is the farthest from the mainland shore of Stony Creek (Fig. 1).

Salinity of the water in both sites is approximately 25 parts per thousand (‰), and water temperature ranges from 0° C during the winter to 22° C during the summer (Costa, 1997; Kruse, 1997).

The sites are exposed to moderate wave action and are dominated by the brown alga, *Fucus vesiculosus,* and the red alga, *Chondrus crispus,* in the eulittoral zone. *F. vesiculosus* is in the higher part of the zone while *C. crispus* is in the lower part of the zone. The collection site at Rocky Neck State Park is steeper than at Outer Island.

There is a mix of other algae such as *Ulva lactuca*, *Codium fragile*, *Enteromorpha* spp., and *Porphyra* spp. in the eulittoral zone, but they are not as common as *F. vesiculosus* and *C. crispus* and do not form the dominant seaweed cover. Large benthic invertebrates found in this zone include amphipods, isopods, polychaetes, gastropods, barnacles, and crabs.

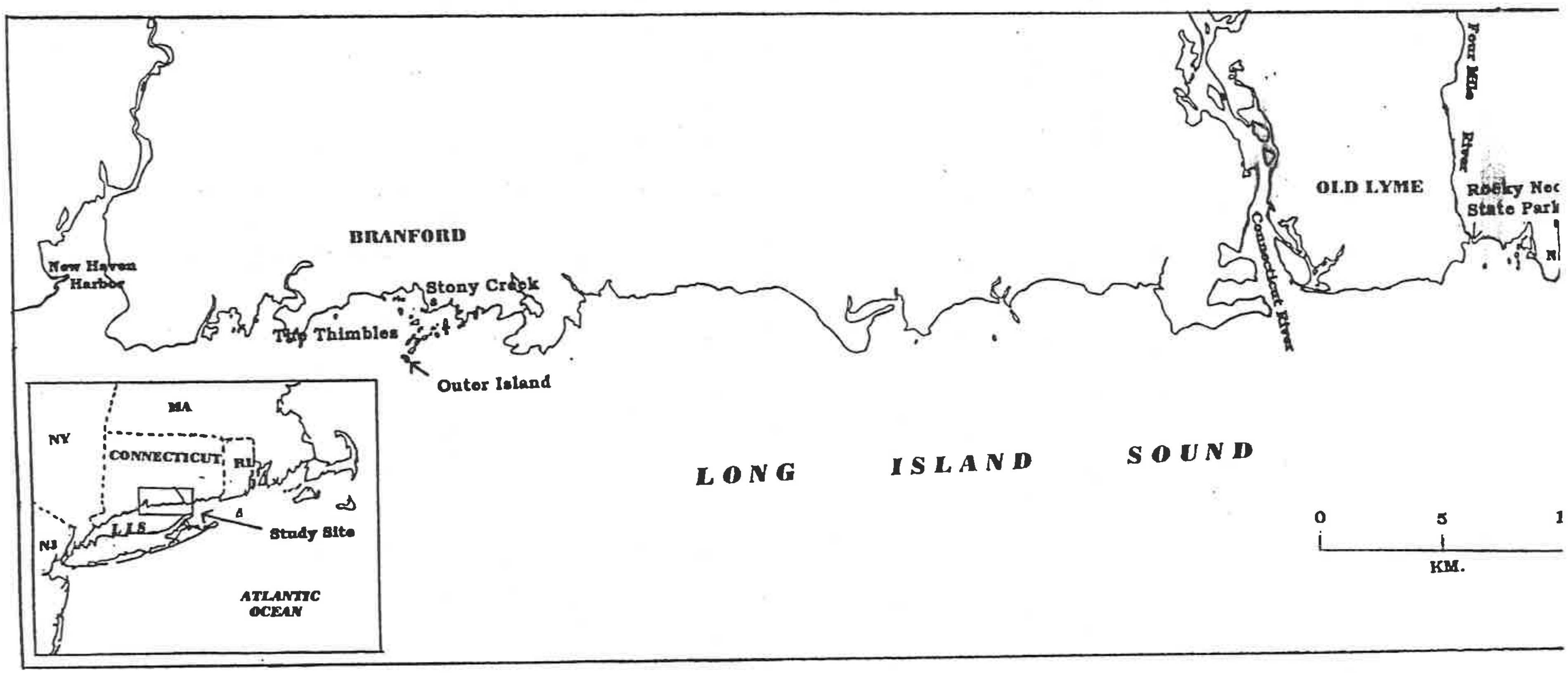

Figure 1. Sampling sites in Long Island Sound: Rocky Neck State Park, East Lyme, Connecticut and Outer Island, Stony Creek, Connecticut.

Sampling Methods and Schedule

Amphipod samples were collected by using a specially designed quadrat placed along a five-meter transect which was stretched parallel to the shore in the *Fucus vesiculosus* and *Chondrus crispus* zones. The distance between the two transects in each zone was not greater than 2.5 meters. The elevation from the mean low water level to a transect line on each *Fucus* and *Chondrus* zone was approximately 67 cm high and 24 cm high respectively. Samples were collected one meter apart along the transect of each zone. The quadrat (0.25x0.25 meters) was designed and constructed to prevent escape of crawling and jumping amphipods. The quadrat was surrounded by an eight-cm-high mesh. The mesh was held with monofilament fishing line to the quadrat frame. Five samples were taken from the *Fucus* zone and three from the *Chondrus* zone. Numbers of samples in the *Chondrus* zone were limited at each sampling period because of the short duration of low tide. The *Chondrus* zone is exposed to the air during a low tide for approximately three hours while the *Fucus* zone is exposed for greater than three hours. Collections were made on August 20, September 6, September 22, and September 27, 1996; April 4, May 2, and June 2, 1997 at Rocky Neck State Park and on August 22, October 11, October 25, 1996; April 5, May 3, and June 1, 1997 at Outer Island (Table 1).

