Winter 2002

Impacts of the introduced crabs, Carcinus maenas and Hemigrapsus sanguineus, in northern New England

Megan Conlon Tyrrell
University of New Hampshire, Durham

Recommended Citation
Tyrrell, Megan Conlon, "Impacts of the introduced crabs, Carcinus maenas and Hemigrapsus sanguineus, in northern New England" (2002). *Doctoral Dissertations*. 117.
https://scholars.unh.edu/dissertation/117

IMPACTS OF THE INTRODUCED CRABS, *Carcinus maenas* and *Hemigrapsus sanguineus*, IN NORTHERN NEW ENGLAND

BY

Megan Conlon Tyrrell
B.A. Macalester College, 1994
M.S. University of New Hampshire, 1999

DISSERTATION

Submitted to the University of New Hampshire
in Partial Fulfillment of
the Requirements for the Degree of

Doctor of Philosophy

in
Zoology

December, 2002

ProQuest Information and Learning Company
300 North Zeeb Road
P.O. Box 1346
Ann Arbor, MI 48106-1346

This dissertation has been examined and approved.

Larry G. Harris

Dissertation Director, Dr. Larry G. Harris
Professor of Zoology

Thomas D. Lee

Dr. Thomas D. Lee, Associate Professor of
Natural Resources

James F. Haney

Dr. James F. Haney, Professor of Zoology

Dr. C. Sarah Cohen, Research Associate,
Harvard University, Cambridge, MA

L. David Smith

Dr. L. David Smith, Assistant Professor of
Biology, Smith College, Northampton, MA

December 4, 2002
Date

ACKNOWLEDGMENTS

Thank you to Dr. Larry Harris for encouraging me to study the impacts of a crab species that is still very uncommon in northern New England. I truly appreciate the opportunities and experiences you have provided for me.

Thank you to my committee members Drs. James Haney, Tom Lee and David Smith for constructive comments and insights on this work. Dr. Sarah Cohen was a mentor and supporter from beginning to end. Thank you to Dr. Jeb Byers for helpful discussions and to Dr. Chris Neefus for advice on statistical analysis. Thank you to Dr. Dan Hornbach at Macalester College in St. Paul, MN for starting me on this path.

Thank you to Harris lab members for support and patience. Thank you especially to Tricia Madigan, who conducted the first set of microcosm experiments and who has been an outstanding colleague and friend. Other people that made this work possible through their friendship and support include: Christa Biche, Jeff Markert, Gabby Martinez, Bruce Sommer, Ann Stork, Sally Turtle, Rebecca Weisman, and Zoology Department graduate students, past and present.

Penny Beuning, Lara Gengarelly and Petra Bertilsson-Friedman were vital colleagues and counselors. Thank you for your friendship and for always being there via email or phone. Thank you to Joe Tyrrell for field assistance on a blustery day and for support throughout this process. Thank you to Mary Tyrrell who has unceasingly encouraging. I guess you were right that cold afternoon in January 1996. Paul Evans has been a loving and wonderful partner throughout this process. This dissertation would not be possible without his love and understanding.

This work was supported by grants from the Center for Marine Biology and the Graduate School of the University of New Hampshire. Additional grant support was provided by the A.V. Fund of the Norcross Wildlife Foundation. Two fellowships, one from the NOAA Estuarine Research Reserve for Great Bay Reserve and one from the University of New Hampshire dissertation fellowship provided vital support.

TABLE OF CONTENTS

III. ABUNDANCE OF EPHEMERAL ALGAE IN UPPER INTERTIDAL POOLS PRIOR TO THE ESTABLISHMENT OF *Hemigrapsus sanguineus*

IV. EFFECTS OF PREDATION BY TWO SPECIES OF INTRODUCED CRABS: INFERENCES FROM SHORT TERM MICROCOSM EXPERIMENTS

V. EFFECTS OF PREDATION BY TWO SPECIES OF INTRODUCED CRABS: INFERENCES FROM LONG TERM MICROCOSM EXPERIMENTS

LIST OF TABLES

LIST OF FIGURES

FIGURE **PAGE**

ABSTRACT

IMPACTS OF THE INTRODUCED CRABS, *Carcinus maenas* and *Hemigrapsus sanguineus*, IN NORTHERN NEW ENGLAND

by

Megan Conlon Tyrrell

University of New Hampshire, December, 2002

Two introduced crab species are presently found in northern New England, *Carcinus maenas*, which has been in this region for over 100 years, and *Hemigrapsus sanguineus* which was first reported in New Hampshire in 1998. *Carcinus maenas* is a generalized predator and its introduction has had negative effects on several native mollusc species but the community wide impacts of its introduction have been relatively neglected. *Hemigrapsus sanguineus* is just beginning to establish populations in this region, and its effects on the resident community are unknown. Both monitoring and experimental approaches were used to retroactively infer the impacts of *C. maenas* and to predict the impacts of *H. sanguineus* on the rocky intertidal community of northern New England.

The temporal and spatial patterns of *C. maenas*' recruitment were documented in anticipation that this species may decline as *H. sanguineus*' population increases. Microcosm experiments indicated that the two crab species had similar consumption patterns, but that *H. sanguineus* caused a significantly greater decline in barnacles than *C. maenas* in both short and long term field experiments. Temporal variation in the abundance of ephemeral algae was documented twice yearly at three coastal and one estuarine location. These baseline data provide pre-*Hemigrapsus* variability in abundance of *Enteromorpha* sp. and other annual algae species that can be used to compare post-invasion levels of these palatable algal species. Temporal variation in community structure prior to the establishment of *H. sanguineus* was also documented at two coastal and one estuarine location. Both non-metric multidimensional scaling and cluster analysis of the community data indicated that there was low temporal variability between each tidal height at a particular location. *Carcinus maenas* was the dominant crab at all locations, but by the end of the study period, *H. sanguineus* had been found at all three study locations. If *H. sanguineus* exhibits similar behavior in northern New England as it did in the microcosms and in southern New England, the rocky intertidal community could soon be dominated by a "new" introduced crab species that has a higher per capita impact than the "old" introduced crab species.

GENERAL INTRODUCTION

Introduced species are organisms that are brought by humans to an environment where the species has not historically been present. In many instances, the introduction of a species has beneficial effects; many of the major crop species in the US are not native to our continent. However, species that are inadvertently introduced often have negative effects. The United States Office of Technology Assessment has estimated 97 billion dollars in economic losses from 79 introduced species and found that they pose a significant threat to the future health of ecosystems (OTA Report Summary, 1993). In addition to the economic problems they pose, introduced species are second only to habitat destruction as a threat to biodiversity (Wilcove et al., 1998).

The Gulf of Maine has been particularly susceptible to the negative effects of introduced species. In fact, some of the most common species within this ecosystem are introduced. The most common snail in New England, *Littorina littorea*, was introduced about 160 years ago and since then it has displaced a native snail *Ilyanassa obsoleta* (Brenchley and Carlton, 1983), and driven the transformation of habitat from marsh to cobble beach (Bertness, 1984). The introduced green alga *Codium fragile* ssp. *tomentosoides* has replaced *Laminarian* kelp as the dominant canopy forming alga at the Isles of Shoals (Harris and Tyrrell, 2001). The most common crab in the New England intertidal zone, the green crab, *Carcinus maenas* was introduced to the U.S. Atlantic coast and has been well established in this region at least since 1954 (Ropes, 1968).

Carcinus maenas is a generalized predator and its introduction has had negative effects on several native mollusc species. The collapse of the soft shell clam fishery was blamed on predation by *Carcinus* (Ropes, 1968) and two common snail species responded to the increased predation pressure by changing their shell shape (Vermeij, 1982; Seeley, 1986). Despite research into its effects on these organisms, the community wide impacts of the introduction of *C. maenas* have been relatively unstudied. Recently, another introduced crab species, *Hemigrapsus sanguineus*, the Asian shore crab has become extremely abundant along the U.S. Atlantic coast. The first record of *H. sanguineus* in the U.S. was in New Jersey in 1988 (Williams and McDermott, 1990) and since that time, it has expanded to become one of the most conspicuous organisms on rocky shores from Long Island Sound to North Carolina (Lohrer and Whitlatch, 1997; Lohrer, 2000; McDermott, 2001). *Hemigrapsus sanguineus* was found in New Hampshire in 1998 (McDermott, 2001) and since that time, has been discovered at a variety of coastal and estuarine locations (Tyrrell, unpub. data). Because of its extremely high densities in areas where it is already well established (Lohrer, 2000) and omnivorous feeding habits (Lohrer and Whitlatch, 1997; Tyrrell, 1999; Tyrrell and Harris, 2001), *H. sanguineus* is likely to have a substantial impact on recipient communities. Various researchers have noted that where established, the number of *H. sanguineus* equals (McDermott, 2001) or far exceeds (Lohrer and Whitlatch, 1997; Lohrer, 2000) the number of *C. maenas*. In Long Island Sound, Lohrer and Whitlatch (2002) have shown that adult *H. sanguineus* consume juvenile *C. maenas* and that *H. sanguineus* may be completely displacing the previously introduced *C. maenas*.

The objectives of this research were to determine the impacts of the introductions of *C. maenas* (the 'old' invader) and *H. sanguineus* (the 'new' invader) on the northern New England rocky intertidal community. This research built on my master's thesis, which compared the feeding preferences of both introduced crab species and created a predictive model of the potential impacts of *H. sanguineus* if it became established in northern New England. Obviously, because *C. maenas* has been established in northern New England for many years, my findings concerning its impact on the rocky intertidal community are retroactive. Previous research into the impacts of *C. maenas* has taken a single species approach and has been focused on molluscs (e.g. *Mya arenaria*, Glude, 1955; Ropes, 1968; *Nucella lapillus*, Vermeij, 1982; *Littorina obtusata*, Seeley, 1986; Trussell, 1996). My research is distinguished from that of other authors because I have focused on the interactions of these two introduced predators with the rocky intertidal community as a whole, rather than focusing on a single prey item. In contrast to my findings concerning *C. maenas*' impact on the community, my findings concerning *H. sanguineus* are predictive. At the time that I found my first *H. sanguineus* at one of my study sites (Hilton Park, 1999; Chapter II), it was the second specimen to be found in the state of New Hampshire. Since that time, there has been a trend of increasing range and abundance of *H. sanguineus* at all of my study sites (Chapter II). However, at my study site where *H. sanguineus* are most abundant, the Hilton Park 1.0 m site, *H. sanguineus* was still outnumbered by *C. maenas* by 3.2:1 in 2001. Clearly, populations of *H. sanguineus* are increasing in northern New England, but the majority of my data was collected prior to the discovery of any *H. sanguineus* at my study sites. I have found a total of 49 *H. sanguineus* as compared to 5,825 *C. maenas*; at the present moment, the abundance of *C. maenas* far exceeds that of *H. sanguineus* at all of my study sites.

The specific objectives of my dissertation are: (1) to examine the community structure of the rocky intertidal zone with an emphasis on *C. maenas'* patterns of habitat use prior to the establishment of significant populations of *H. sanguineus* (2) to infer some of the impacts of *H. sanguineus* and *C. maenas* by examining their prey selection in short and long term microcosm experiments and (3) to examine temporal fluctuations in the abundance of ephemeral algae in upper intertidal pools prior to the establishment of *H. sanguineus* and (4) to determine the temporal and spatial patterns of recruitment of *C. maenas*, especially in reference to a potential future decline in this species following the establishment of *H. sanguineus*.

The results of this research will contribute to our understanding of the impacts of biological invasions, how they affect established communities and the potential consequences for biodiversity. *Hemigrapsus sanguineus* has generated much interest among invasion biologists and the general public because it has spread rapidly and has been so successful at establishing large populations, even displacing a previously introduced species. The baseline community structure data that was obtained in this project is essential to gauge future changes in the intertidal zone. The results of the microcosm experiments not only elucidated some of the changes that likely occurred with the introduction of the "old" crab invader, but also those that are likely to occur with the population expansion of the "new" crab invader. Information regarding *C. maenas'* recruitment and habitat utilization is important because this introduced crab is a major predator in this community (Menge, 1983). Finally, this project is unique in that it is the first time that a marine ecologist has anticipated a biological invasion (that of *H. sanguineus*) and conducted both monitoring and manipulative experimental work prior to the establishment of substantial populations of the invader in order to predict its impact.

CHAPTER I

TEMPORAL AND SPATIAL PATTERNS IN THE SETTLEMENT AND RECRUITMENT OF THE INTRODUCED GREEN CRAB, *Carcinus maenas*, IN NORTHERN NEW ENGLAND

ABSTRACT

Many authors have emphasized the importance of early life history stages (settlement and recruitment) in regulating adult populations and subsequent community structure (Keough and Downes, 1982; Gaines and Roughgarden, 1985; Underwood and Fairweather, 1989; Menge; 1991; Young, 1994; Harris and Chester, 1996). Although the European green crab, *Carcinus maenas*, is abundant in the New England rocky intertidal zone, the only quantitative studies of recruitment of this species is from soft sediment habitats in northern Europe (Klein Breteler, 1976; Eriksson and Edlund, 1977; Pihl and Rosenberg, 1982; Beukema, 1991; Thiel and Dernedde, 1994). This study examined the patterns of settlement and recruitment of *C. maenas* megalopae and juveniles utilizing artificial substrates as samplers. Two factors were investigated: the variation in the density and size distributions of crabs by height on shore (spatial patterns) and by the time of sample collection (temporal patterns). The study was conducted at two locations for multiple years to assess whether the observed patterns were consistent from year to year and site to site. Results indicate that the timing of peak settlement of megalopae was consistent between years and sites but that the timing of peak recruitment of juvenile crabs was more variable between years and sites. When recruitment was low, the differences in density between tidal heights were small, but these differences became more pronounced when overall recruitment levels were very high.

INTRODUCTION

Carcinus maenas was introduced to the east coast of the United States from the western Atlantic in the early 1800's and populations of this species have spread throughout the world since this initial invasion (Cohen *et al.* 1995; Grosholz and Ruiz, 1996). *Carcinus maenas* is a voracious predator in the northwest Atlantic; it is implicated in the decline of the soft shell clam (*Mya arenaria*) industry (Ropes, 1968) and has caused rapid morphological changes in at least two species of intertidal snails, *Littorina obtusata* (Seeley, 1986) and *Nucella lapillus* (Vermeij, 1982). Although it has been present in northern New England for approximately 100 years (Glude, 1955), some important aspects of this predators' life history in this environment are unknown.

Many authors have emphasized the importance of early life history stages (settlement and recruitment) in regulating community structure and subsequent adult populations (Keough and Downes, 1982; Gaines and Roughgarden, 1985; Menge; 1991;

Young, 1994; Harris and Chester, 1996). The majority of information regarding recruitment of *C. maenas* is from soft sediment habitats in northern Europe (Klein Breteler, 1976; Eriksson and Edlund, 1977; Pihl and Rosenberg, 1982; Beukema, 1991; Thiel and Dernedde, 1994; Moksnes and Wennhage, 2001). There is very little information regarding temporal or spatial aspects of recruitment of *C. maenas* on the rocky shores of the western Atlantic coast. Berrill (1982) found *C. maenas* megalopae from late August to early October in Maine, but he did not determine densities at his study sites. While Moksnes and Wennhage (2001) found that artificial settlement substrates produced reliable estimates of *C. maenas* settlement on the Swedish west coast, thus far, there have been no attempts to quantify settlement or recruitment of *C. maenas* in northern New England using artificial substrates. This research was designed to describe and quantify patterns in the early life history stages of this crab and use this information to draw conclusions regarding some of the impacts of its introduction.

Information regarding density and size distributions of megalopae and juvenile crabs by spatial (height on shore) and temporal (time of collection) patterns of settlement and recruitment is important to assess the impacts of this introduced predator. By utilizing artificial substrates, I was able to eliminate variability associated with substrate selection. This allowed me to directly compare densities between various tidal heights and locations and consequently, to infer where larval flux is greatest. The spatial distribution of newly recruited *C. maenas* at various tidal heights may indicate the relative importance of physical or biological factors influencing densities of juvenile crabs. Although the diet of young of the year crabs has a higher proportion of plant matter than adults (Ropes, 1968), they have been described as micro-carnivores (Eriksson and Edlund, 1977). The timing of recruitment of *C. maenas* may impact survival of other newly recruited prey (e.g. *Littorina obtusata, Mytilus edulis*) and consequently favor earlier recruiting prey species that can achieve a refuge from predation by their size. The life history dynamics of this important predator have implications for many other intertidal species, and may in turn, affect their life histories.

The objective of this study was to investigate the temporal and spatial (tidal height) patterns of recruitment of *C. maenas*. This baseline information on *C. maenas* recruitment was particularly relevant because it appears that the Asian shore crab, *H. sanguineus* inhibits recruitment of *C. maenas* via disproportionate predation on newly recruited *C. maenas* versus conspecific recruits (Lohrer and Whitlatch, 2002). In southern New England, *H. sanguineus* appears to have displaced *C. maenas* from rocky intertidal habitats (Lohrer and Whitlatch, 2002). As populations of *H. sanguineus* continue to expand in northern New England, declines in densities of juvenile *C. maenas* may result. These data will provide a valuable baseline against which future comparisons of *C. maenas* recruitment and settlement can be made.

MATERIALS and METHODS

Study sites

Recruitment studies were carried out at two coastal and one estuarine location in New Hampshire (Fig. 1.1). The two coastal locations were: Fort Stark, Newcastle, NH (43°03.51N, 70°42.75W) and Odiorne State Park, Rye, NH (43°02.62N, 70°42.97W).