Algae and trapped amphipods were removed from each quadrat and placed in labeled plastic bags. Amphipods that were not trapped with the algae were then picked out of the quadrat with forceps. In the laboratory, amphipods were removed from the algae, fixed in 75% ethanol, identified to species, and measured using a dissection microscope. Bousfield (1973) and Weiss (1995) were used to identify amphipods. Amphipods were measured from the first thoracic segment to the fifth thoracic segment. After measuring, they were divided into three size classes: small (0.1-1.00 mm), medium (1.01-2.00 mm), and large (>2.00 mm).

Table 1. Summary of sampling frequency and replicate number of quadrats taken on each sample date for the two habitats in two study sites.

	Sites			
	Rocky Neck State Park		**Outer Island**	
	Fucus vesiculosus	***Chondrus crispus***	***Fucus vesiculosus***	***Chondrus crispus***
1996				
August 20	5	3		
August 22			5	3
September 6	5	3		
September 22	5			
September 27		3		
October 11			5	3
October 25			5	3
1997				
April 4	5	3		
April 5			5	3
May 2	5	3		
May 3			5	3
June 1			5	3
June 2	5	3		

Laboratory Experiment

A laboratory experiment was conducted to determine habitat selection by amphipods while submerged. All experiments were conducted in 20-gallon glass aquaria (76x31 cm, 31 cm high). The experiments were run at room temperature (18-24 °C) and salinity of 25 °/₀₀.

Amphipods were collected in clumps of algae within a quadrat from each *Fucus* and *Chondrus* zone from the study sites and brought back to the laboratory. Collections were made following the field sampling on April 4, May 2, and June 2, 1997 at Rocky Neck and on April 5, May 3 and June 1, 1997 at Outer Island; except on April 16 at Rocky Neck State Park and April 19, 1997 at Outer Island, when collections were made separately. Samples of *Fucus* and *Chondrus* with the amphipods were held in a separate bucket with seawater and brought back to the laboratory. Two replicates were taken at each study site except on April 4 at Rocky Neck State Park and on April 5, 1997 at Outer Island, where one sample was taken.

In the laboratory, the experimental trials were run immediately after collecting the samples on each date. Amphipods that were not alive were removed from the algae. Clumps of *Fucus* and *Chondrus* were placed separately into each side of the aquarium. Plant anchors made of lead were used to keep the algae in place. The tanks were aerated with airstones. The aquaria were left undisturbed over night (approximately 18 hours; 12 hours dark and six hours with fluorescent lighting). At the end of the experimental trial, a divider was used to separate the two sides of the tank. Each species of algae was removed from the tanks, and live amphipods were removed from the algae, fixed in 75% ethanol and identified to species using a dissection microscope.

Statistical Analysis

Nonparametric statistical tests were used to test for differences between sites and seaweeds in number of species, total abundance, and species occurrence of amphipods. Nonparametric statistics are applied when the assumptions of homogeneous variance and normal distribution are not met (Zar, 1996). All statistical analyses were performed using SPSS-PC (Norusis, 1993). These included Mann-Whitney U test and one-way Kruskal Wallis ANOVA.

The Mann-Whitney U test was used to test for differences in number of species and total abundance of amphipods in the two seaweeds between Rocky Neck State Park and Outer Island. The data on August 20, 1996, April 4, May 2, and June 2, 1997 from Rocky Neck State Park and the data on August 22, 1996, April 5, May 3, and June 1, 1997 from Outer Island were used.

Differences in number of species and total abundance in *Fucus vesiculosus* and *Chondrus crispus* and between collection dates were tested on all data from Rocky Neck State Park and Outer Island. The two locations were tested separately. Mann-Whitney U tests were used to test for differences in number of species and total abundance of amphipods in the two seaweeds, and one-way Kruskal Wallis ANOVA were used to test ~~for differences in~~ number of species and total abundance of amphipods between the collection dates.

A Mann-Whitney U test was used to test for differences in habitat selection of amphipods in the laboratory. *Hyale nilssoni*, *Erichthonius difformis*, and *Gammarellus angulosus* were chosen to test for habitat selection because of their higher densities. The proportion of amphipods collected in *Fucus* in the field at low tide was compared with the proportion of amphipods selecting *Fucus* in the laboratory experiment. All data from laboratory experiment were used to compare with the data from the field on April 4, May 2, and June 2, 1997 from Rocky Neck State Park and April 5, May 3, and June 1, 1997 from Outer Island.

Results

A total of 9,773 amphipods of eight species were collected from the two study sites. Five species were found at Rocky Neck State Park while seven species were found at Outer Island. These species were *Hyale nilssoni, Ampithoe rubricata, Erichthonius difformis, Corophium insidiosum, Gammarellus angulosus, Calliopius laeviusculus, Ampithoe longimana,* and *Gammarus oceanicus* (Table 2). There was no significant difference between the two study sites in the number of amphipod species (Mann-Whitney U test, $P > 0.5$); however, there were significant differences between the two study sites in the total abundance of amphipods (Mann-Whitney U test, $P < 0.0005$) (Table 3). The zonation patterns of the species are summarized in Table 2 and are described below.

At Rocky Neck State Park there were significant differences between the two habitats, *Fucus vesiculosus* (upper zone) and *Chondrus crispus* (lower zone), in number of species (Mann-Whitney U test, $P = 0.0001$) and total abundance of amphipods (Mann-Whitney U test, $P < 0.0001$) (Table 4). *Hyale nilssoni* seemed to be the numerically dominant species (1539 individuals) in the upper zone, while in the lower zone, *E. difformis* was most common (5440 individuals) (Table 2). No *H. nilssoni* were found in the lower zone. Similar to *E. difformis*, *Co. insidiosum* also occurred in the upper zone (3 individuals), but the numbers of individuals were not as great as in the lower zone (71 individuals). *G. angulosus* (635 individuals) were found only in the lower zone. A small number of individuals of *A. rubricata* occurred in both upper and lower zones. No *Ca. laeviusculus, A. longimana,* or *G. oceanicus* were found at Rocky Neck State Park.

At Outer Island, the differences between *Fucus* and *Chondrus* in the number of species and the total abundance of amphipods were statistically significant (Mann-Whitney U test, $P < 0.001$ for both) (Table 5). *Hyale nilssoni* was the most abundant species in the upper zone (342 individuals) (Table 2). In the lower zone, the dominant species was *E. difformis* (730 individuals). However, a large number of *A. rubricata* (233 individuals) and *Co. insidiosum* (436 individuals) also were found in the lower zone. A high number of *A. rubricata* (105 individuals) also occurred in the upper zone. Similar to Rocky Neck State Park, no *H. nilssoni* were found in the lower zone. A small number of *Ca. laeviusculus, A. longimana,* and *G. oceanicus* occurred only in the lower zone. No *G. angulosus* was found at Outer Island.

Table 2. Total number of amphipods found in *Fucus vesiculosus* and *Chondrus crispus* at Rocky Neck State Park and Outer Island.

	Sites			
	Rocky Neck State Park		**Outer Island**	
	Fucus vesiculosus **(Upper Zone)**	***Chondrus crispus*** **(Lower Zone)**	***Fucus vesiculosus*** **(Upper Zone)**	***Chondrus crispus*** **(Lower Zone)**
Hyale nilssoni	1539		342	
Ampithoe rubricata	2	1	105	233
Erichthonius difformis	164	5440	33	730
Corophium insidiosum	3	71	10	436
Gammarellus angulosus		635		
Calliopius laeviusculus				7
Ampithoe longimana				4
Gammarus oceanicus				18
Total	1708	6147	490	1428

Table 3. Results of Mann-Whitney U test on effect of location on number of species and total abundance of amphipods for Rocky Neck State Park and Outer Island.

Test	Mean Rank		N	*P*
	Rocky Neck State Park	Outer Island	(Total)	
Number of Species	32.35	33.67	64	0.7677
Total Abundance	41.11	23.89	64	0.0002

Table 4. Results of Mann-Whitney U test on effect of habitat on number of species and total abundance of amphipods for *Fucus vesiculosus* and *Chondrus crispus* at Rocky Neck State Park.

Test	Mean Rank *Fucus vesiculosus*	Mean Rank *Chondrus crispus*	N (Total)	*P*
Number of Species	18.80	34.00	48	0.0001
Total Abundance	16.93	37.11	48	0.0000

Table 5. Results of Mann-Whitney U test on effect of habitat on number of species and total abundance of amphipods for *Fucus vesiculosus* and *Chondrus crispus* at Outer Island.

Test	Mean Rank *Fucus vesiculosus*	Mean Rank *Chondrus crispus*	N (Total)	*P*
Number of Species	17.27	36.56	48	0.0000
Total Abundance	19.18	33.36	48	0.0007

(104.7 individuals/quadrat), and *Co. insidiosum* (109.7 individuals/quadrat) occurred in August 1996 (Fig. 7).

Table 8. Results of one-way Kruskal Wallis ANOVA testing for difference in number of species and total abundance of amphipods between sampling dates at Rocky Neck State Park.

Test	Mean Rank						*P*
	1996			1997			
	20 Aug	6 Sep	22, 27 Sep	4 Apr	2 May	2 Jun	
Number of Species	23.25	29.25	23.06	27.19	25.13	19.13	0.7210
Total Abundance	32.88	33.56	26.00	12.38	19.44	22.75	0.0193

Table 9. Results of one-way Kruskal Wallis ANOVA testing for difference in number of species and total abundance of amphipods between sampling dates at Outer Island.

Test	Mean Rank						*P*
	1996			1997			
	22 Aug	11 Oct	25 Oct	4 Apr	3 May	1 Jun	
Number of Species	34.31	27.81	17.44	18.44	22.06	26.94	0.1088
Total Abundance	39.56	26.38	19.25	11.50	21.63	28.69	0.0024

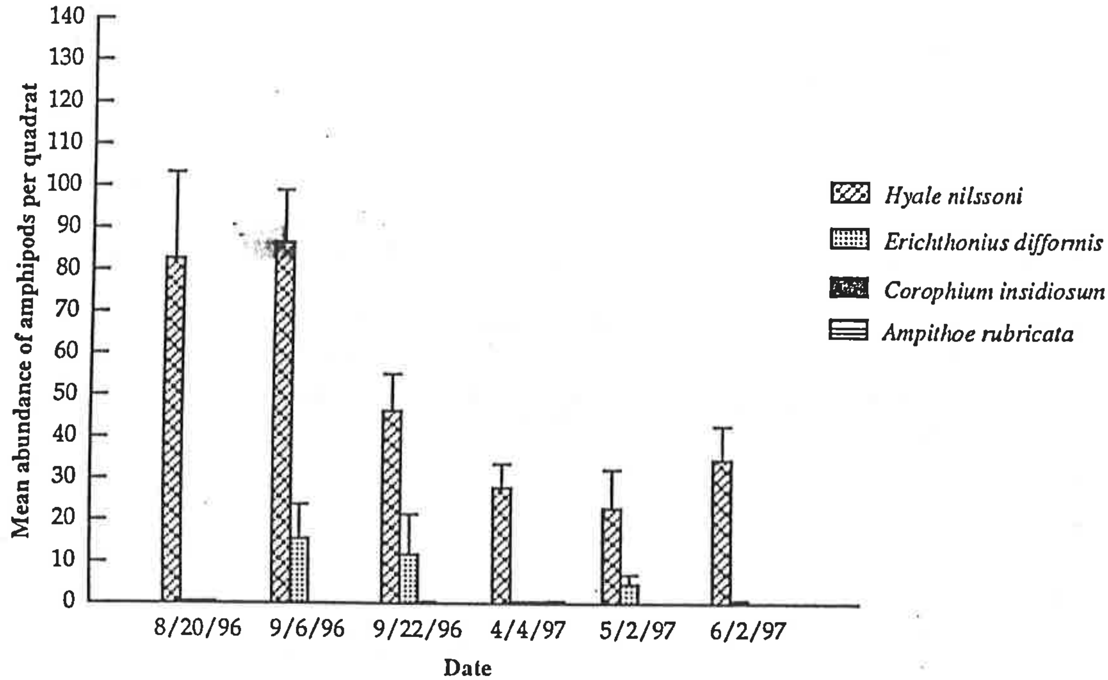

Figure 4. Mean abundance of each amphipod species collected on *Fucus vesiculosus* at Rocky Neck State Park.