These are rocky habitats along the coast with little to moderate exposure to wave action. The two coastal sites were chosen based on their similarity in species composition and abundance. In addition, I have been monitoring intertidal community structure at these two sites since 1997. I also examined recruitment at an estuarine location, Hilton Park, Dover Point, NH (43 07.00N, 70 50.00W). This site is a tidal rapids (fast-moving water driven by tidal currents) with little exposure to waves. In contrast to the coastal sites, Hilton Park has less rock bench substrate, a higher proportion of sand and a lower abundance of canopy fucoid algae (Chapter II) it also has a higher number of *H. sanguineus* than the two other coastal sites. The panels from the Hilton Park are currently being processed and analyzed, but a preliminary examination of panels that were deployed during peak recruitment at the coastal sites has revealed very low densities of juvenile *C. maenas* on the Hilton Park panels.

Artificial recruitment panels were used to eliminate substrate selection by newly recruited crabs. In order to standardize substrates between tidal heights and sampling locations, I utilized small pieces of artificial grass (also known as Astroturf) as a substrate. These mats have been successfully used to examine recruitment of the green sea urchin, *Strongylocentrotus droebachiensis* in the Gulf of Maine (Harris and Chester, 1996; Harris et al., 2001). Each replicate consisted of two small (approximately $15\ cm^2$) panels of artificial grass that were arranged so that the "grass" of each piece faced inwards, creating a sandwich. The two panels were loosely secured to each other with cable ties in each corner. Five of the panel sandwiches were attached to a plasticized wire grid (sampler).

Field component

Samplers were deployed at three tidal heights (0.5, 1.0 and 2.0 m above mean lower low water [MLLW]) at both of the coastal locations. Tidal heights were determined using data from Harbormaster (Zihua software Marlborough, CT). A metal bolt was drilled into the rock bench at each tidal height and the samplers were fastened to the bolt using cable ties. Cobbles were also placed over all of the samplers to secure and camouflage them.

Sampling was initiated at the coastal sites in 1997; the first set of samplers were deployed at Ft. Stark on May 24 and on June 2 at Odiorne Park. I exchanged the sandwiches every two weeks. Each sandwich was placed into a quart sized bag and the contents were preserved with 95% ethanol within two hours of collection. The last set of sandwiches were picked up on September 8, 1997 at Ft. Stark and September 10, 1997 at Odiorne Park. Sampling dates for 1998 were: May 11 to November 1 at Ft. Stark and May 12 to October 20 at Odiorne Park. In 1998, the last set of samplers at Odiorne were left in the field for one month (9/18 to 10/20). Because of the difference in the amount of time these samplers were deployed, the data from these sets of samplers were excluded from statistical analyses. In 1999, sampling dates at Ft. Stark were: April 26 to November 8 and June 8 to October 26 at Odiorne. Only the panels from July 6 to September 14, 1999 from Odiorne have been processed and analyzed at this time. In addition, in most cases for the 1999 panels, only three of the five replicates have been processed and analyzed at this time.

Laboratory Component

Extraction of organisms on the panels was accomplished by gently hitting the panel against a dishpan and rinsing with ethanol until all material was dislodged from the panel. Each panel was closely inspected in insure that all crabs and amphipods (which can harbor small crabs or megalopae between their legs) were removed. All material that was retained on a 200 micron mesh was examined under a dissecting microscope (the minimum size of megalopae was 0.8 mm). Numbers of megalopae (settlement stage) and juvenile crabs (recruitment stage) and their sizes were recorded using an ocular micrometer. Crabs that were over 10 mm were measured using a digital calipers, but these individuals were not included in the analysis because they may have been over one year old (Ericksson and Edlund, 1977). Size of megalopae was determined between the eyes (the widest part of the body), while carapace width was recorded for juvenile crabs. Size of the panels was also recorded to determine density of crabs and all densities were calculated per m^2.

Analyses

Differences in density and size distributions of megalopae and juvenile crabs were compared by spatial (height on shore) and temporal (time of collection) patterns of settlement and recruitment. The results from each location were analyzed separately for each year. Dates are reported as Julian day to facilitate comparisons of results between years.

Statistical analyses were conducted using Systat 10 (SAS Institute). Densities of megalopae and juvenile crabs were square root transformed prior to statistical analyses. For the 1999 samples, a two-way ANOVA was used to determine the effect of sampling date, tidal height and their interaction on the densities of *C. maenas* (megalopae plus juvenile *C. maenas*) at each location. For the 1997 and 1998 samples, an ANOVA was used to examine the influence of date and tidal height on the densities of *C. maenas*. Several samplers were lost due to storms in 1998 and 1999 (Appendix A), which precluded testing of the interaction term of tide height and date.

RESULTS

Density

The recruitment panels were successful in attracting both *C. maenas* megalopae and juvenile crabs at all tidal heights but the overall number of juvenile crabs outnumbered megalopae by a ratio of 27:1. Only one crab was found that was not *C. maenas* and it was likely to be the lady crab, *Ovalipes ocellatus*. A total of 4161 juvenile *C. maenas* (<10 mm CW) were encountered in the panels; 58 *C. maenas* were not included in analyses because their carapace width exceeded 10 mm. Larger crabs were also often observed underneath the panels, indicating a possible shortage of shelter for adult crabs.

At both Ft. Stark and Odiorne Park, the density of *C. maenas* megalopae was highest during mid-August in 1997 (Figs. 1.2 and 1.3) and 1998 (Figs. 1.4 and 1.5) but megalopae densities peaked in late August in 1999 (Figs. 1.6 and 1.7). In most cases, megalopae density at Ft. Stark was highest at the 0.5 m tidal height and decreased with increasing tidal height (Figs. 1.2, 1.6 and 1.7). In the two cases when densities of megalopae at the Ft. Stark 1.0 m tidal height exceeded those of the 0.5 m tidal height, the same number of megalopae were actually encountered on the panels: the higher densities at the 1.0 m tidal height were due to the fact that the average sizes of the panels at the 1.0 m tidal height were slightly smaller than at the 0.5 m tidal height. Throughout the three years of sampling, only one *C. maenas* megalopae was found at the Ft. Stark 2.0 m tidal height, in late August of 1997 (Fig. 1.2). In contrast to the relatively consistent spatial pattern at Ft. Stark, the tidal height with the highest density of megalopae at Odiorne varied between sampling periods (Figs. 1.3, 1.5 and 1.7). The 2.0 m tidal height had the highest density of all three tidal heights at Odiorne once during each year.

The timing of peak densities of juvenile crabs at Ft. Stark was less variable than at Odiorne. At Ft. Stark, the highest densities of *C. maenas* generally occurred from late August to late September in 1997 and 1999 (Figs. 1.8 and 1.12). Unfortunately, sampling for the year was terminated on September 8, 1997 at Ft. Stark, which was when the highest densities of juvenile *C. maenas* occurred at both the 0.5 and 1.0 m tidal heights. In 1998 at Ft. Stark, there appeared to be two periods of high densities: mid May to June and late September to early November (Fig. 1.10). At Odiorne, the overall recruitment levels in 1997 were lower than at Ft. Stark and the peak densities occurred earlier (mid to late August) (Fig. 1.9). In 1998, the highest numbers of juvenile *C. maenas* at Odiorne were found in late May at the 2.0 m height, in mid July at the 1.0 m height and in late October at the 0.5 m height (Fig. 1.11). Densities between the 1.0 and 2.0 m tidal heights were similar throughout much of the 1998 sampling period at Odiorne Park. However, many samplers at the 1.0 m height were lost due to storms in 1997 and 1998 and consequently, the results from this tidal height should be interpreted with caution because of the large amount of missing data. Finally, for the 1999 Odiorne samples, it appears that crab recruitment levels were still elevated into mid- September, although the peak for the 0.5 and 1.0 m tidal heights may have occurred in late August (Fig. 1.13).

Generally, the spatial pattern of decreasing densities with increasing tidal height that was observed for the megalopae at Ft. Stark was similar for the juvenile crabs at this site (Figs. 1.8, 1.10 and 1.12). At Odiorne, there was not a consistent relationship between densities of crabs and tidal height, which was the same result that was observed for megalopae. In 1998 and 1999, densities at Odiorne were generally inversely related to tidal height at times when recruitment was highest (Figs. 1.11 and 1.13). However, in 1997, a sharp increase in densities from mid to late August at the 2.0 m tidal height preceded the peak densities at the two lower tidal heights (Fig. 1.9).

When megalopae and juvenile crabs are considered simultaneously, the results for each site largely reflect the patterns for juvenile crabs because they strongly outnumbered megalopae even during peak settlement (Figs. 1.14 – 1.19). The results of the ANOVA indicated that the density of juvenile *C. maenas* in the panels was significantly influenced by tidal height and sampling date for all three years at Ft. Stark and for the Odiorne 1998 samples (Table 1.1). Because of the loss of various samplers at both locations in 1997 and 1998 (Table 1.2), I was unable to test for the interaction of tidal height and sampling date. In 1999, the interaction term was significant at Ft. Stark and not statistically significant at Odiorne Park (Table 1.1).

Size

The size of *C. maenas* megalopae was very consistent between individuals (range 0.8 to 1.4 mm) and therefore average size results for megalopae are not depicted graphically. In 1998 and 1999, the ranges of average sizes of juvenile *C. maenas* were more variable at Odiorne Park than at Ft. Stark (Figs. 1.22 to 1.25) but in 1997, the opposite was true (Figs. 1.20 and 1.21). There were six instances when peak recruitment at a particular tidal height coincided with the lowest average size for that tidal height (in 1997: Ft. Stark 2.0 m, Odiorne 0.5 and 2.0 m; 1998: Ft. Stark, 1.0 m; 1999: Odiorne, 0.5 and 1.0 m). Unlike the density data, there was no consistent spatial pattern in the size of crabs occurring at particular tidal heights.

DISCUSSION

In New Hampshire, there is a settlement pulse of *Carcinus maenas* in mid to late July that extends to the end of September, with some megalopae settling into the samplers as late as the first of November. This timing is slightly later than that recorded by Klein Breteler (1976) and Beukema (1991) who report peak numbers of megalopae at the end of June and the beginning of July in the Dutch Wadden Sea (temperatures are warmer there than in the Gulf of Maine). In Sweden, where water temperatures are comparable to those of Maine (Berrill, 1982), Eriksson and Edlund (1977) and Pihl and Rosenberg (1982) report settlement of *C. maenas* as occurring from late July to September.

Morgan et al. (1996) investigated the correlation between settlement of *Callinectes sapidus* and water temperature, wind stress, tidal amplitude, and lunar phase. They determined daily settlement densities for two years and found that peak settlement of *C. sapidus* coincided with the minimum amplitude tides for the month. It is likely that most megalopae quickly metamorphosed into juveniles in my samplers, and therefore the megalopae densities reflected settlement in the last day or two before sampler collection. The timing of my collection of samplers coincided with neap tides in August in 1997 and 1998 but not in 1999. In 1997 and 1998, I also found that the peak density of megalopae coincided with the minimum amplitude tides for August. However, because my sampling frequency was only every two weeks, I do not feel that further conclusions regarding lunar or tidal periodicity in *C. maenas* settlement are warranted for this study design.

Beukema (1991) and Thiel and Dernedde (1994) report that *C. maenas* megalopae settle in the high intertidal zone of the Wadden Sea, but these authors do not quantify these references to tidal height. Thiel and Dernedde (1994) observe that predation pressure is depressed in the high intertidal zone, which may offset the increased physiological stress associated with this area. The results from Ft. Stark generally indicate that given the same substrates, densities of megalopae and juvenile crabs are highest in the lower intertidal zone. At Odiorne, the same pattern was generally applicable during times of peak recruitment in 1998 and 1999 but not in 1997. In addition, the ratio of *C. maenas* at the Odiorne 2.0 m site to the Ft. Stark 2.0 m site could be as high as 35:1. It is possible that the differences in orientation of the two sites (Ft. Stark faces northwest and Odiorne faces northeast) contributed to the differences in spatial pattern of *C. maenas* recruitment. Microhabitat differences between the locations of the 2.0 m samplers at each site may also have contributed to the differences in results for the two locations. The samplers were hidden under cobble but at the 2.0 m Odiorne site they were also covered by a thick canopy of *Ascophyllum nodosum*, while there was no algal canopy over the samplers at the 2.0 m Ft. Stark site. The algal canopy at the

Odiorne 2.0 m site may have ameliorated the physical stress enough to account for the differences in densities between the two locations.

The differences in timing of peak recruitment between years and between locations that was observed in this study testify to the importance of conducting multi-year and multi-site investigations. While at Ft. Stark, it generally appeared that densities of juvenile crabs and megalopae were consistently inversely related to tidal height, this pattern was not apparent at Odiorne. If this research had only been conducted at Odiorne Park in 1999, there would be no indication that the interaction of tidal height and sampling date could significantly affect densities of *C. maenas* recruits. In contrast, the interaction of these two factors was statistically significant at Ft. Stark in 1999, which supports the conclusion that there may be important physical or biological factors that contribute to the differences between the two sites. In order to assess the timing or peak settlement and recruitment for a particular species, a multi-year and multi-site investigation is necessary because variable results can be obtained from year to year and site to site because of differences in environmental and biological conditions.

The role of predation by adult *C. maenas* in influencing the recruitment and abundance of intertidal organisms has been documented by several authors (*Cerastoderma edule*, Sanchez-Salazar et al., 1987; Beukema, 1991; *C. edule* and *Macoma balthica*, Richards et al. 1999; various species of soft sediment macrofauna, Reise, 1977). However, the feeding behavior of juvenile *C. maenas* has been comparatively neglected (Mascaro and Seed, 2001) but see Rangeley and Thomas (1987). The potential of these micro-carnivores to influence the survival of other newly recruited prey species is considerable. Klein Breteler (1976) estimated that young of the year and

1 year old *C. maenas* consumed 5% of the total organic matter produced by the macrofauna at Balgzand in the Dutch Wadden Sea.

The timing of peak *C. maenas* recruitment into the rocky intertidal zone appears to be several months later than that of several of its prey items. *Semibalanus balanoides* settle and recruit in April and May and *Nucella lapillus* also emerge from their egg capsules in spring (Bertness, 1999). Keough (1983) reports recruitment of *Spirorbis* sp. during the Austral summer which could mean that this species also recruits during the summer months in the Gulf of Maine. Although they have various life history strategies that range from planktotrophic (*Littorina littorea*) to non-planktotrophic with intracapsular metamorphsis (*L. obtusata*) to ovoviviparous (*L. saxatilis*), the timing of spawning of these three species appears to extend from March to November (Reid, 1996). Peak spawning coincides with favorable temperatures (Reid, 1996) and recruitment of Littorinid snails is likely to occur several weeks after spawning (possibly July and August). In contrast to the previous organisms, *Mytilus edulis* appears to have a prolonged recruitment period, newly recruited juveniles can be encountered in high densities at various times of the year in the Gulf of Maine (Harris and Tyrrell, 2001). It is interesting to note that several potential prey species (*S. balanoides*, *N. lapillus*, *Spirorbis* sp.) experience recruitment peaks months before that of *C. maenas*, and the time lapse between peak recruitment of prey and predator may allow prey to reach some refuge from crab predation due to their size. However, extensive experimental work would need to be performed before causation could be implied between these observations.

There is ample evidence that spatial refuges are critical to the survival of early benthic stage decapod crustaceans (Wahle and Steneck, 1991; McDonald et al., 2001) and for *C. maenas* in particular (Thiel and Dernedde, 1994; Moksnes et al., 1998; Tyrrell, 1999). The artificial settlement/recruitment samplers used in this study provided much higher densities of juvenile crabs than naturally exist at the two sites (Chapter II; Table 1.3) which indicates that the structure provided by the turf of the samplers may have attracted megalopae and juvenile *C. maenas* or temporarily enhanced their survival. In order to make this comparison, I calculated the average density of crabs from the samplers for the two or three sampling periods that encompassed the same dates as when the quadrat sampling was accomplished. For the Odiorne 1997 recruitment samples, only one sampling period overlapped with the quadrat sampling dates, so the averages are based on the averages of five replicates from 8/26 to 9/9/97. The ratio of density estimates based on the artificial substrates exceeded naturally occurring densities by as much as 115.6:1.

Throughout its life history, *Carcinus maenas* appears to have less specific habitat requirements than *Hemigrapsus sanguineus*. For example, in a short term experiment designed to investigate recruitment patterns of *C. maenas* and *H. sanguineus* in a variety of habitat types, Lohrer (2000) found that *H. sanguineus* megalopae and juvenile crabs were predominantly found in rocky intertidal habitats while *C. maenas* recruited into a variety of habitat types other than the rocky intertidal zone. However, for those *C. maenas* that settle in the rocky intertidal zone, they face the threat of cannibalism as well as disproportionate predation by adult *H. sanguineus* (Lohrer and Whitlatch, 2002). These authors have suggested that significant predation on newly recruited *C. maenas* is one of the factors responsible for the decline in *C. maenas* in rocky intertidal habitats of southern New England. *Hemigrapsus sanguineus* are just beginning to become established in New Hampshire (Chapter II) and it is possible that declines in the successful recruitment of *C. maenas* will follow. Tyrrell and Harris (2001) predicted that the establishment of *H. sanguineus* would lead to a decline in the abundance and recruitment of *C. maenas* in northern New England and that *C. maenas* would become rare in the rocky intertidal zone. It may take several years to test the predictions of that model but the data provided in this study will provide a valuable baseline against which future comparisons of *C. maenas* settlement and recruitment can be made. Microhabitat differences between the tidal heights at the three locations appeared to exert a strong influence on crab densities in the samplers, and therefore, future comparisons of *C. maenas* settlement and recruitment would ideally take place at the same locations.

Table 1.1: ANOVA of the total number of *Carcinus maenas* (juvenile crabs + megalopae) on recruitment panels and the year, tide height and the interaction of these two factors. Testing the interaction of tide height and year was only possible in 1999 at each location because of the loss of samplers to storms in 1997 and 1998. Values in bold indicate statistical significance.

Location	Year	Factor	F ratio	df	p value
Ft. Stark	1997	Date	22.925	8	**0.000**
		Tide height	49.388	2	**0.000**
	1998	Date	9.467	12	**0.000**
		Tide height	155.387	2	**0.000**
	1999	Date	16.133	13	**0.000**
		Tide height	290.044	2	**0.000**
		Date*tide height	2.966	26	**0.000**
Odiorne	1997	Date	11.161	6	**0.000**
		Tide height	2.080	2	0.132
	1998	Date	5.950	8	**0.000**
		Tide height	32.321	2	**0.000**
	1999	Date	20.767	4	**0.000**
		Tide height	2.431	2	0.105
		Date*tide height	.833	8	0.581

Table 1.2: List of crab recruitment replicates that were lost due to storms at Ft. Stark and Odiorne Park, NH in 1997 and 1998.

Location	Year	Date (Julian day)	Tidal Height	Replicates missing
Ft. Stark	1997	5/24 to 6/2 (144 to 153)	2	1-5
		6/11 to 6/16 (162 to 167)	0.5	1-5
			1	4.5
			2	1-5
	1998	8/3 to 8/18 (215 to 230)	2	1-5
Odiorne	1997	6/2 to 6/17 (153 to 168)	1	1-5
			2	1-5
		6/16 to 7/1 (167 to 182)	1	1-5
		8/12 to 8/26 (224 to 238)	1	1-5
		8/26 to 9/10 (238 to 253)	1	3-5
	1998	5/12 to 5/26 (132 to 146)	0.5	1-5
			1	1-5
		6/10 to 6/23 (161 to 174)	0.5	1-5
			1	3-5
		9/1 to 9/18 (244 to 261)	1	1-5
		9/18 to 10/20 (261 to 293)	1	1-5

Table 1.3: Comparison of the average density/m^2 of juvenile *Carcinus maenas* in artificial settlement/recruitment samplers versus the naturally occurring density/m^2 at the same location. The distance separating the quadrat sampling location and the recruitment sampling location at Odiorne Park is several hundred meters. MLLW is meters above mean lower low water and CW is carapace width. In all cases, all *C. maenas* with >10 mm CW were excluded from density estimates.

Location	Year	Tidal Height (m above MLLW)	Quadrat sampling	Recruitment sampling
Ft. Stark	1997	0.5	2.3	266
		1.0	1.3	143.3
		2.0	5.5	5
	1998	0.5	8.1	125
		1.0	9.5	46.5
		2.0	13.5	8
	1999	0.5	19.6	177
		1.0	13.5	124
		2.0	15.5	20.3
Odiorne Park	1997	0.5	12.3	451
		1.0	14.4	337
		2.0	14.8	274
	1998	0.5	19.8	384.5
		1.0	18.8	174
		2.0	8.4	36.5
	1999	0.5	29.1	514
		1.0	33.2	499.5
		2.0	14.3	294

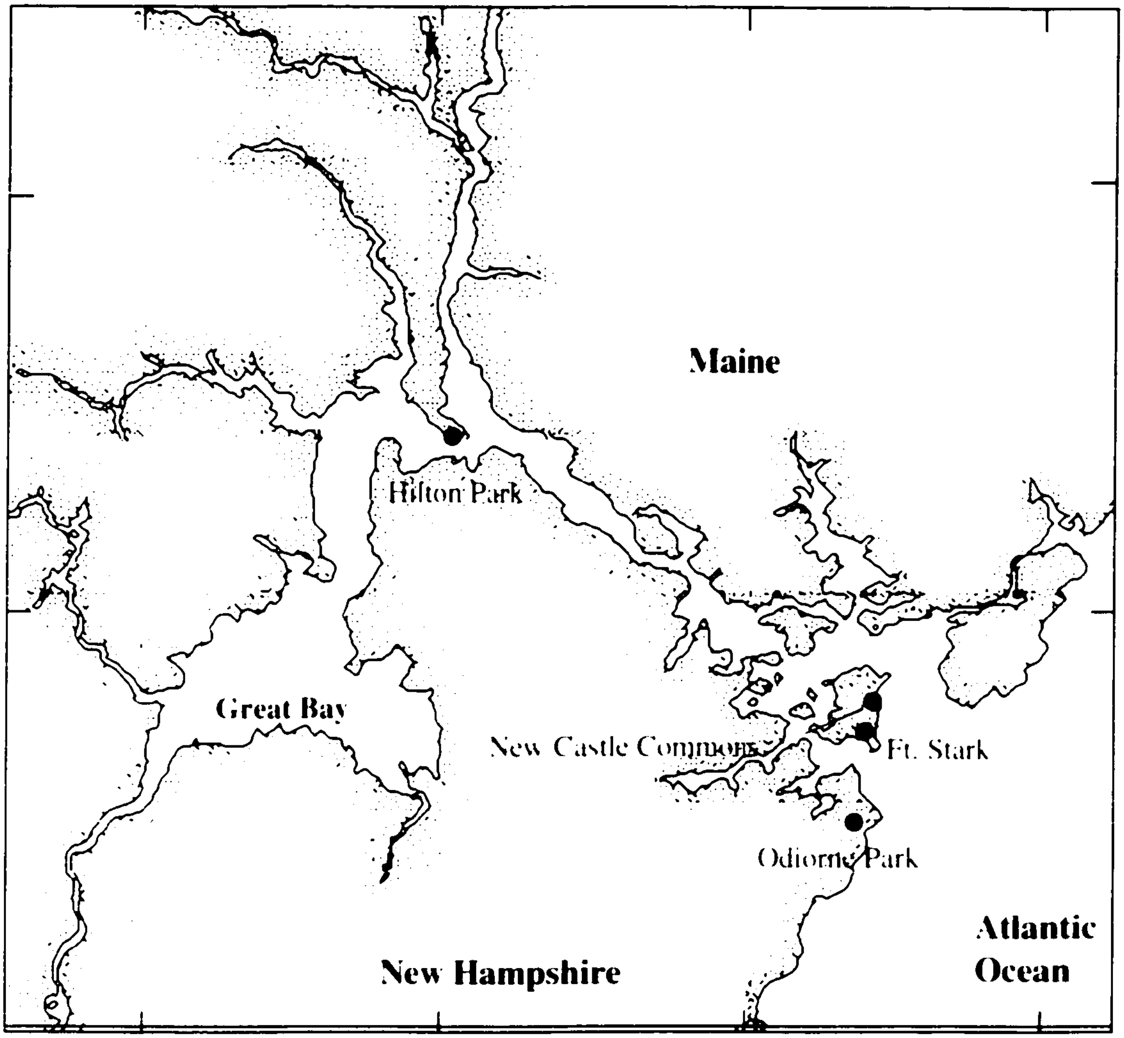


Figure 1.1. Map of the New Hampshire coast and Great Bay estuary showing study locations for *Carcinus maenas* recruitment and settlement.

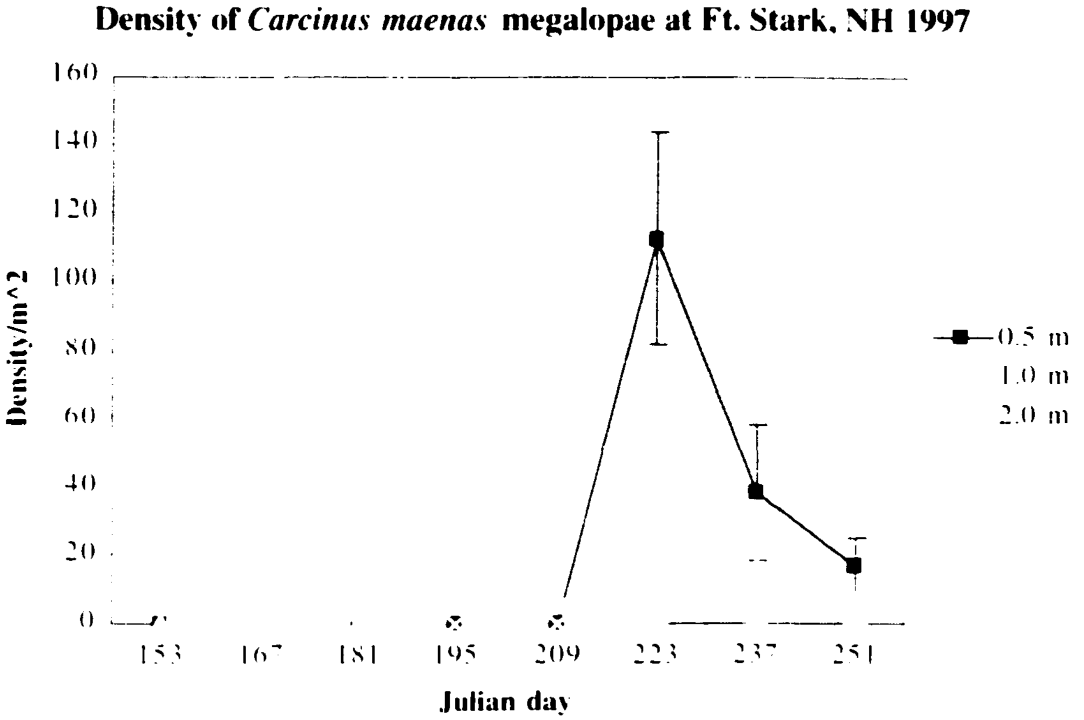


Figure 1.2: Average density and standard error of *C. maenas* megalopae in artifical settlement/recruitment panels deployed at three tidal heights (0.5, 1.0 and 2.0 m above mean lower low water) at Ft. Stark, NH in 1997.

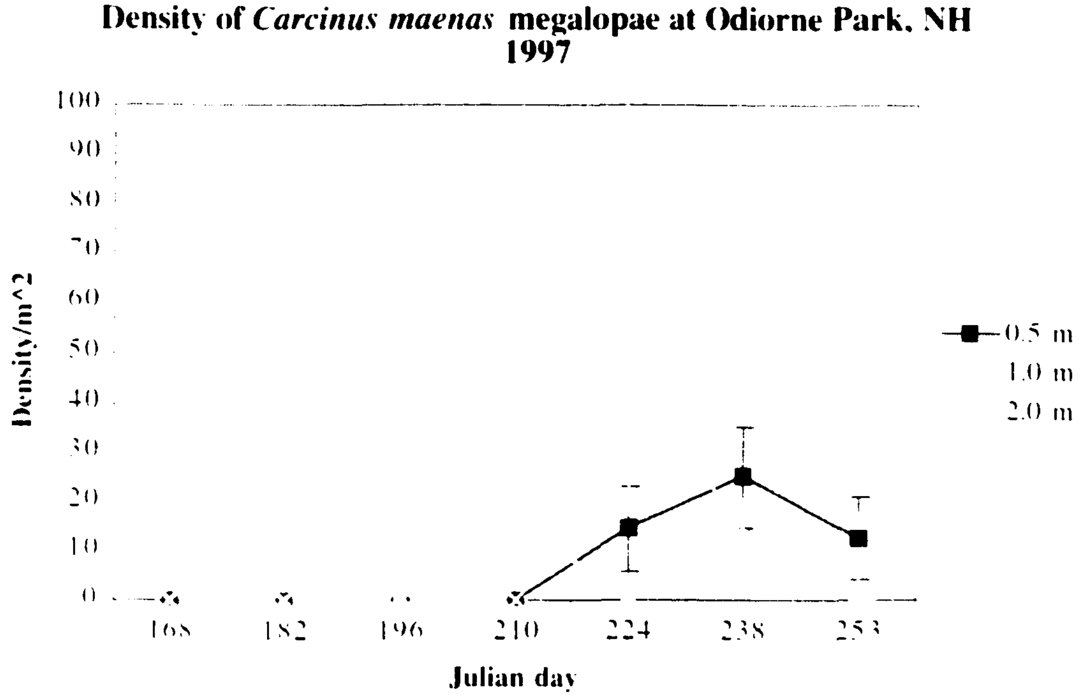


Figure 1.3: Average density and standard error of *C. maenas* megalopae in artifical settlement/recruitment panels deployed at three tidal heights (0.5, 1.0 and 2.0 m above mean lower low water) at Odiorne Park, NH in 1997.

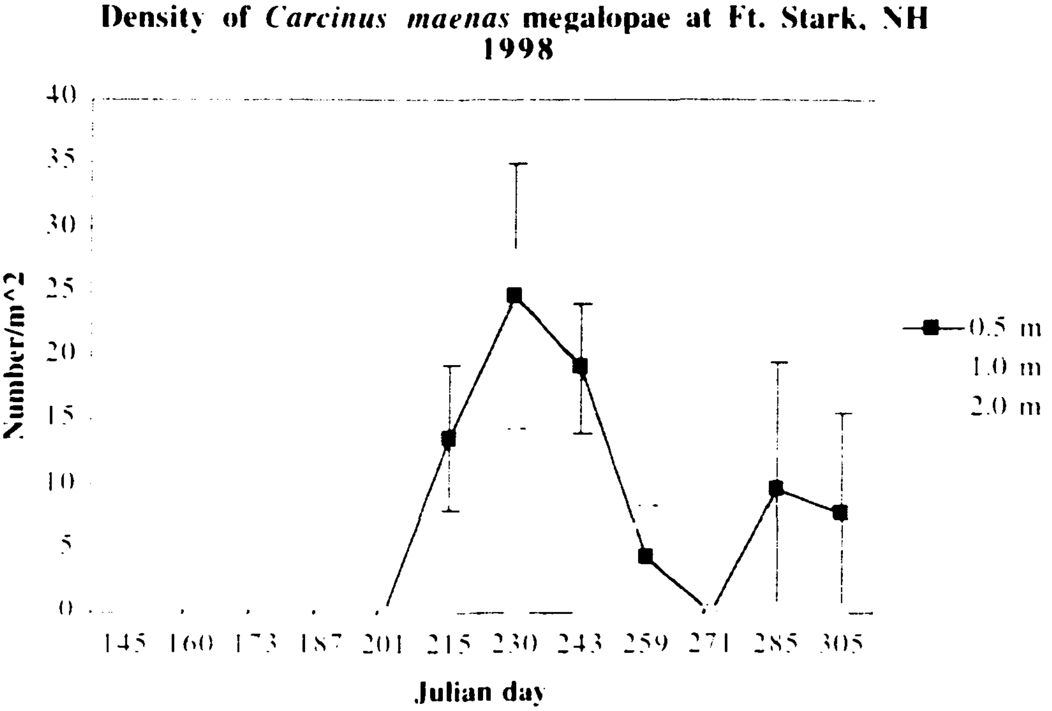


Figure 1.4: Average density and standard error of *C. maenas* megalopae in artifical settlement/recruitment panels deployed at three tidal heights (0.5, 1.0 and 2.0 m above mean lower low water) at Ft. Stark, NH in 1998.

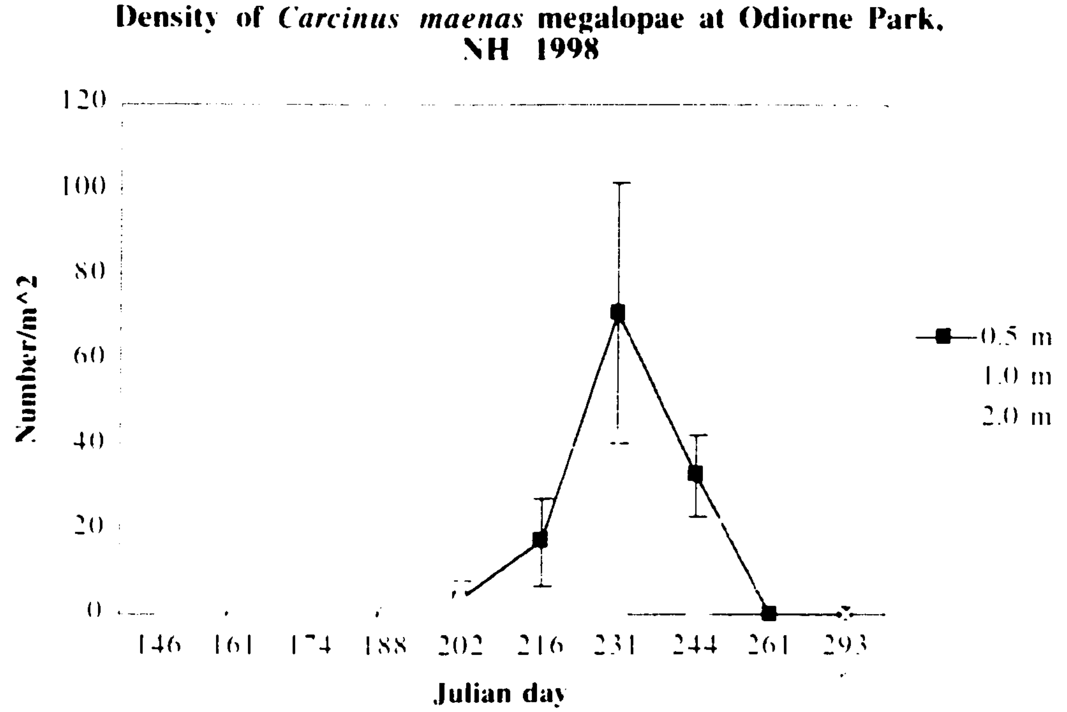


Figure 1.5: Average density and standard error of *C. maenas* megalopae in artifical settlement/recruitment panels deployed at three tidal heights (0.5, 1.0 and 2.0 m above mean lower low water) at Odiorne Park, NH in 1998. Asterick indicates that the last set of samplers were deployed for one month rather than the usual interval of two weeks.