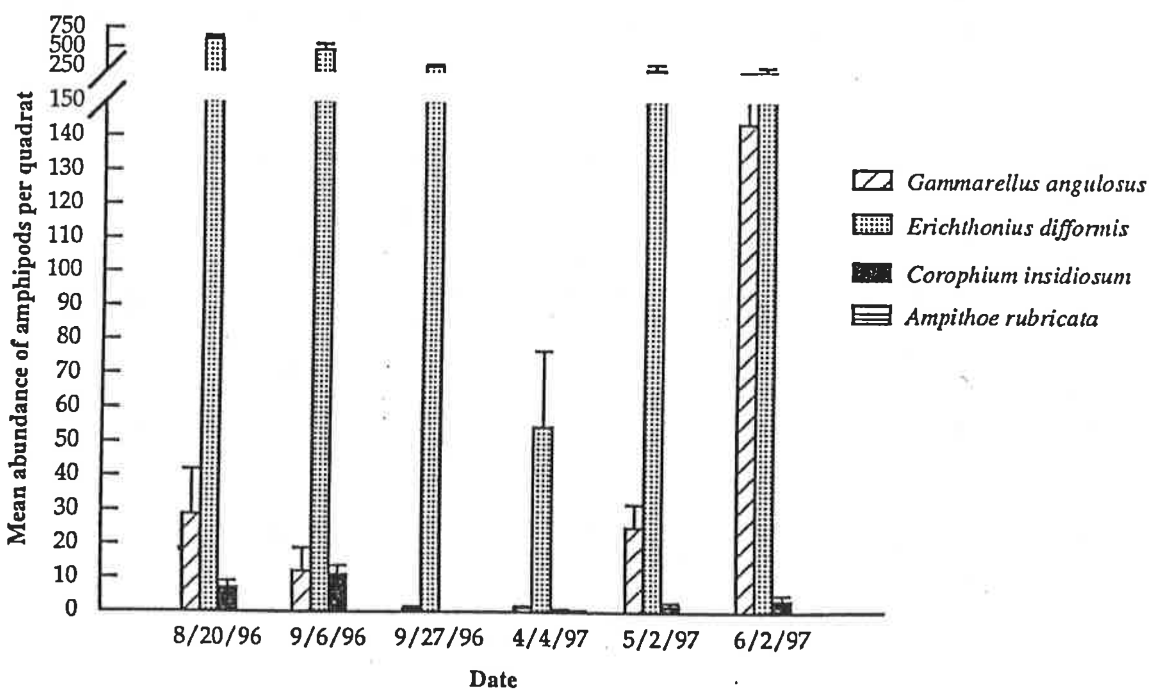

Figure 5. Mean abundance of each amphipod species collected on *Chondrus crispus* at Rocky Neck State Park.

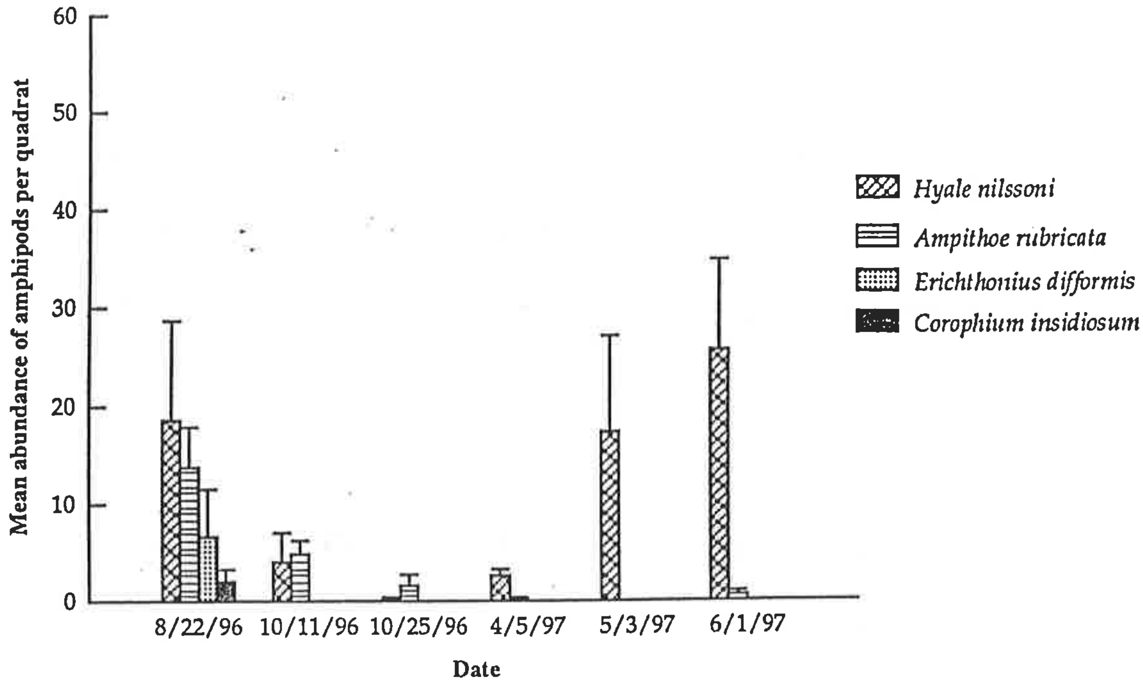

Figure 6. Mean abundance of each amphipod species collected on *Fucus vesiculosus* at Outer Island.