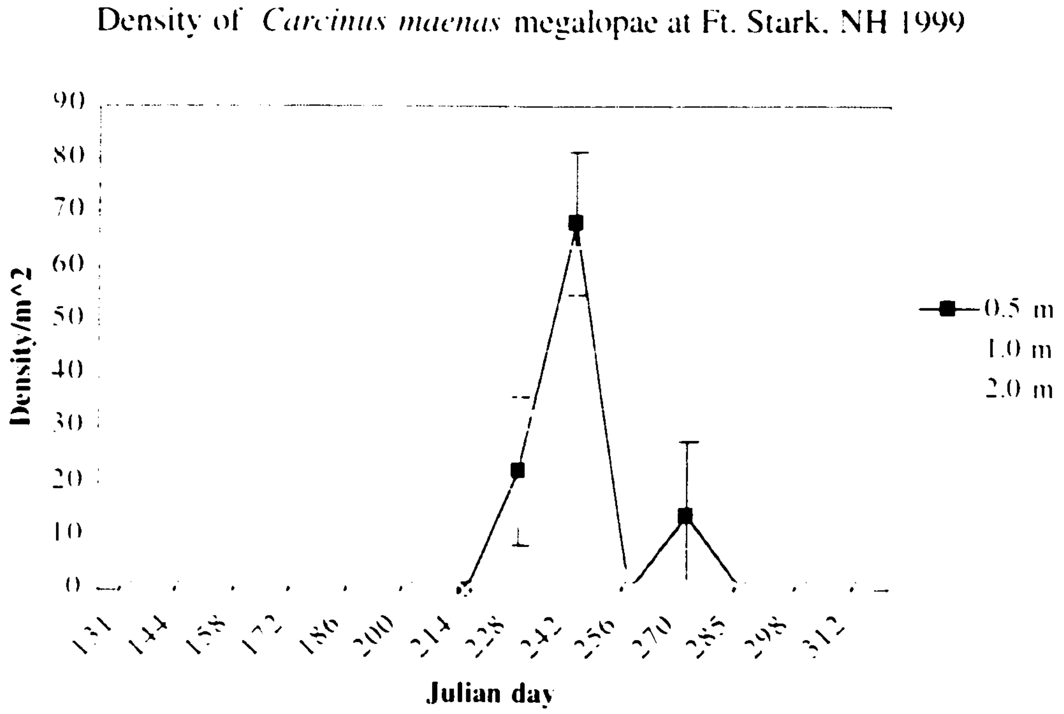


Figure 1.6: Average density and standard error of *C. maenas* megalopae in artifical settlement/recruitment panels deployed at three tidal heights (0.5, 1.0 and 2.0 m above mean lower low water) at Ft. Stark, NH in 1999.

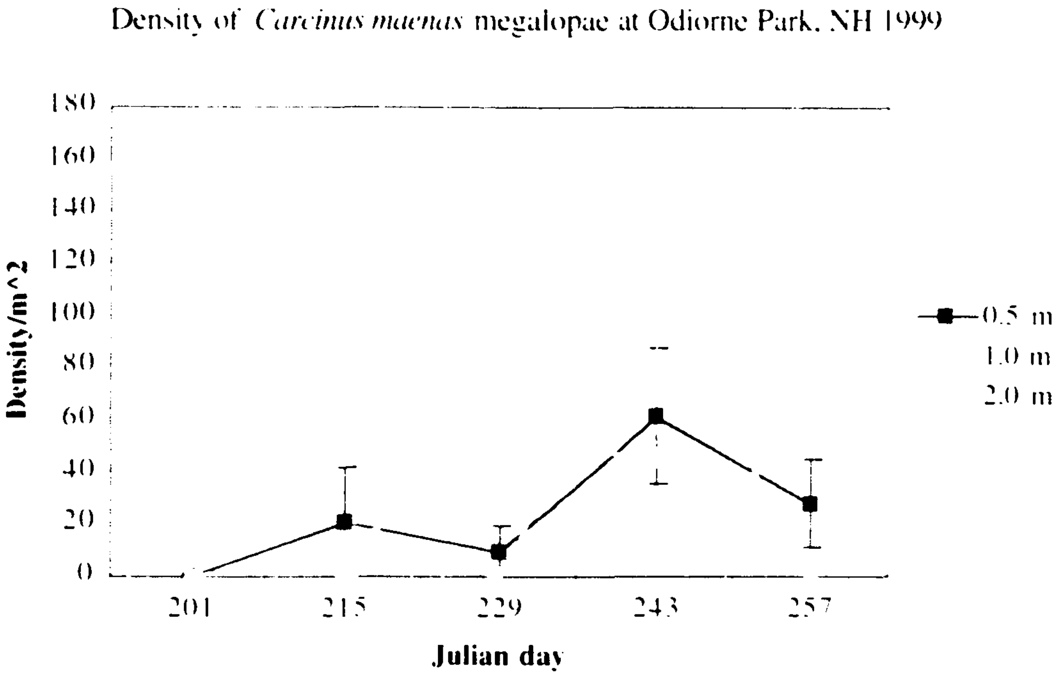


Figure 1.7: Average density and standard error of *C. maenas* megalopae in artifical settlement/recruitment panels deployed at three tidal heights (0.5, 1.0 and 2.0 m above mean lower low water) at Odiorne Park, NH in 1999.

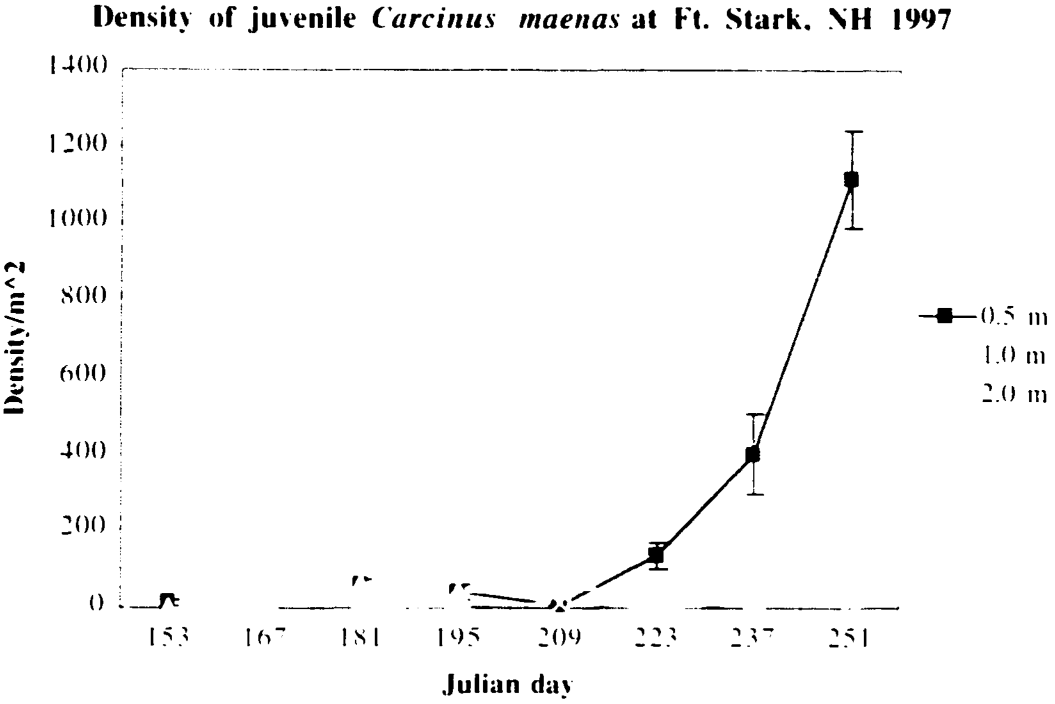


Figure 1.8: Average density and standard error of juvenile *C. maenas* in artifical settlement/recruitment panels deployed at three tidal heights (0.5, 1.0 and 2.0 m above mean lower low water) at Ft. Stark, NH in 1997.

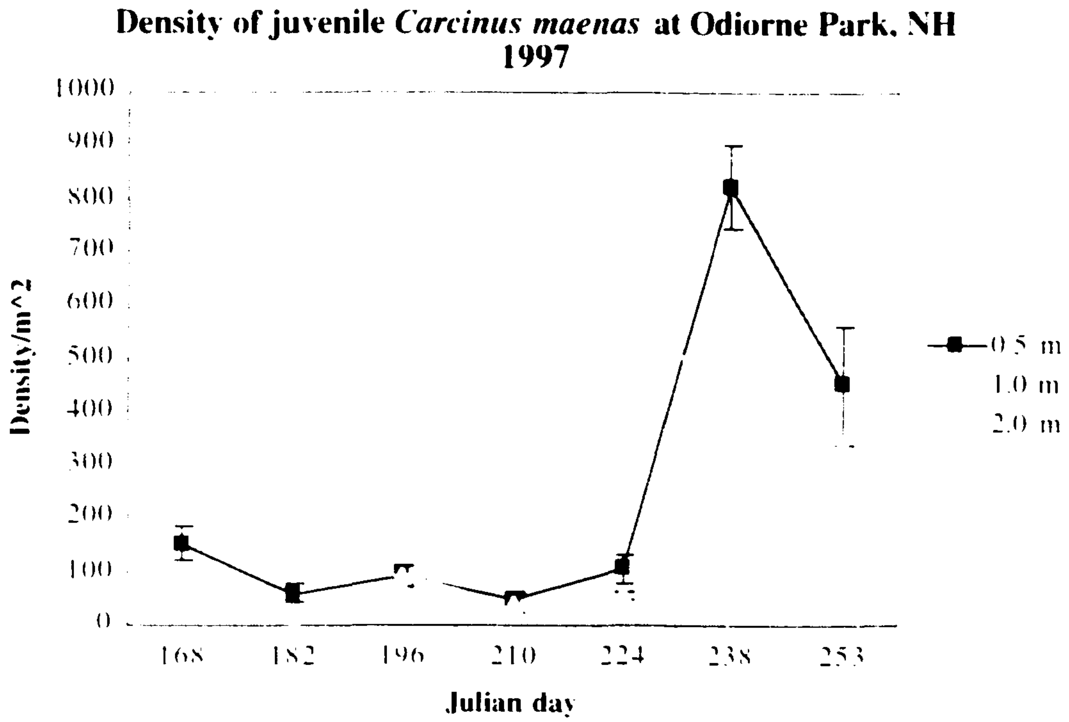


Figure 1.9: Average density and standard error of juvenile *C. maenas* in artifical settlement/recruitment panels deployed at three tidal heights (0.5, 1.0 and 2.0 m above mean lower low water) at Odiorne Park, NH in 1997.

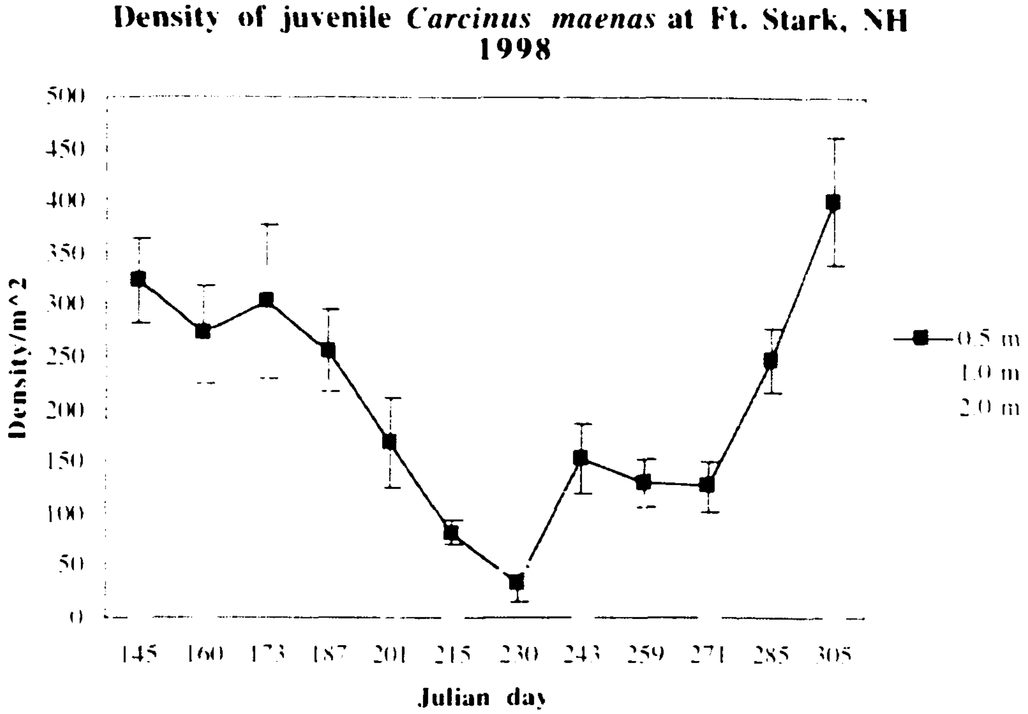


Figure 1.10: Average density and standard error of juvenile *C. maenas* in artifical settlement/recruitment panels deployed at three tidal heights (0.5, 1.0 and 2.0 m above mean lower low water) at Ft. Stark, NH in 1998.

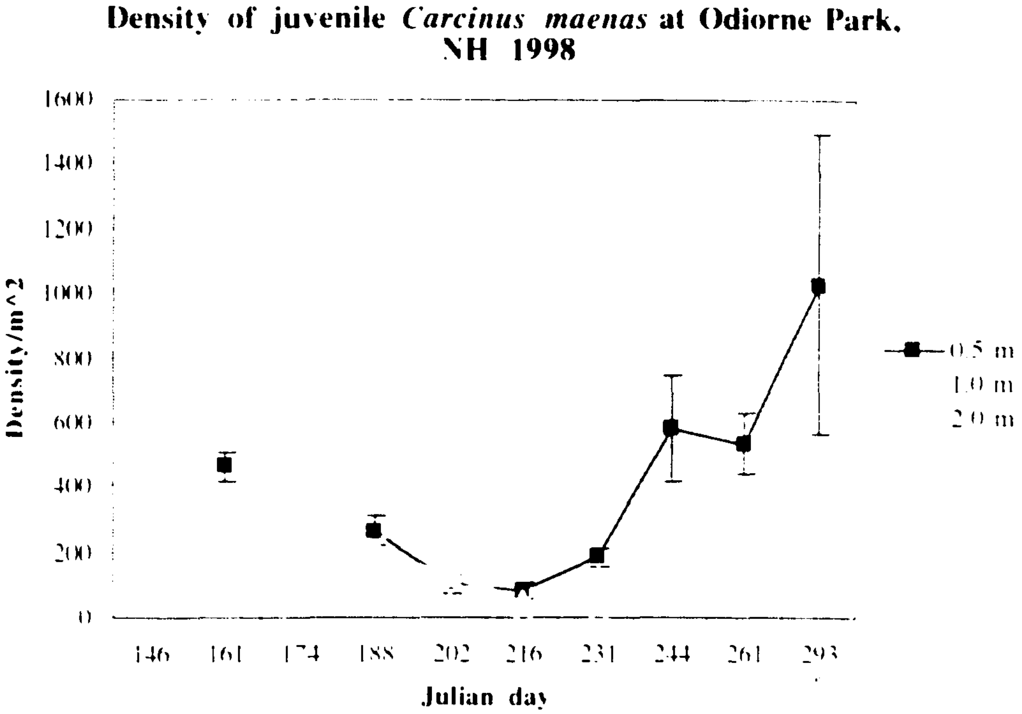


Figure 1.11: Average density and standard error of juvenile *C. maenas* in artifical settlement/recruitment panels deployed at three tidal heights (0.5, 1.0 and 2.0 m above mean lower low water) at Odiorne Park, NH in 1998. Asterick indicates that the last set of samplers were deployed for one month rather than the usual interval of two weeks.

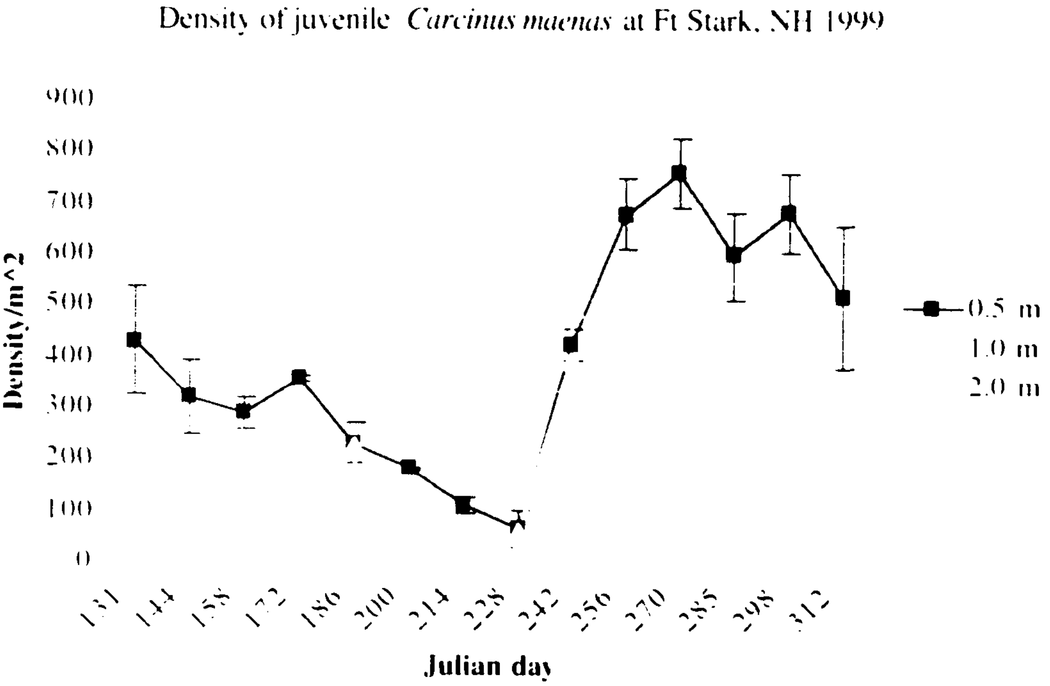


Figure 1.12: Average density and standard error of juvenile *C. maenas* in artifical settlement/recruitment panels deployed at three tidal heights (0.5, 1.0 and 2.0 m above mean lower low water) at Ft. Stark, NH in 1999.