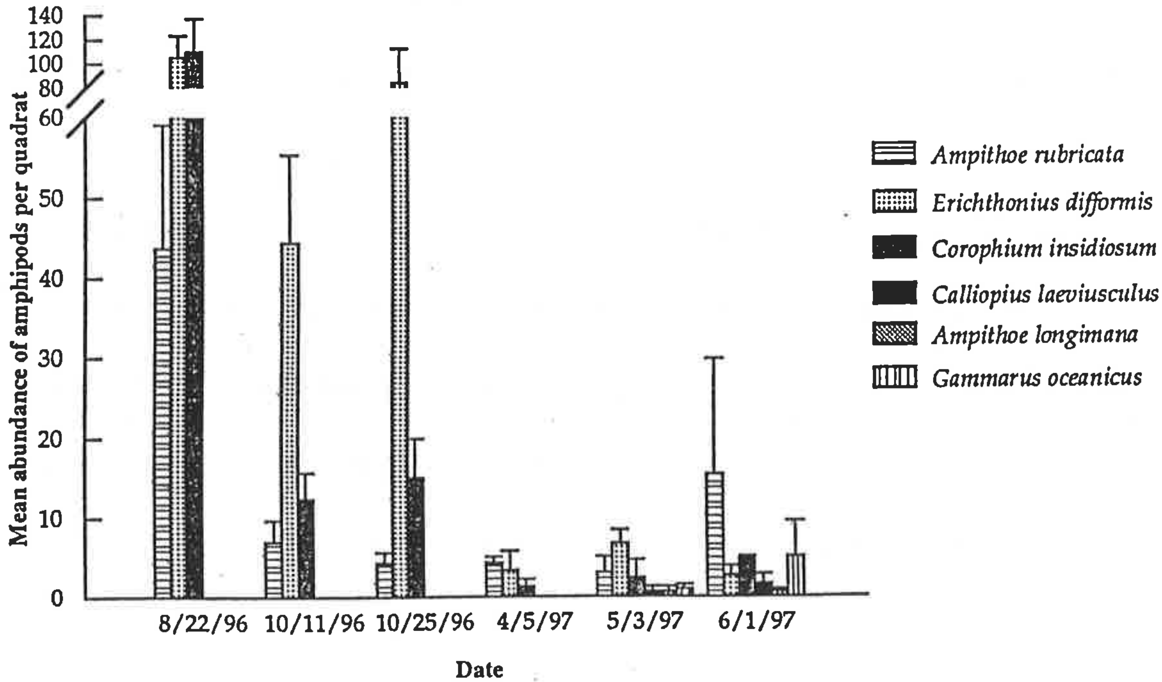

Figure 7. Mean abundance of each amphipod species collected on *Chondrus crispus* at Outer Island.

Life History of Amphipods

Seasonal changes in the population numbers of each amphipod species at Rocky Neck State Park and Outer Island are shown in Figures 8-12 and are described individually below. Due to a small number of individuals in the sample collections, the life histories of *Co. insidiosum, G. oceanicus, Ca. laeviusculus*, and *A. longimana* are not included.

Hyale nilssoni on *Fucus vesiculosus* at Rocky Neck State Park and Outer Island (Figs. 8, 9):

The number of individuals in the small-size class on September 6, 1996 (162 individuals) was higher than on other collection dates. A large proportion of individuals in the large-size class (47.7-96.6%) occurred in spring 1997. No individuals in the small-size class were collected on October 25, 1996 and April 5, 1997 while no large individuals were collected on October 11, 1996.

Erichthonius difformis on *Chondrus crispus* at Rocky Neck State Park (Fig. 10):

A large number of individuals in the small-size class (117 individuals) were collected on September 27, 1996. The large proportion of individuals in the medium-size class (73.6-83.1%) occurred in the late summer and the beginning of fall 1996 while the large proportion of large-size class individuals (66.3-85.8%) occurred in the spring 1997.

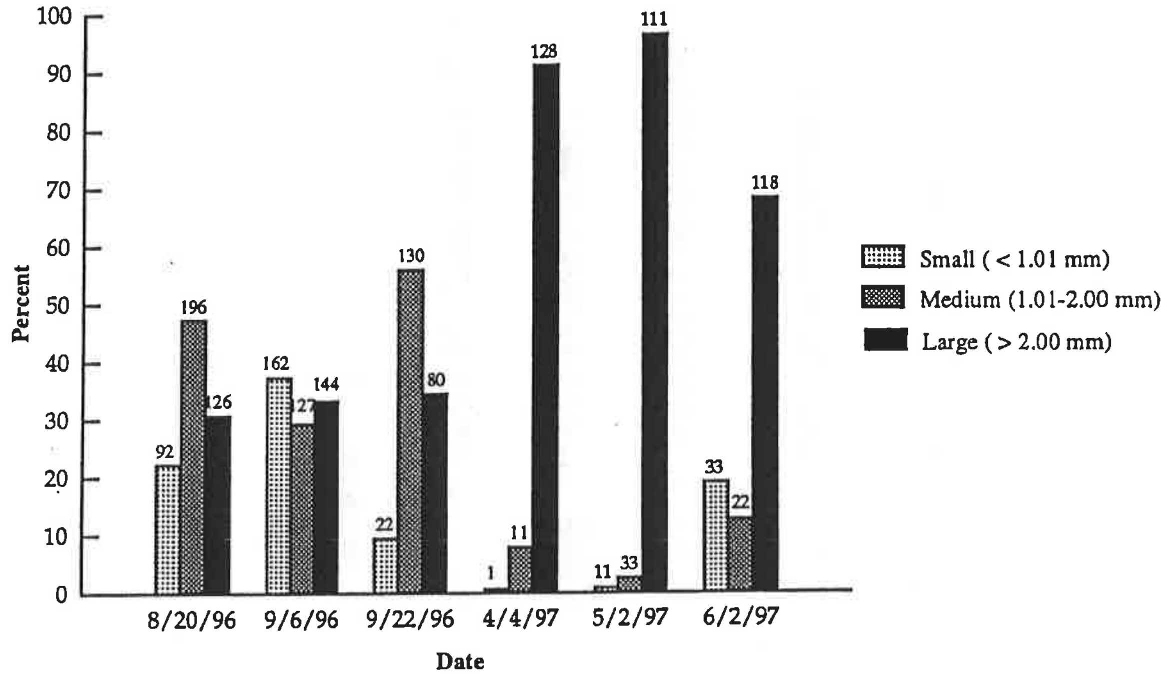

Figure 8. Percentage of *Hyale nilssoni* in each size class by date in *Fucus vesiculosus* at Rocky Neck State Park.