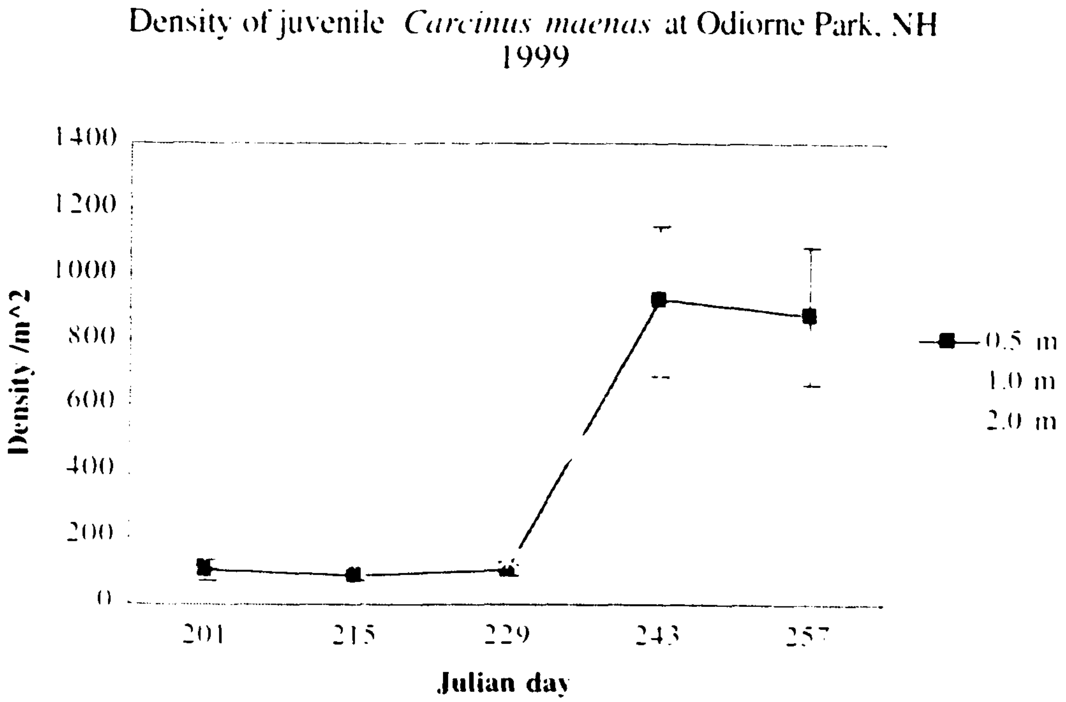


Figure 1.13: Average density and standard error of juvenile *C. maenas* in artifical settlement/recruitment panels deployed at three tidal heights (0.5, 1.0 and 2.0 m above mean lower low water) at Odiorne Park, NH in 1999.

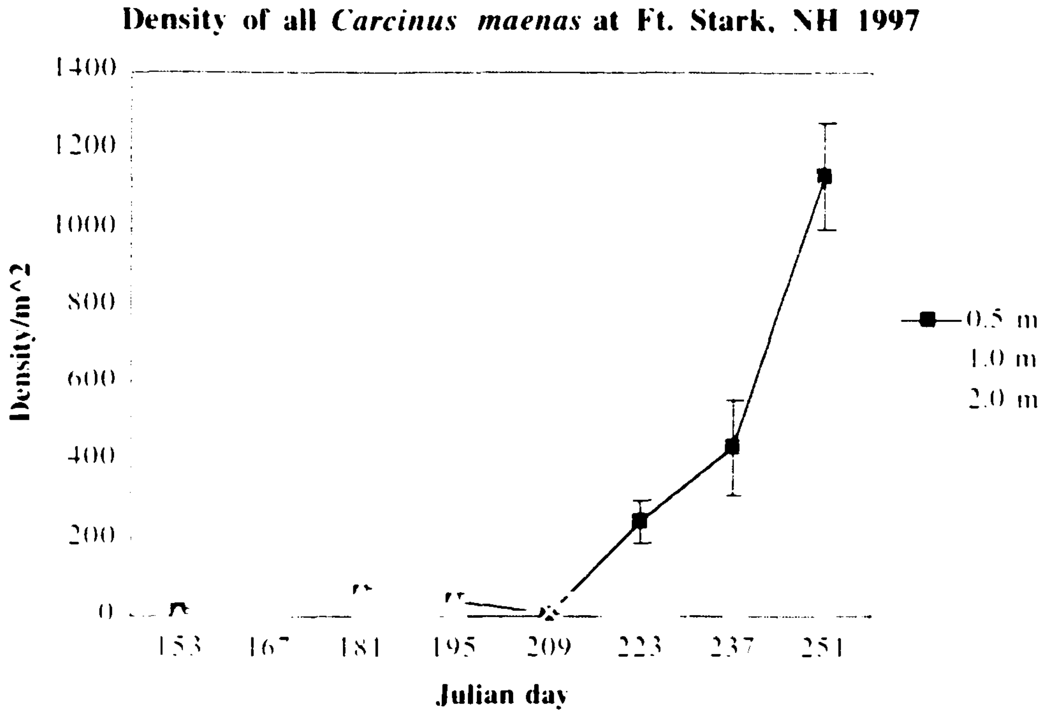


Figure 1.14: Average density and standard error of megalopae and juvenile *C. maenas* in artificial settlement/recruitment panels deployed at three tidal heights (0.5, 1.0 and 2.0 m above mean lower low water) at Ft. Stark, NH in 1997.

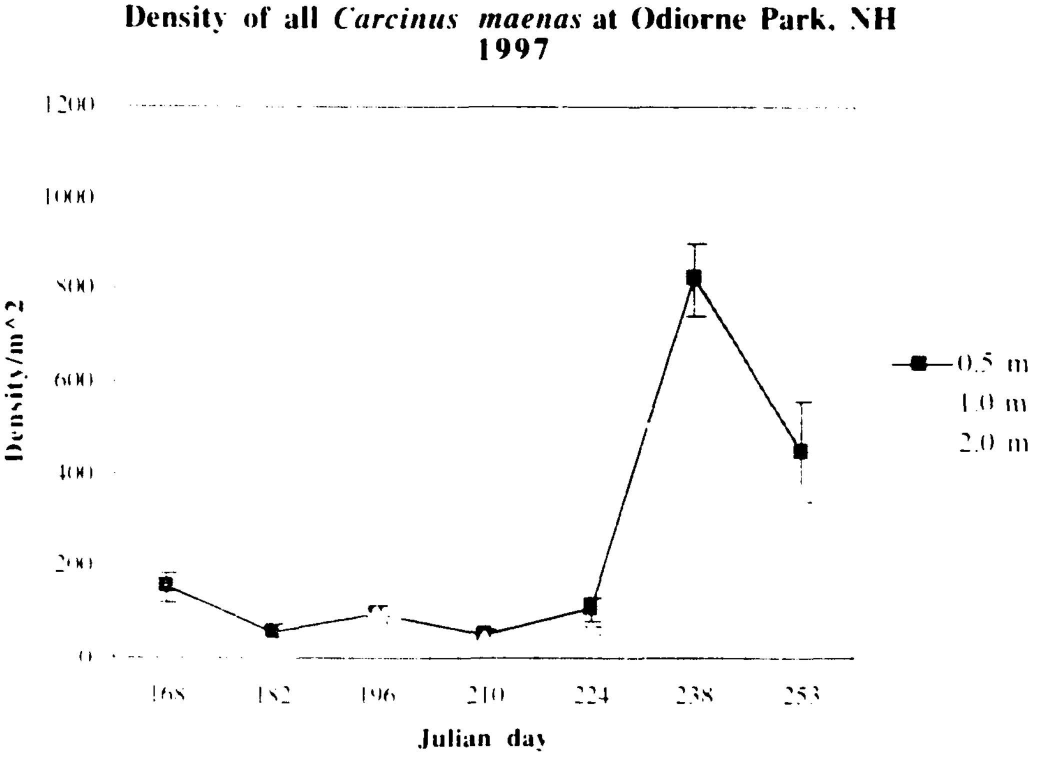


Figure 1.15: Average density and standard error of megalopae and juvenile *C. maenas* in artifical settlement/recruitment panels deployed at three tidal heights (0.5, 1.0 and 2.0 m above mean lower low water) at Odiorne Park, NH in 1997.

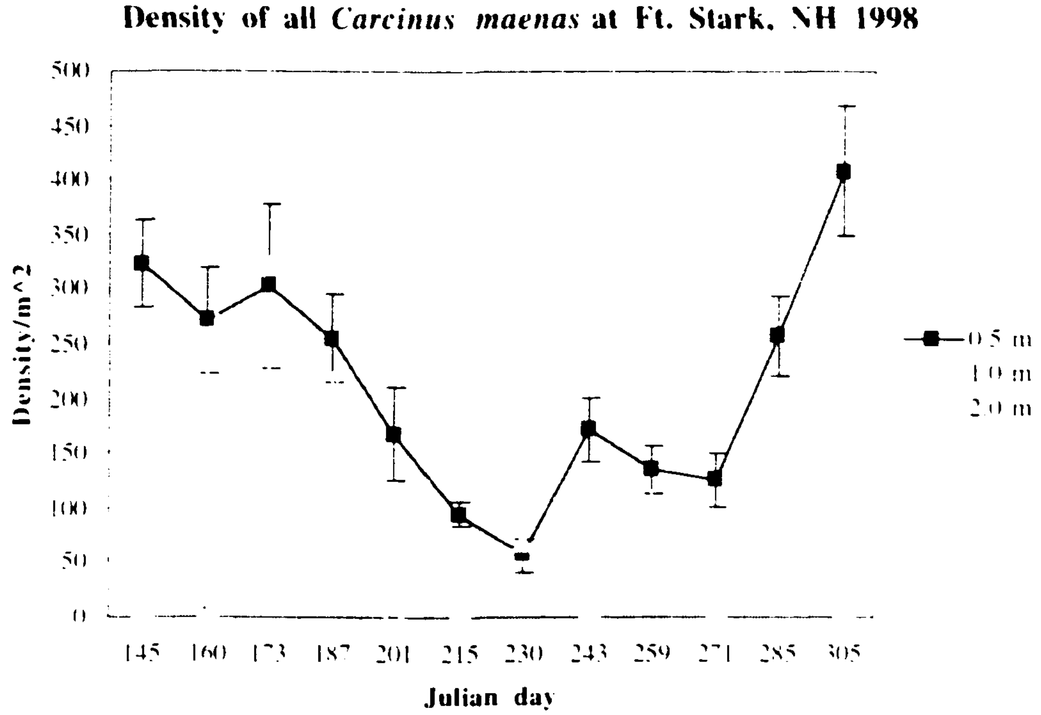


Figure 1.16: Average density and standard error of megalopae and juvenile *C. maenas* in artifical settlement/recruitment panels deployed at three tidal heights (0.5, 1.0 and 2.0 m above mean lower low water) at Ft. Stark, NH in 1998.

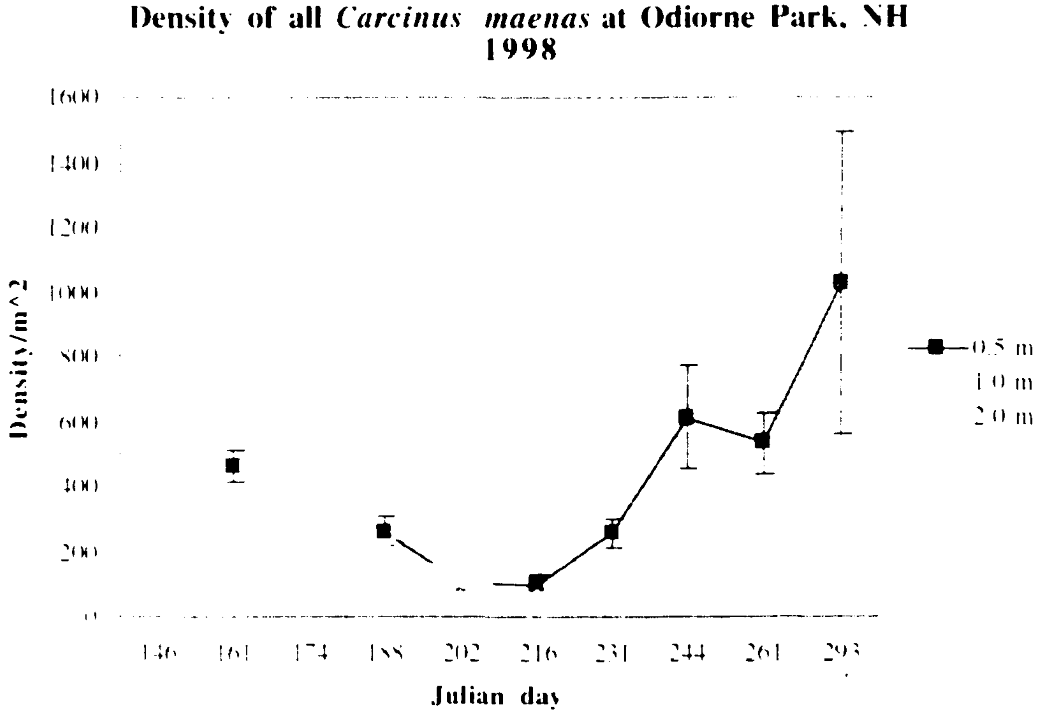


Figure 1.17: Average density and standard error of megalopae and juvenile *C. maenas* in artificial settlement/recruitment panels deployed at three tidal heights (0.5, 1.0 and 2.0 m above mean lower low water) at Odiorne Park, NH in 1998. Asterick indicates that the last set of samplers were deployed for one month rather than the usual interval of two weeks.

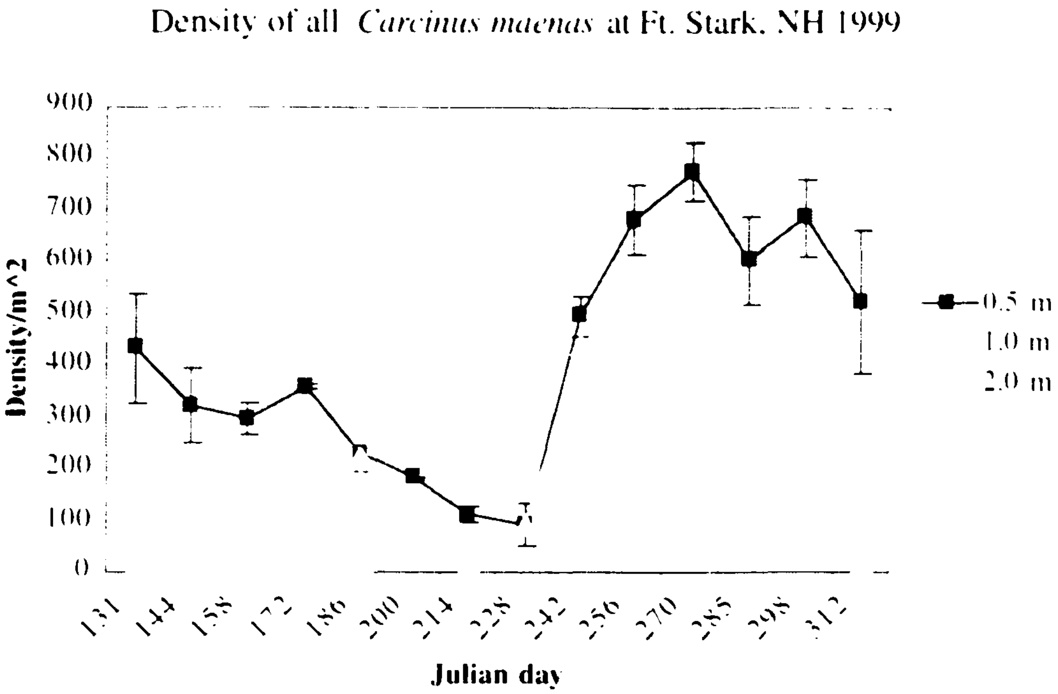


Figure 1.18: Average density and standard error of megalopae and juvenile *C. maenas* in artifical settlement/recruitment panels deployed at three tidal heights (0.5, 1.0 and 2.0 m above mean lower low water) at Ft. Stark, NH in 1999.