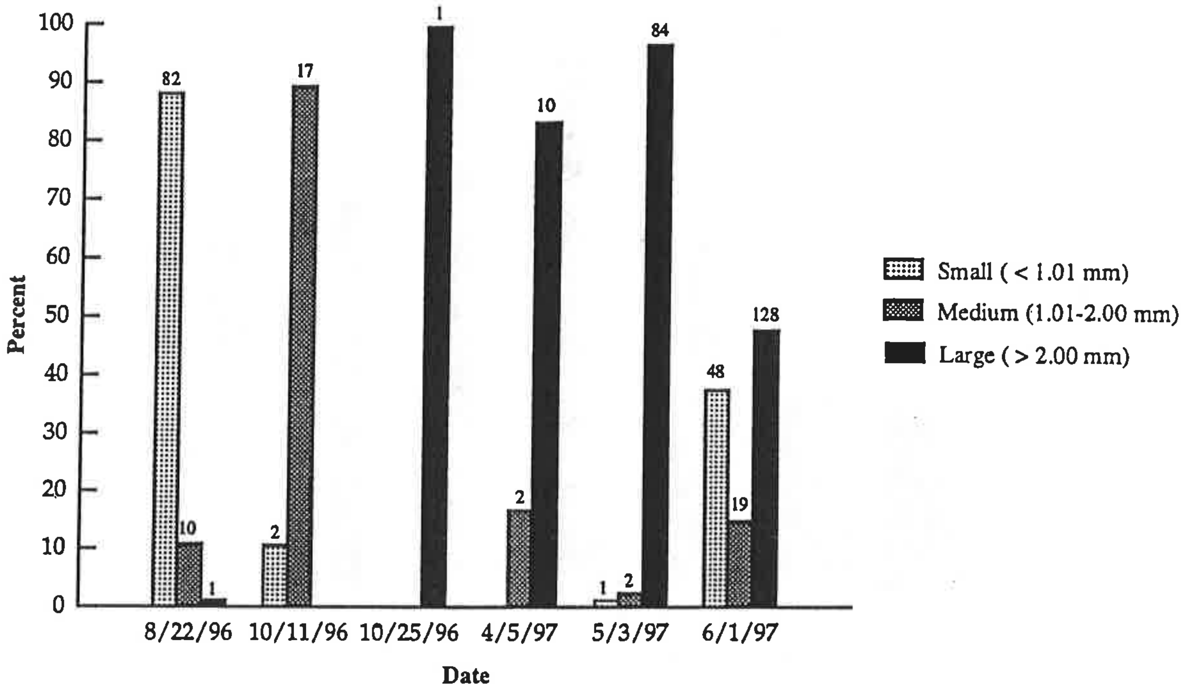

Figure 9. Percentage of *Hyale nilssoni* in each size class by date in *Fucus vesiculosus* at Outer Island.

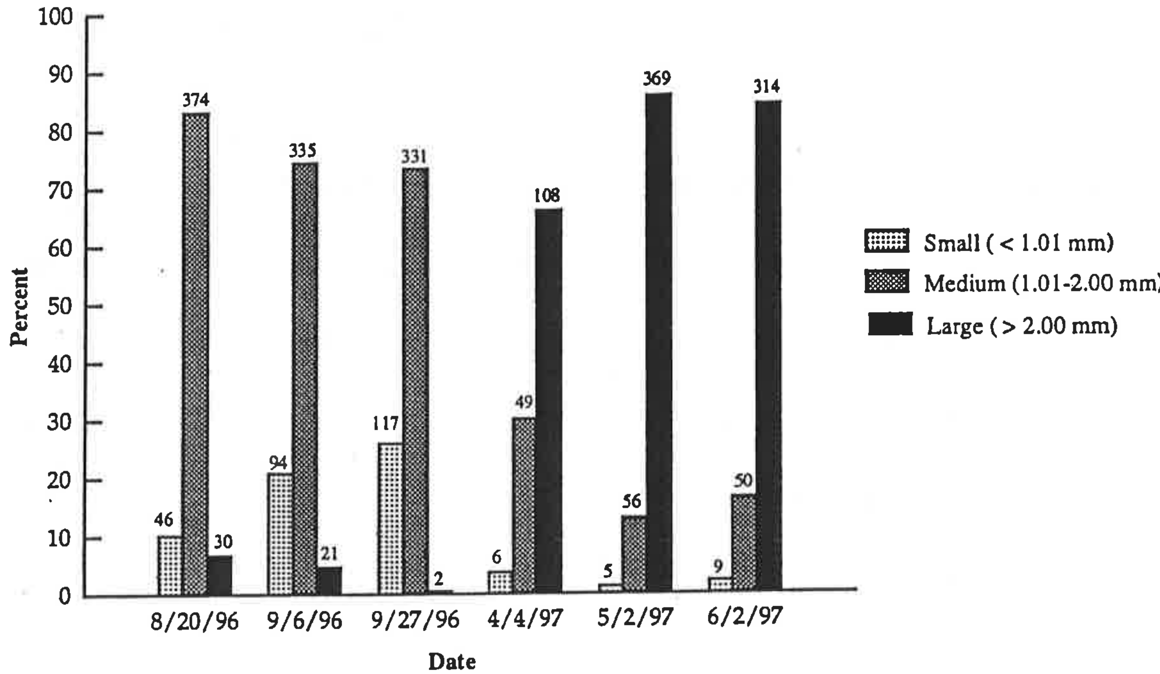

Figure 10. Percentage of *Erichthonius difformis* in each size class by date in *Chondrus crispus* at Rocky Neck State Park.