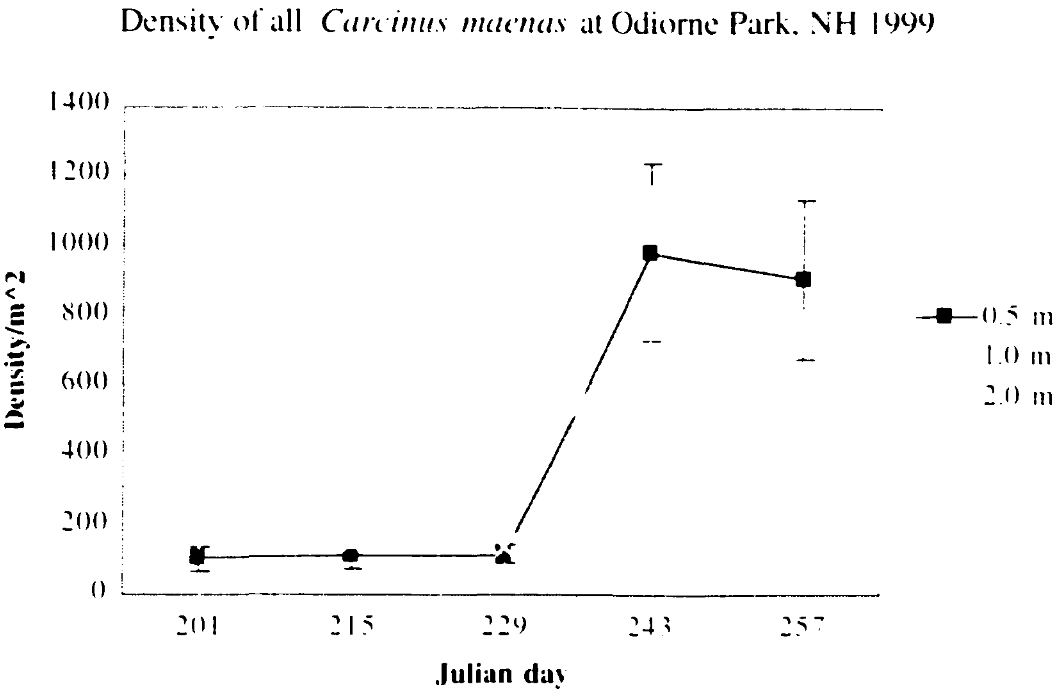


Figure 1.19: Average density and standard error of megalopae and juvenile *C. maenas* in artifical settlement/recruitment panels deployed at three tidal heights (0.5, 1.0 and 2.0 m above mean lower low water) at Odiorne Park, NH in 1999.

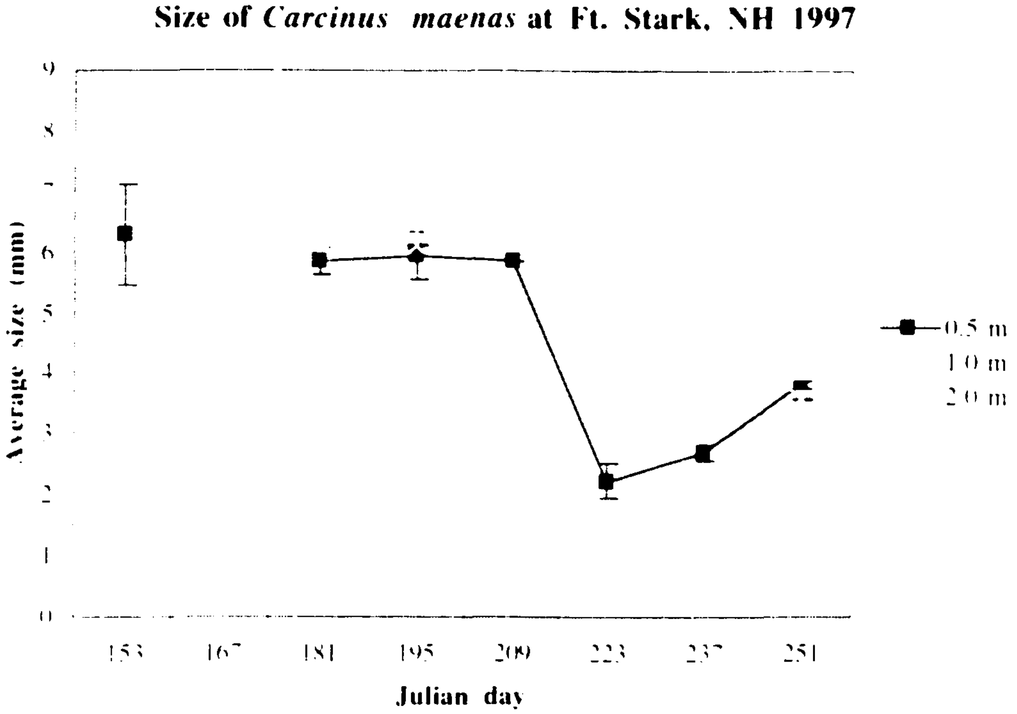


Figure 1.20: Average size and standard error of juvenile *C. maenas* in artifical settlement/recruitment panels deployed at three tidal heights (0.5, 1.0 and 2.0 m above mean lower low water) at Ft. Stark, NH in 1997.

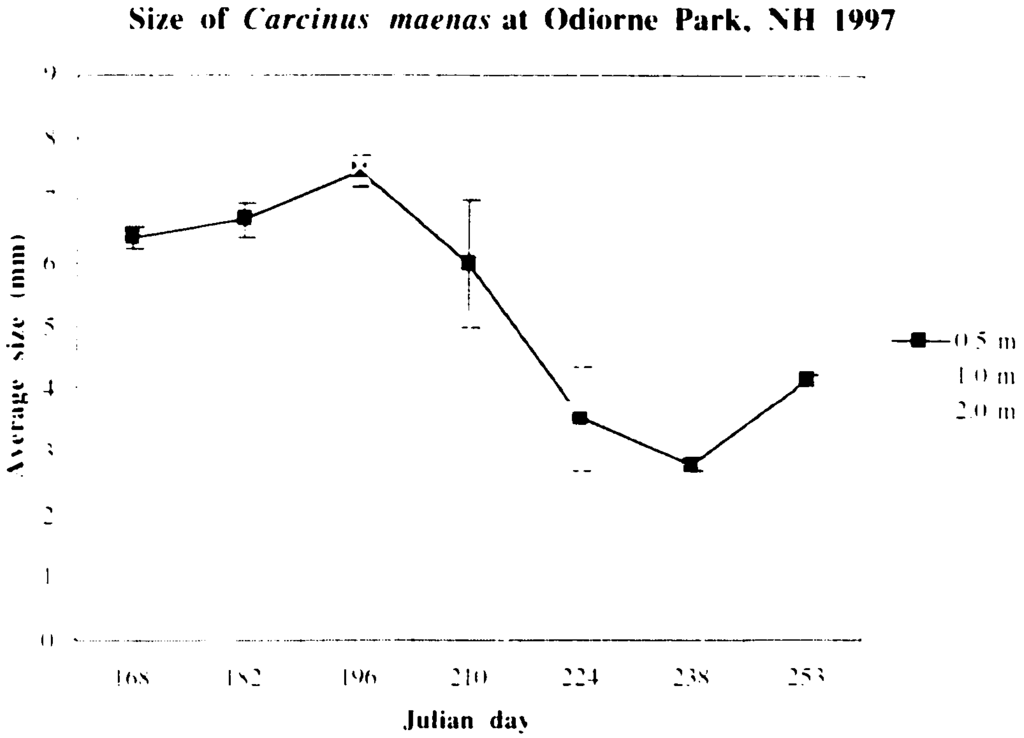


Figure 1.21: Average size and standard error of juvenile *C. maenas* in artifical settlement/recruitment panels deployed at three tidal heights (0.5, 1.0 and 2.0 m above mean lower low water) at Odiorne Park, NH in 1997.

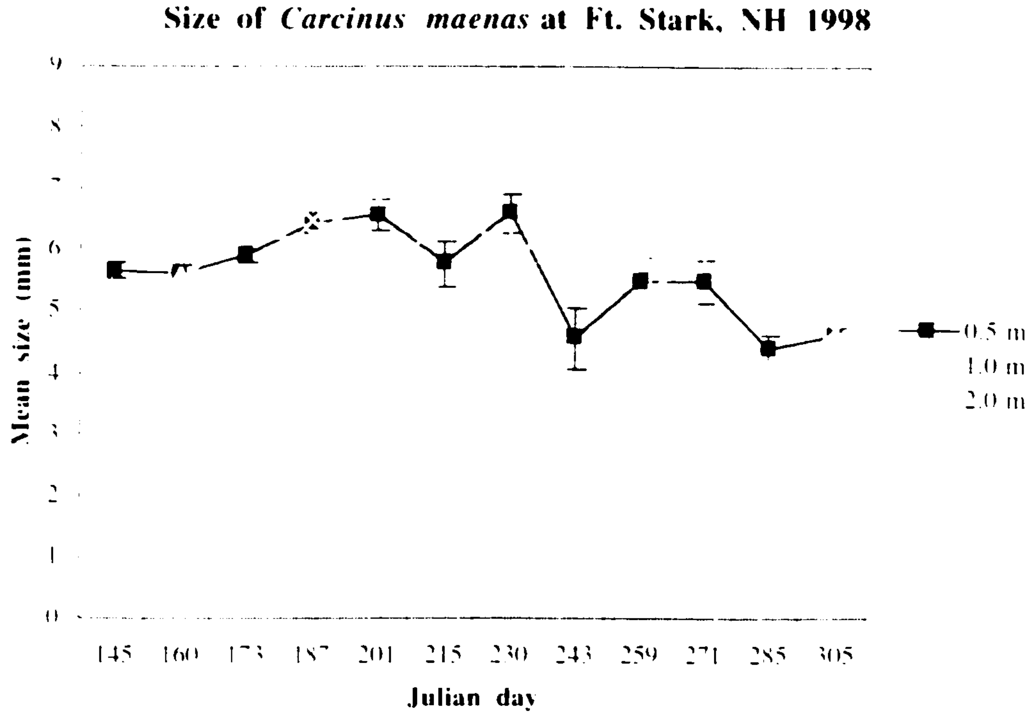


Figure 1.22: Average size and standard error of juvenile *C. maenas* in artifical settlement/recruitment panels deployed at three tidal heights (0.5, 1.0 and 2.0 m above mean lower low water) at Ft. Stark, NH in 1998. Asterick indicates that the last set of samplers were deployed for one month rather than the usual interval of two weeks.

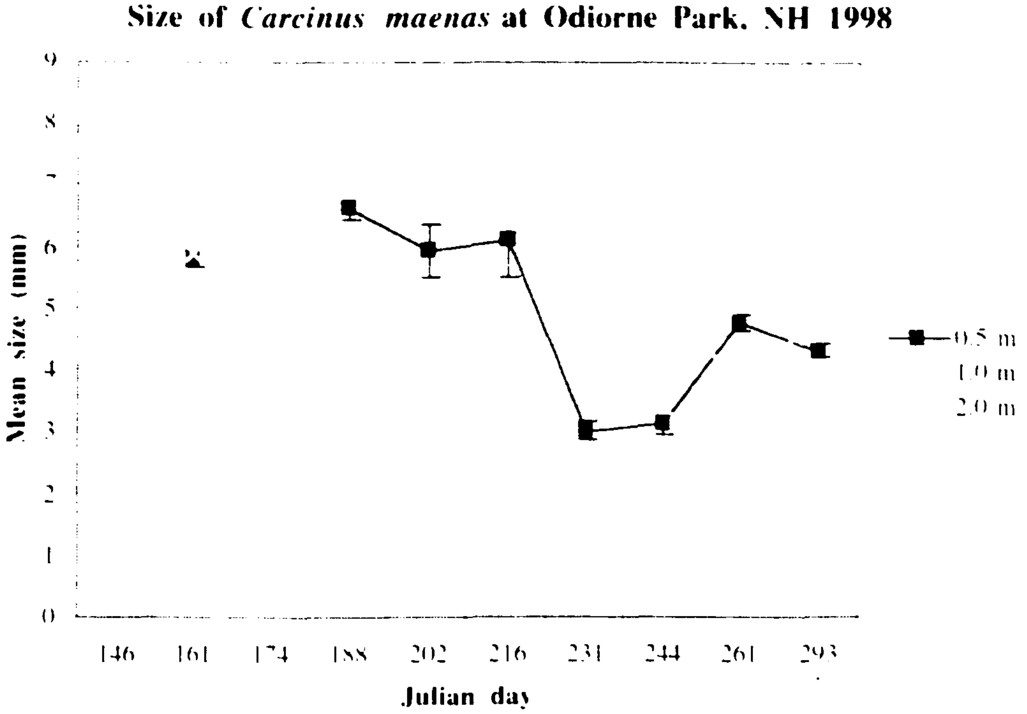


Figure 1.23: Average size and standard error of juvenile *C. maenas* in artifical settlement/recruitment panels deployed at three tidal heights (0.5, 1.0 and 2.0 m above mean lower low water) at Odiorne Park, NH in 1998.

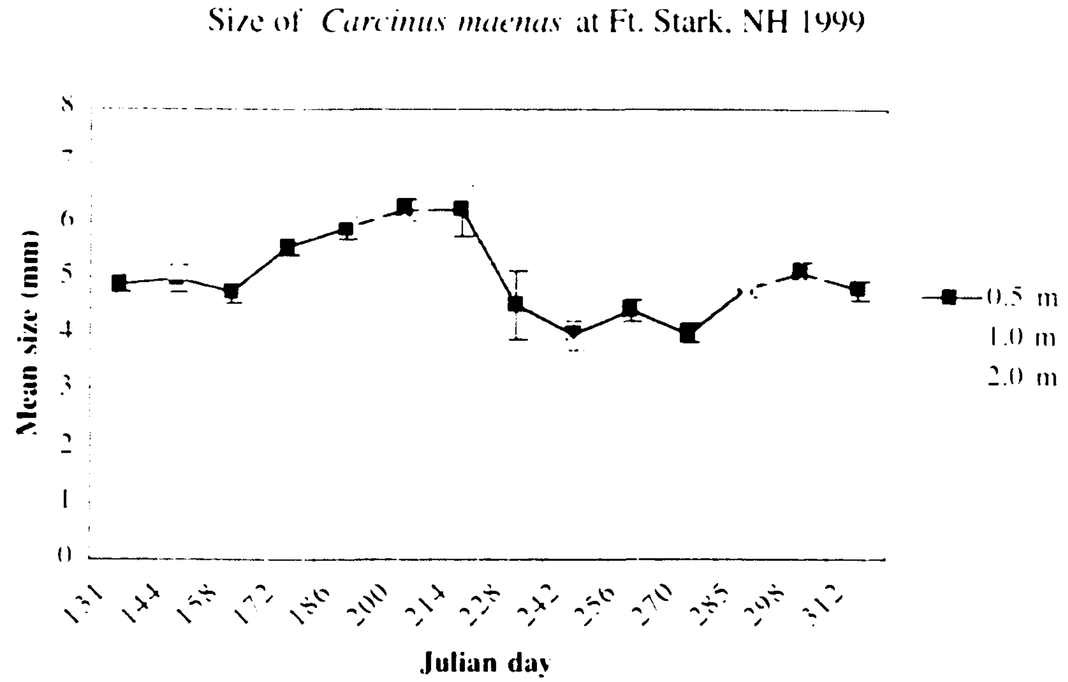


Figure 1.24: Average size and standard error of juvenile *C. maenas* in artifical settlement/recruitment panels deployed at three tidal heights (0.5, 1.0 and 2.0 m above mean lower low water) at Ft. Stark, NH in 1999.

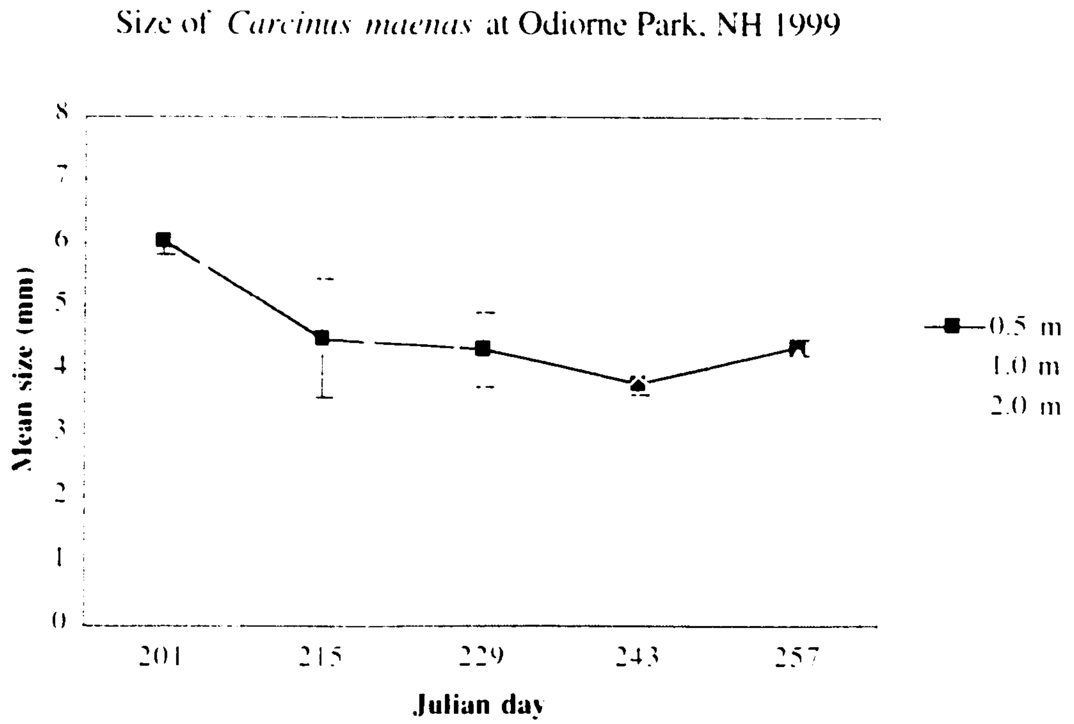


Figure 1.25: Average size and standard error of juvenile *C. maenas* in artifical settlement/recruitment panels deployed at three tidal heights (0.5, 1.0 and 2.0 m above mean lower low water) at Odiorne Park, NH in 1999.