Gammarellus angulosus on *Chondrus crispus* at Rocky Neck State Park (Fig. 11):

A large number of individuals in the small-size class (21 individuals), medium-size class (158 individuals), and large-size class (179 individuals) were collected in June 1997. No small-size class individuals occurred on September 27, 1996 and April 4, 1997 while no medium-size class individuals were found on September 27, 1996.

Ampithoe rubricata on *Chondrus crispus* at Rocky Neck State Park (Fig. 12):

A large proportion of individuals in the small-size class (47.83%) occurred on June 1997. No small-size class individuals were collected on April and May 1997. A large number of individuals in medium (89 individuals) and large (23 individuals) size classes occurred on August 22, 1996.

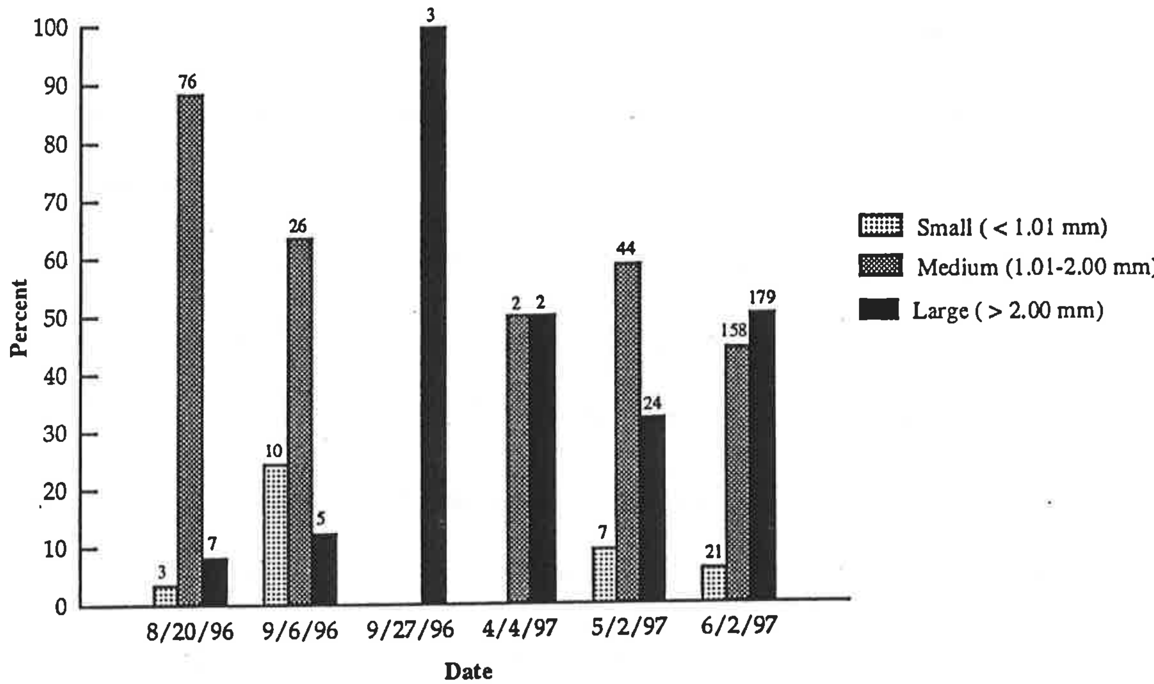

Figure 11. Percentage of *Gammarellus angulosus* in each size class by date in *Chondrus crispus* at Rocky Neck State Park.

amphipods during low and high tides. Amphipods living on algae have different ways to adapt to environmental changes. These include migration, physiological adaptations such as specialized respiratory mechanisms, and rhythmic activity (Raffaelli and Hawkins, 1996). Rhythms may be related to behaviors during high tide and low tide or daytime and nighttime (Williams, 1983). Williams (1983) has suggested that the semi-terrestrial amphipod, *Talitrus,* has a circadian rhythm, foraging only at night. Physiological adaptations in respiratory mechanisms also play an important role in habitat selection (Raffaelli and Hawkins, 1996). Different intertidal species have differences in the consumption of oxygen in air and water in order to cope with a variety of factors (Branch and Newell, 1978).

Members of the genus *Hyale* are well adapted to live in algae in the higher littoral zone (Wieser, 1952; Tararam *et al.*, 1986; Baldinger and Gable, 1995). These amphipods may have the ability to reduce water loss through the gills or exoskeletons as in the terrestrial amphipod, *Arcitalitrus sylvaticus* (Lazo-Wasem, 1984). Viejo and Arrontes (1992) have suggested that *H. nilssoni* is an opportunistic feeder on *Fucus vesiculosus* but they tend to prefer soft algae such as some epiphytes over firm and rigid algae as food (McBane and Croker, 1983). It might be possible that during low tide, *H. nilssoni* remains in the upper zone (*F. vesiculosus*) to avoid competition for food sources in the lower zone (*C. crispus*). However, during high tide, *H. nilssoni* may move away from the *Fucus* habitat to search for a softer food such as epiphytes. This could explain differences in habitat selection by *H. nilssoni* in the field and laboratory. McBane and Croker (1983) also suggested that *Hyale nilssoni* prefer ephemeral algae, which are softer, over perennial macroalgae. Other studies also found that amphipods graze on a variety of epiphytic filamentous algae (D' Antonio, 1985; Steele and Whittick, 1991). The effect of epiphytes on *Fucus* and *Chondrus* on habitat selection by amphipods might be a subject for consideration.

Competition between grazers is an important factor leading to zonation patterns; however, overlap in feeding on the same algal species by some species of grazers has been suggested to play an important role in providing suitable feeding for other grazers (Viejo and Arrontes, 1992). Viejo and Arrontes (1992) showed that the feeding activity of the isopod, *Dynamene bidentata,* was beneficial for the amphipod, *Hyale nilssoni,* by providing suitable feeding surface on *Fucus vesiculosus.* In addition, competition may be reduced by preference of different parts of algae by each mesograzer (Hacker and Steneck, 1990; Duffy and Hay, 1991).