CHAPTER II

COMMUNITY STRUCTURE OF THE NEW HAMPSHIRE ROCKY INTERTIDAL ZONE PRIOR TO THE ESTABLISHMENT OF *Hemigrapsus sanguineus*

ABSTRACT

Documentation of the effects of the establishment of an introduced species in marine habitats is much less common than for terrestrial systems. The Asian shore crab, *Hemigrapsus sanguineus*, was reported on the U.S. Atlantic coast fourteen years ago but has already become the numerically dominant crab species in rocky habitats along the mid-Atlantic coast. *Hemigrapsus sanguineus* is just beginning to establish populations in New Hampshire and northern New England. The objective of this research was to obtain baseline data documenting the temporal variation in community structure within three New Hampshire locations prior to the establishment of *H. sanguineus*. After this crab species becomes abundant at each location, before and after comparisons in community

structure can be made. While the major focus of this research was to document temporal variation in community structure within each location, some between site comparisons were also made to examine the commonality of abundance patterns between locations. Quantitative community sampling at three tidal heights was initiated at Ft. Stark and Odiorne Park in 1997 and continued for five years. An estuarine tidal rapids site, Hilton Park, was added in 1999 and data was obtained at two tidal heights for three years. Sampling at each location took place during the summer. The two coastal sites had very similar species composition which differed from that of the estuarine site, especially for algae. Species richness and evenness generally declined with increasing tidal height at all three study sites. The estuarine site had the lowest species richness and evenness overall. The distributions of several organisms appeared to be strongly affected by tidal height, there were two mollusk and one algal species that were either never or only once encountered at the highest tidal height at the two coastal sites. Both non-metric multidimensional scaling and cluster analysis of the community data indicated that there was low temporal variability between each tidal height at a particular location. A stepwise multiple regression between the density of *C. maenas* and several physical and biological factors at each site revealed that only the density of gastropods was consistently positively related to densities of *C. maenas*. *Carcinus maenas* was the dominant crab species at all locations, but by the end of the study period, *H. sanguineus* had been found at all three study locations. The densities of *H. sanguineus* were highest at the estuarine site, but it was still outnumbered by *C. maenas* by 11:1 in the final year of the study. Overall, the results of this community structure monitoring indicated that there were no consistent trends between sites in the abundance of any of the species monitored for this study which implies that these data will be useful for assessing changes that may occur after *H. sanguineus* becomes more abundant.

INTRODUCTION

Introduced species have the potential to drastically alter the recipient community, although their effects have rarely been quantified in marine habitats (Grosholz and Ruiz, 1996) but see Schwindt et al. (2001) on the reef building polychaete, *Ficopomatus enigmaticus*, in Argentina, Bertness (1984) on the gastropod, *Littorina littorea*, in New England and Nichols et al. (1990) on the Asiatic clam, *Potamocorbula amurensis*, in San Francisco Bay for important studies. In the rare instances where pre- and post- invasion data on the recipient community is available, the effects of the introduced species have been substantial. For example, the Asian clam, *Potamocorbula amurensis*, appeared to cause drastic declines in the abundance of zooplankton in San Francisco Bay shortly after its introduction in 1986 (Kimmerer et al., 1994). Nine years of data on invertebrate and shorebird abundance were utilized by Grosholz et al. (2000) to examine the impacts of the introduction of the green crab, *Carcinus maenas*, in Bodega Harbor, CA. These authors found that *C. maenas* exerted strong top down control on prey, and within three years after its arrival, it significantly reduced the abundance of two mollusk and one grapsid crab species.

The number of introduced species in the Gulf of Maine is much lower than heavily invaded regions such as San Francisco Bay, yet the success of some of the species that have been introduced is evident. In fact, some of the most common species within the Gulf of Maine ecosystem are introduced. The most common snail in New England, *Littorina littorea*, was introduced and has displaced a native snail *Ilyanassa obsoleta* (Brenchley and Carlton, 1983) and it also transforms habitat from marsh to cobble beach (Bertness, 1984). The introduced green alga *Codium fragile* has replaced *Laminarian* kelp as the dominant canopy forming algae at the Isles of Shoals (Harris and Tyrrell, 2001). *Carcinus maenas* was also introduced to the U.S. Atlantic coast and was blamed for the collapse of Maine's soft shell clam, *Mya arenaria*, industry (Ropes, 1968).

Recently, another introduced species, the Asian shore crab, *Hemigrapsus sanguineus*, has become extremely abundant along the U.S. Atlantic coast. The first record of *H. sanguineus* in the U.S. was in New Jersey in 1988 (Williams and McDermott, 1990) and since that time, it has expanded to become one of the most conspicuous organisms on rocky shores from Long Island Sound to North Carolina (Lohrer and Whitlatch, 1997; Lohrer, 2000; McDermott, 2001). *Hemigrapsus sanguineus* was found in New Hampshire in 1998 (McDermott, 2001) and since that time, has been discovered at a variety of coastal and estuarine locations (Tyrrell, unpub. data). Because of its extremely high densities in areas where it is already well established (New Jersey, McDermott, 1998; Long Island Sound, Lohrer, 2000; southern Massachusetts, Ledesma and O'Connor, 2001) and omnivorous feeding habits (Lohrer and Whitlatch, 1997; Tyrrell, 1999; Tyrrell and Harris, 2001), *H. sanguineus* is likely to have a substantial impact on the recipient community.

The ongoing range expansion of *Hemigrapsus sanguineus* along the Atlantic coast of the U.S. provided a rare opportunity to determine the effects of an invasion by obtaining data on the community before the invasion occurs. In anticipation that *H. sanguineus* would become established in northern New England, I began collecting quantitative community data at two coastal sites in 1997. Grosholz et al. (2000) used long term community structure monitoring data in combination with laboratory feeding experiments to document the impacts of the introduction and establishment of *C. maenas* in Bodega Harbor, CA. This is the first study that documents temporal variation in rocky intertidal community structure in anticipation of the establishment of a marine invader.

In a recent review, Brown et al. (2001) emphasized the utility of long term experiments in elucidating complex interactions between the fluctuating abundances of species and variable environmental conditions. By combining my observations from this long term community structure monitoring data with the results of feeding and microcosm experiments, I provide insight into potential changes in the rocky intertidal community that may occur as *H. sanguineus* becomes prominent in the community.

MATERIALS and METHODS

Study sites

I conducted long term monitoring of community structure using quadrat sampling at two coastal and one estuarine site in New Hampshire (Fig. 2.1). *Carcinus maenas* is abundant at all of the study locations, indicating that each site provides suitable habitat for intertidal crabs. I selected the coastal sites because these communities had similar species composition and abundance: Fort Stark, Newcastle, NH (43 03.51N, 70 42.75W) and Odiorne State Park, Rye, NH (43 02.62N, 70 42.97W). These are rocky habitats along the coast with little to moderate exposure to wave action. Canopy forming fucoid algae dominate both coastal sites. Two years after I began conducting this research at the two coastal sites, I added an estuarine site to my sampling regime to increase the scope of habitat being monitored. I conducted long term community structure monitoring in these two different habitats (coastal and estuarine) because *Hemigrapsus sanguineus* can become established in both types of habitats (for coastal habitats, Lohrer and Whitlatch, 1997; pers. obs.; for estuarine habitats, Epifanio et al., 1998; McDermott, 1998, Ledesma and O'Connor, 2001, pers. obs.). The estuarine site, Hilton Park, Dover Point, NH (43 07.00N, 70 50.00W) is a tidal rapids with little exposure to waves. In contrast to the coastal sites, Hilton Park has less rock bench substrate, a higher proportion of sand and a lower abundance of canopy fucoid algae.

Quadrat sampling

To reduce variability at a particular site between years, I finished all of the sampling at a particular site before I started sampling at another site. The quadrat sampling was labor intensive and it took at least two weeks and up to two months to complete sampling at each site. Sampling dates for each site are shown in table 2.1.

Table 2.1: Sampling dates for long term community structure monitoring prior to the establishment of *H. sanguineus* in New Hampshire.

Year	Ft. Stark	Odiorne Park	Hilton Park
1997	8/8 to 9/7	9/14 to 9/30	N/A
1998	7/10 to 8/4	8/13 to 8/27	N/A
1999	6/18 to 8/2	8/5 to 8/27	9/2 to 9/29
2000	6/9 to 7/6	7/11 to 7/31	8/21 to 10/21
2001	6/14 to 7/4	7/9 to 7/31	9/10 to 9/23

Using tidal data from Harbormaster (Zihua Software, Marlborough, CT), I established three tidal heights (0.5 m, 1.0 m and 2.0 m) above mean lower low water (MLLW) at both coastal sites. These tidal heights were used as a reference point in order to locate quadrats at the same tidal height on subsequent sampling dates. At Hilton Park, I only conducted quadrat sampling at the lower two tidal heights because the substrate at 2.0 m above MLLW was very large boulders which prohibited my sampling design. Each day, I attached a 30 m transect line to the reference point and used a random numbers table to determine where each quadrat would be placed. Ten quadrats (0.25 m^2) were randomly located along the transect at each tidal height. Each quadrat was positioned so that it was horizontal or nearly horizontal on the substrate.

I collected data on three different aspects of the community: the canopy algae (or in cases where the canopy was incomplete, the substrate), the understory algae and substrates, and the animals that occurred within the quadrat. The type of canopy cover (mostly fucoid algae) was determined under 25 intersections of monofilament line. In cases where the algal canopy was incomplete, the type of substrate (rock bench, cobble, pebbles, etc.) was recorded. There was a consistently thick algal canopy at Ft. Stark and I displaced canopy algae outside the quadrat to obtain subcanopy (substrate and understory algae) data. Odiorne algal canopy cover was patchier than that at Ft. Stark and therefore separate subcanopy data were not taken at Odiorne in 1997. However, in subsequent years, I recorded subcanopy data at each site. I carefully checked all canopy algae for the presence of snails before displacing it outside of the quadrat.

The subcanopy data were also obtained under 25 intersections of monofilament line. The numbers of barnacles (*Semibalanus balanoides*) and mussels (*Mytilus edulis*) were counted in four (69 cm-^{2}) subsections of the quadrat. These subsections were created by the monofilament line and counts were performed in subsections arranged along a diagonal of the quadrat. The proportions of barnacles and mussels in varying size classes were also estimated. Gastropods (mostly littorinids and *Nucella lapillus*) were counted, and the number in each size class was recorded. These gastropods were measured from the tip of the spire to the end of the siphonal canal using calipers. Limpets, *Notoacmea testudinalis*, were not removed nor measured, but they were counted.

I collected all crabs from within the quadrat by overturning all rocks and sifting through the softer substrates (shell hash, mud etc.). The carapace width (CW) of each crab was measured using calipers and sex was recorded if it could be determined. Missing chelae and legs were recorded as well as the occurrence of ovigerous females. Megalopae and very small crabs (less than 2 mm CW) were counted but not measured due to their extremely small size and fragility. I noted the presence of amphipods, isopods and annelids, but I did not count these organisms due to their high abundance and rapid movement. Finally, I also recorded the number of urchins, *Strongylocentrotus droebachiensis*, and the presence of other rare organisms (anemones, nudibranchs).

A total of 361 0.25m^2 quadrats were analyzed in this study (60 at Hilton Park, 151 at Odiorne and 150 at Ft. Stark). Results from individual quadrats were averaged from each tidal height at each site for every year. To facilitate analysis, I created several categories for algal species that either had similar life histories (annual or ephemeral periodicity) or that were encountered as unattached drift. The ephemeral/drift algae category included the drift algae as well as various uncommon ephemeral red and green algal species. The subcanopy algae category was mostly *Mastocarpus stellatus* but *Chondrus crispus*, crustose algae and various ephemeral red and green species also comprised this category.

Statistical analysis

To examine temporal variability in community structure, I tested the abundance of a species or substrate type (subcanopy analyses only) at a particular tidal height at each sampling location. Canopy and subcanopy percent cover data were square root arcsine transformed prior to statistical analysis. Count data (*S. balanoides*, *M. edulis*, littorinids and *C. maenas*) were also square root transformed prior to statistical analysis. After transformation, I examined the data for normality. If the distribution was heavily skewed or bimodal, I used the non-parametric Kruskall-Wallis test in place of Analysis of Variance (ANOVA). To compare size distributions of potential prey species through the years, I calculated the percent of the total in each size class. I then compared the percent in a particular size class through the sampling period (e.g. percent of *L. littorea* in the 0-

10 mm size class at the 0.5 m tidal height at Ft. Stark from 1997-2001). Post hoc tests were Tukey's for ANOVA and Dunn's test for Kruskall-Wallis. Statistical analyses were performed using Instat version 2.01 (Graphic software) and Systat version 9.0 (SAS Institute).

Multiple regressions were used to examine relationships between the number of *C. maenas* and various physical and biological factors. The physical factors consisted of two categories: tidal height (0.5, 1 or 2.0 m) and the sum of the amount of substrate that was classified as either pebble/shell, cobble or large rock for each quadrat. The biological factors were: the abundance of canopy algae, the number of snails (Littorinids, *N. lapillus* and *N. testudinalis*), the number of *S. balanoides* and the number of *M. edulis*.

I calculated the species richness and Pielou's J equitability (evenness) at each tidal height at each site. I chose these two indices because they are simple to calculate (versus other indices) and because they each emphasize different aspects of species diversity (richness and evenness) (Magurran, 1988). For the evenness calculations, I excluded quadrats that had only one algal species (Table 2.2)

Table 2.2: Number of quadrats with only 1 algal species. Only quadrats that had more than one algal species were included in evenness calculations.

Location	Year	Tidal height 0.5	1.0	2.0
Hilton Park	1999	1	3	
	2000	3	3	
	2001	4	5	
Odiorne Park	1997	6	4	5
	1998	5	0	6
	1999	0	1	5
	2000	3	0	7
	2001	2	1	5
Ft. Stark	1997	0	0	2
	1998	0	4	2
	1999	0	0	3
	2000	0	3	5
	2001	0	1	7

I used Shannon-Wiener diversity estimates for the algal percent cover data (both canopy and subcanopy categories combined) to calculate Pielou's J. Richness was calculated in two ways: once when only organisms that were identified to species were included in the estimate and once when groups of organisms (those not identified to species- e.g. amphipods, isopods, anemones, etc.) were included in the estimate.

To examine the relationships between the communities at different tidal heights at each site, cluster analysis and a form of ordination known as nonmetric multidimensional scaling (MDS) were performed. MDS calculates coordinates for samples so that the distances between them reflect their dissimilarities as closely as possible. The stress of an MDS plot, a measure of confidence, reflects the amount of distortion that was required to compress the distances between the samples into the particular amount of dimensions (Field et al., 1982). Stress of an MDS plot always rises as number of dimensions are reduced. Stress levels that are between 0.1 and 0.2 generally indicate that the MDS is a good representation of the data but when stress values approach 0.2, the MDS plot is better suited for interpreting coarse scale rather than fine scale patterns in the data (Clark and Warwick, 1994).

Both count and percent cover data were analyzed in the ordinations simultaneously, so to minimize the count data (especially *S. balanoides* which could reach densities of thousands per m^2) relative to the percent cover data (canopy and subcanopy), the data were log transformed ($\log_{10}$ [1+y]). Following the suggestions of Clarke and Warwick (1994), I chose to severely transform the data rather than to standardize it because I considered the differences in total abundance of species between sites to be relevant information for discriminating between the sample years and study locations. There were 28 categories which consisted of algae and substrates observed in canopy analysis, algae and substrates observed in subcanopy analysis, and total number of: each mollusc species, *S. balanoides* and *C. maenas*. The one exception was Odiorne 1997 data; no subcanopy data were taken during this year so the groups are based on average values of 19 categories of abundance for this site in 1997. The average value for all 10 quadrats at a particular tidal height in a particular year in each of the 28 categories was utilized for both the cluster analysis and the MDS. The cluster analysis utilized Ward's minimum variance and Euclidean distances. The cluster analysis was performed for each site individually and for all sites simultaneously. The MDS was performed on a Bray-Curtis dissimilarity matrix and all sites were examined simultaneously for the MDS. Finally, I examined the relationship between the scores for each MDS axis (response variable) and the year, tidal height and location using analysis of variance (ANOVA). I checked the distributions of the scores for normality prior to performing the ANOVA. In order to have a complete factorial design for the ANOVA, I only utilized data from the 0.5 and 1.0 m tidal heights and for the years 1999-2001.

RESULTS

Ft. Stark

The evenness of algae at Ft. Stark was very consistent and relatively high at the 0.5 m tidal height throughout the sampling period (Fig. 2.2). At the 1.0 m tidal height, the algal evenness fluctuated from 1997 to 2001. Evenness declined at the 2.0 m tidal height from 1997 to 1999, held steady from 1999 to 2000, and then declined greatly in 2001. Both methods to estimate richness produced very similar results at Ft. Stark: richness was always lowest at the 2.0 m tidal height and highest at the 0.5 m tidal height (Figs. 2.3a and b). There was a small but steady increase in richness from 1997 to 2000 at both the 0.5 and 1.0 m tidal heights and then a slight decline in 2001 (Figs. 2.3a and b).

Fucoid algae dominated the rocky intertidal zone at Ft. Stark. *Fucus vesiculosus* and *Ascophyllum nodosum* co-dominated at the 0.5 m tidal height and through the years the rank order of abundance of these two species fluctuated (Fig. 2.4a). In 1998, the abundance of *F. vesiculosus* at this tidal height was significantly higher than that of 2001 (Table 2.3). A similar pattern of fluctuating co-dominance occurred at the 2.0 m tidal height but the fluctuation was between *A. nodosum* and *F. spiralis* (Fig. 2.4c). The peak abundance of *F. vesiculosus* at the 2.0 m tidal height in 1998 was significantly higher than both 1999 and 2001 (Table 2.3). In contrast to the temporal shifts in relative abundance of the upper and lower zones, *A. nodosum* was consistently the most abundant canopy species at the 1.0 m tidal height (Fig. 2.4b). The ephemeral/drift algae category comprised relatively little of the percent cover at all tidal heights through the years. This category was primarily composed of drift algae with some ephemeral red algal species.