Several studies have emphasized the importance of algal morphology as a factor that can affect the abundance pattern of animals inhabiting seaweeds (Heck and Wetstone, 1977; McBane and Croker, 1983; Hicks, 1986; Buschmann, 1990; Hacker and Steneck, 1990; Edgar and Robertson, 1992). Generally, more complex habitats seem to offer animals greater protection from predators. *F. vesiculosus* seems to have more a complex structure than *C. crispus*. *Fucus* has more a branched-like structure than *Chondrus*. This structure may serve as a refuge from predators during high tide (Hacker and Steneck, 1990). However, during low tide, most amphipods, except

Hyale nilssoni, seem to live on *Chondrus*, which is less complex, probably to reduce desiccation stress. This could explain the differences in habitat selection by *E. difformis* and *G. angulosus* in the field and the laboratory. However, more experiments are needed to distinguish between the factors and interactions that might affect abundance and habitat selection by amphipods in the rocky intertidal.

When comparing Rocky Neck State Park and Outer Island, statistical tests showed no significant differences in the number of species but significant differences in total abundance of amphipods. In addition, there were differences in amphipod species occurring between study sites. The salinity and water temperature of two study sites were almost the same (pers. obs.) and so probably do not play an important role in the differences in the occurrence of species in the study sites. Both study sites also have moderate exposure to wave action. The factors that might influence the diversity and abundance differences could be topography and composition of the substratum (Foster *et al.*, 1988; Jazdzewski *et al.*, 1995). Breaking waves can be reduced by topography (Foster *et al.*, 1988). Gently sloping beaches may drain more slowly, as a result, the extension of the upper limit of lower intertidal organisms is formed (Seapy and Littler, 1978; Foster *et al.*, 1988). In this study, collection sites at Rocky Neck State Park were steeper than at Outer Island (pers. obs.). This may lead to differences in zonation and amphipod abundance between study sites. Other factors including types of predators, epiphytes, nutrients, and productivity also may influence the differences between study sites.

Seasonal changes in the population biology of amphipods have been demonstrated in Hyalidae (Hiwatari and Kajihara, 1984), Gammaridae (Kolding and Fenchel, 1981), and Corophiidae (Sheader, 1978; Peer *et al.*, 1986). However, the life history of most amphipod species is not well known. Patterns in population biology are discussed below for each species found from Rocky Neck State Park and Outer Island.

Hyale nilssoni: Large numbers of large-size class individuals occurred during April to June (Figs. 8, 9). Brooding females also were found in this period. As a result, high juvenile recruitment into the population occurred in summer corresponding with the reproductive season reported by Bousfield (1973). He reported that ovigerous females occur during April to August.

Erichthonius difformis: A large number of individuals in the large-size class, including ovigerous females, occurred in April to June (Fig. 10). Brooding females in the medium-size class also were found in late summer. As a result, high juvenile recruitment into the population occurred in late summer and in the beginning of fall. These results are similar to findings in other study (Bousfield, 1973). Bousfield (1973) reported that ovigerous females occur from March to July. However, no collections were made in March and July in this study. The data also show that large numbers of small-size class individuals (juveniles) continued to be found until the end of October at

Outer Island. It is interesting to note that *E. difformis* seems to be found in colder water areas and colder weather (Bousfield, 1973; this study) where other species are not likely to be found.

Gammarellus angulosus: Juveniles that were found in May to June and August to September probably resulted from brooding females in May to June (Fig. 11). The data correspond with the reproductive season shown by Bousfield (1973) who reported that ovigerous females normally are found from April to June.

Corophium insidiosum: There were very few individuals collected in spring. Therefore, their size distribution is not included in this study. However, Bousfield (1973) reported that ovigerous females normally occur from April to August.

Ampithoe rubricata: Juveniles present in June and August to October probably resulted from medium and large-size class individuals in April to June (Fig. 12). Bousfield (1973) reported that ovigerous females occur from April to July.

Gammarus oceanicus: Due to the small number of individuals in the sample collections, the size distribution is not included in this study. However, Bousfield (1973) found that ovigerous females mainly occur from March to July.

***Ampithoe longimana*:** A small number of *A. longimana* was found from May to June (Fig. 7). Bousfield (1973) reported that ovigerous females occurred from May to September.

***Calliopius laeviusculus*:** A small number of ovigerous females were found during May to June (Fig. 7). Therefore, conclusions are difficult to make. However, other studies have shown that ovigerous females occur from March to June (Bousfield, 1973; DeBlois and Leggett, 1993b).

Most of the population patterns of the amphipod species (except *E. difformis*) correspond with Bousfield (1973). The population pattern of *E. difformis* in this study seemed to have a longer period of ovigerous females than the data reported by Bousfield (1973). Water temperature is an important factor in the seasonal reproductive patterns of amphipods (Stoner, 1980). The critical water temperature can affect the reproductive activity and development of amphipod eggs (Stoner, 1980). Because of incomplete year-round sampling, caution should be applied in using this study to interpret the population biology of amphipods.

My study found that species of amphipods have differences in seasonal abundance. Greze (1968) suggested that different seasonal distributions of dominant species were due to different life cycles, competition, and grazing adaptations to epiphytes. The seasonal macrophyte biomass and physical characteristics of a habitat such as habitat space and habitat complexity also influence the seasonal pattern of amphipod abundance (Heck and Wetstone, 1977). Steele and Whittick (1991) have demonstrated that seasonal abundance of the amphipod, *Gammarus lawrencianus,* is related to the seasonal abundance of the brown alga, *Pilayella littoralis*.

Because there is variability among reproductive times of different species, reproductive patterns must be described before life history can be understood. At present, little is known about the life histories of amphipods. In this study, the samples were collected over six months. Ideally, the growth and reproductive biology of amphipod species should be studied year-round.

The results of this study suggest that rocky intertidal amphipods of southern New England occur in zones associated with seaweeds. In addition, this study shows that seasonal changes had effects on species abundance and population biology of amphipods. Very little is known about the ecology of amphipods in the rocky intertidal zone in New England. Further investigation is needed to understand factors causing zonation of amphipods, the life history of amphipods, and seasonal changes corresponding with amphipod abundance.

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