The lower intertidal zone of Ft. Stark was mostly composed of pebble/shell substrates (Fig. 2.5a). The relative proportion of soft substrates (mud/sand) in the lower intertidal zone was significantly lower in 1997 as compared to 1999, 2000 and 2001 (Table 2.4). *Mastocarpus stellatus* was the most common subcanopy algal species in the lower intertidal zone at Ft. Stark and the percent cover of subcanopy algae category showed an increasing, but non-significant trend from 1998 to 2001 (Table 2.4; Figure 2.5a). The mid intertidal zone at Ft. Stark was mostly composed of rock bench substrates (Figs. 2.5b) with some cobble and pebble/shell substrates. The subcanopy algae category at the 1.0 m tidal height was composed of a mixture of *M. stellatus* and crustose algae. An increase in the amount of substrate that was categorized as rock bench occurred at the 2.0 m tidal height from 1997 as compared to 1999 and 2001 (Table 2.4; Figure 2.5c). In contrast, the amount of substrates that were categorized as large rock was significantly lower in 1999 and 2000 as compared to 1997 (Table 2.4). There were no subcanopy algae at the highest tidal height throughout the sampling period (Fig. 2.5c).

There were large fluctuations in the abundance of *S. balanoides* at Ft. Stark throughout the sampling period (Figs. 2.6a – c), particularly at the 2.0 m tidal height (Table 2.5). From 1998 to 1999, the density of *S. balanoides* in the high intertidal zone dropped by an order of magnitude, but by the following year, the density was almost double that in 1998 (Fig. 2.6c) and significantly higher than in 1999 (Table 2.5). The high volatility in barnacle densities continued into 2001 and resulted in a significant decline from 2000 to 2001 (Table 2.5). In the mid zone, the densities of *S. balanoides* were also highest in 2000 (Fig. 2.6b) and this tidal height had the highest densities of *S. balanoides* overall. Similar to the 1.0 and 2.0 m tidal heights, there were also large fluctuations in the density of *S. balanoides* at the 0.5 m tidal height. The peak in densities in 1998 at the 0.5 m tidal height was significantly higher than densities the following year (Table 2.5)

The increase in *S. balanoides* at the 2.0 m tidal height in 2000 was apparently due to a successful recruitment event because the proportion of barnacles in the smallest size class was significantly higher in 2000 than in both 1999 and 1998 (Table 2.6; Fig. 2.7c). Conversely, the proportion of *S. balanoides* in the largest size class was significantly higher in 1998 versus 2000 and 2001 and the 1999 values were also significantly greater than in 2000. The largest size class was a smaller proportion of the overall size class distribution at the 1.0 m tidal height than at the 2.0 m tidal height. There were no significant differences in the proportions in any of the size classes between any of the years at the 1.0 m tidal height (Table 2.6; Fig. 2.7b). Finally, at the 0.5 m tidal height, the proportion of *S. balanoides* in the smallest size class was significantly larger in 1998 than in 2000 (Table 2.6; Fig. 2.7a).

From 1998 to 2001 at Ft. Stark, there appeared to be a general trend of declining densities of *M. edulis* at both the lower and mid tidal heights (Fig. 2.6a and b). Densities were an order of magnitude lower at the 2.0 m tidal height and this species was completely absent from this tidal height in 3 of the 5 years (Fig. 2.6c). The size class distribution data for *M. edulis* at the lowest tidal height indicated that larger animals composed the majority of the population especially since 1999 (Fig. 2.8a). The proportion in the 30 – 50 mm size class was significantly greater in 1997 and 1998 than in 2001 and conversely, the proportion in the largest size class (>50 mm) was significantly less in the later sampling years as compared to both 1997 and 1998 (Table 2.7). Smaller *M. edulis* were more common in the mid to upper intertidal zone (Figs. 2.8b and c) and a similar pattern of shifts in size class distributions through the sampling period was observed at the 1.0 m tidal height. There were significantly lower proportions in the 21 – 30 mm and 31 – 50 mm size classes in 1998 versus 2000 while the proportion in the largest size class in 2000 was significantly greater than 1998 levels (Table 2.7). Finally, the proportion of *M. edulis* in the 31 – 50 mm size class was significantly greater in 1999 than in 2000 at the 1.0 m tidal height (Table 2.7).

The densities of *N. lapillus* and *N. testudinalis* at Ft. Stark were highest at the 0.5 m tidal height, declined greatly at the 1.0 m tidal height and neither of these species were ever found at the 2.0 m tidal height (Fig. 2.9a and b). The density of *N. lapillus* was highest in 1997 in the lower intertidal zone and since that time densities declined except for a slight rebound in 1999 (Fig. 2.9a). In contrast, *N. lapillus* were not found in the mid zone in 1999 and densities of this species increased since that time (Fig. 2.9b). The majority of the *N. lapillus* at the 0.5 m tidal height were in the largest size class in 1997 and the relative proportion in that size class decreased sharply since that time (Fig. 2.10a). There were no consistent patterns in the size distributions of *N. lapillus* at the 1.0 m tidal height through the sampling period (Fig. 2.10b).

Littorinids, particularly *Littorina littorea*, were much more common at Ft. Stark than *N. lapillus* or *N. testudinalis*. In 1998, *L. littorea* reached peak abundance at the Ft. Stark 0.5 m tidal height (Fig. 2.11a) and densities were significantly higher than the previous year (Table 2.8). *Littorina obtusata* peaked a year later at the 0.5 m tidal height (Fig. 2.11a). *Littorina obtusata* declined since 1999 at the 0.5 m tidal height but the densities of *L. littorea* have fluctuated since 1998. *Littorina saxatilis* was never found at the lowest tidal height at Ft. Stark. There were large fluctuations in the density of *L. littorea* at the 1.0 m tidal height from 1997 to 2001; the difference between the years with the lowest and highest density was seven-fold (Fig. 2.11b) but there were no statistically significant differences (Table 2.8). *Littorina obtusata* increased from 1997 to 1999 at the 1.0 m tidal height, but then declined until 2001; this is the same pattern that occurred at the lower tidal height (Fig. 2.11b). The densities of *L. obtusata* were significantly lower in 1997 as compared to 1999, 2000 and 2001 (Table 2.8). The densities of *L. saxatilis* were very low at the 1.0 m tidal height at Ft. Stark and none were found in 1998 (Fig. 2.11b). At the 2.0 m tidal height, there was a trend of declining densities of *L. littorea* from 1997 to 2001, with a slight rebound in 2000 (Fig. 2.11c). In contrast, the density of *L. obtusata* was significantly higher than the 1997 densities for each year subsequent to 1997 (Table 2.8). The trend of slightly increasing densities of *L. obtusata* at the 2.0 m tidal height declined in 2001 (Fig. 2.11c). There were large fluctuations in the density of *L. saxatilis* at the highest tidal height throughout the sampling period and no consistent patterns (Fig. 2.11c).

The size distributions of *L. littorea* in the low intertidal zone were generally consistent from 1997 to 2001 (Fig. 2.12a). The two exceptions were a significantly lower proportion of snails in the smallest size class in 1997 versus 1999 (Table 2.9) and a non-significant trend of a decreased proportion of the largest size class in 1997 compared to subsequent years. In comparison, the size distributions of *L. obtusata* at the 0.5 m tidal height were much less consistent throughout the sampling period (Table 2.10; Fig. 2.12b). There was a trend of decreased relative abundance of the 2-10 mm size class in 1997 and 1998 as compared to subsequent years and the proportion in the largest size class (>10mm) was highly variable through the sampling period.

At the 1.0 m tidal height, the proportion of *L. littorea* in the largest size class was lower in 1997 as compared to 1999, 2000 and 2001 (Table 2.9). Generally the size distributions were less even and more heavily dominated by smaller size classes since 1997 (Fig. 2.13a). At the 1.0 m tidal height, the proportion of *L. obtusata* in the 2-10 size classes was significantly lower in 1997 versus 1999, 2000 and 2001 (Table 2.10; Fig. 2.13b). The low numbers of *L. saxatilis* at the 1.0 m tidal height make conclusions regarding their size class distributions difficult (Fig. 2.13c).

At the 2.0 m tidal height, the proportion of *L. littorea* in the smallest size class was consistently high through the sampling period (Fig. 2.14a) and the only statistically significant differences were due to a decline in the proportion of the largest size class in 1997 versus subsequent years (Table 2.9). *Littorina obtusata* in the smallest size class were relatively uncommon at the 2.0 m tidal height at Ft. Stark (Fig. 2.14b) and the proportion of snails in the intermediate and largest size classes were highly variable throughout the sampling period (Table 2.10). There was a significantly higher proportion of *L. saxatilis* in the smallest size class at the 2.0 m tidal height in 1997 compared to subsequent years (Table 2.11) and a trend of increased relative abundance of the largest size class (Figure 2.14c).

From 1997 to 1999, the density of *C. maenas* increased at all three tidal heights (Fig. 2.15). At the 1.0 m tidal height, in particular, the density increased by fourfold from 1997 to 1998 and the difference between densities recorded in 1997 and all subsequent years was statistically significant (Table 2.5). At the 0.5 m tidal height, the general increase in densities resulted in significant increases from 1997 levels compared to 1999, 2000 and 2001 as well as a significant increase from 1998 to 1999 (Table 2.5). The stepwise multiple regression indicated that the number of *C. maenas* at Ft. Stark and the amount of substrate that was categorized as pebble/shell, cobble or large rock, the number of snails and the number of *S. balanoides* were significantly related ($p<0.001$; Table 2.12). The only statistically significant changes in proportions in a size class between years occurred between 1997 and subsequent years for the two smallest size classes (0 – 5 and 6 – 10 mm) (Table 2.13). At all three tidal heights the proportion in the 6 – 10 mm size class was significantly lower in 1997 than most of the subsequent years while at the 2.0 m tidal height, the proportion in the 0 – 5 mm size class was significantly higher in 1997 than all subsequent years (Table 2.13, Fig. 2.16a - c).

Finally, two *H. sanguineus* were found at Ft. Stark during the 2001 sampling: one was at the 2.0 m tidal height and one was at the 1.0 m tidal height. Both crabs were less than 4 mm carapace width (data not shown).

Odiorne Park

Algal evenness was lowest at the Odiorne 2.0 m tidal height in all years except 1997 and the overall difference in evenness between the highest tidal height and the two lower tidal heights was very large at Odiorne (Fig. 2.17). The overall evenness at the 0.5 and 1.0 m tidal heights was much higher in the years after 1997. Similar to Ft. Stark, both methods to estimate richness produced very similar results at Odiorne. Generally, richness was lowest at the 2.0 m tidal height, but it was also very consistent throughout the sampling period (Fig. 2.18a and b). Richness was similar between the two lower tidal heights from 1997 to 2001, and it peaked in 1999 for both types of estimates.

Ascophyllum nodosum was the dominant algal canopy species throughout the intertidal zone at Odiorne (Fig. 2.19a – c) and the only significant difference was between 1997 and 1999 abundance at the 1.0 m tidal height (Table 2.3). Interestingly, both *F. vesiculosus* and *F. spiralis* were found at all tidal heights at Odiorne, but at Ft. Stark, *F. spiralis* was only found at the highest tidal height. There appears to be more ephemeral/drift algae at Odiorne than at Ft. Stark. In 1999, the abundance of all three major canopy species (*A. nodosum*, *F. vesiculosus* and *F. spiralis*) peaked in the low zone at Odiorne, but otherwise, there were few strong trends in the abundance of canopy algae through the five year sampling period.

Overall, the substrates throughout the intertidal zone at Odiorne are mostly composed of large rocks, cobble and pebble/shell (Figs. 2.20a - c). The proportion of substrate that was categorized as large rock at the 0.5 m tidal height was significantly higher in 1999 as compared to 2000 and 2001 (Table 2.4). There was much less rock bench substrate at Odiorne as compared to Ft. Stark, especially at the 1.0 m tidal height and the relative abundance of each type of substrate was consistent through the years at this tidal height (Table 2.4; Fig. 2.20b). At the 2.0 m tidal height, the proportion of substrate that was categorized as rock bench was significantly lower in 2001 as compared to 1998 and the opposite pattern occurred for pebble/shell substrates (Table 2.4). Subcanopy algae were encountered at all three tidal heights at Odiorne, but their abundance was lowest at the 2.0 m tidal height (Figs. 2.20a - c).

There were large fluctuations in the density of *S. balanoides* at Odiorne Park from 1997 to 2001, especially at the 0.5 m and 2.0 m tidal heights (Fig. 2.21a – c). In both 1997 and 1998, the density of *S. balanoides* at the 0.5 m tidal height was extremely low (3.6/m in 1998) and densities in the three following years were significantly higher than in 1998 (Table 2.5). In addition, the peak in 2000 (almost 12,000/m^2) was also significantly higher than the 1997 densities (Table 2.5). In contrast, *S. balanoides* increased from 1997 to 1999 in the mid zone and remained fairly consistent since that time. In the high zone, *S. balanoides* decreased from 1997 to 1999 and the difference in densities between 1997 and 1999 was statistically significant (Table 2.5). From 1999 to 2000, there was a slight rebound in *S. balanoides* densities but they dropped again in 2001. Similar to Ft. Stark, the density of barnacles was generally much higher at the 1.0 m tidal height compared to the 2.0 m tidal height; at Odiorne, the overall average density was 2 times higher (5,600/m^2 vs. 2,500/m^2).

At the 0.5 m tidal height, there appeared to be a general trend of declining proportions of *S. balanoides* in the smallest size class since 1997 (Fig. 2.22a). In 1997, 62% of the *S. balanoides* were in 0-2 mm the size class. The proportion of *S. balanoides* in the smallest size class in 1997 was significantly greater in 1997 than in 1999 and 2000 while the proportion in the medium size class (2 – 5 mm) was significantly lower in 1997 than in 1999, 2000 and 2001 (Table 2.6). At the 1.0 m and 2.0 m tidal heights, the size class distributions were relatively constant through the sampling period (Table 2.6; Figs. 2.22b and c).

Mytilus edulis were never found at the 0.5 m tidal height at Odiorne throughout the five year sampling period. There was a small dip in densities at the 1.0 m tidal height in 1999 (Fig. 2.21b) and the *M. edulis* at this tidal height were also usually in the larger size classes (Fig. 2. 23a). At the 2.0 m tidal height at Odiorne, the density dropped by an order of magnitude from 1997 to 1998, and stayed very low except for a slight rebound in 2000 (Fig. 2.21c). The difference between 1997 densities and those of 1998, 1999 and 2000 were statistically significant (Table 2.5) for the 2.0 m tidal height. There were no statistically significant differences in the proportions of *M. edulis* in any of the size classes at the 1.0 m tidal height (Table 2.7; Fig. 2.23a) and there weren't enough *M. edulis* at the 2.0 m tidal height to compare proportions in the various size classes between years (Table 2.7; Fig. 2.23b).

The densities of *N. lapillus* and *N. testudinalis* were similar between Ft. Stark and Odiorne Park. *Nucella lapillus* densities were very consistent at the Odiorne 0.5 m tidal height from 1997 to 2001 but *N. testudinalis* had a sharp peak in 1998 (Fig. 2.24a). In the mid zone, the density of *N. lapillus* increased from 1997 to 1998, but declined since that time (Fig. 2.24b). The density of *N. testudinalis* was consistently low at the 1.0 m tidal height and was zero in the final year of sampling (Fig. 2.24b). *Notoacmea testudinalis* was never found at the 2.0 m tidal height and *N. lapillus* was only found at this tidal height once in 1997 at Odiorne (data not shown). There were big fluctuations in the size class distributions of *N. lapillus* at the low and mid tidal heights, but no consistent patterns through time (Fig. 2.25a and b).

Littorinids, particularly *Littorina littorea*, were much more common at Odiorne than any other snail species. *Littorina littorea* was particularly abundant in the low zone. The density of this species at the 0.5 m tidal height increased from 1997 to 2000 (Fig. 2.26a) and the 1997 densities were significantly lower than each of the subsequent years (Table 2.8). In 2000, the average density of *L. littorea* was over 1,100/m^2 at the 0.5 m tidal height. In contrast, the density of this species was at its lowest point at the 1.0 m tidal height in 2000 (Fig. 2.26b). *Littorina obtusata* increased by an order of magnitude from 1998 to 1999 at the 0.5 m tidal height (Fig. 2.26a) and its densities in 1999 were significantly higher than those of 1997 and 1998 (Table 2.8). *Littorina saxatilis* was found at the 0.5 m tidal height at Odiorne, in contrast to at Ft. Stark, where it never occurred in the low zone and was only found in very low densities at the 1.0 m tidal height. The density of *L. saxatilis* at the 0.5 m tidal height increased steadily from 1998 to 2001 (Fig. 2.26a) and there were significant differences between both the 1997 and 1998 densities and the 2000 and 2001 densities (Table 2.8).

The densities of *L. littorea* were more consistent at the 1.0 m tidal height than at the 0.5 m tidal height (Fig 2.26 a and b). The densities of *L. obtusata* increased from 1997 to 2000 at the 1.0 m tidal height (Fig 2.26b) and resulted in significant differences between the 1997 and 1999, 2000 and 2001 densities (Table 2.8). In addition, the 1998 densities were also significantly lower than the 1999 and 2000 densities. By the end of the sampling period, the density of *L. obtusata* was over four times that recorded in 1997 (133 vs. 32/m^2). Overall, the density of *L. saxatilis* at the 1.0 m tidal height was slightly lower in 1997 than in subsequent years, but the high variability did not result in any significant differences between the densities in any of the years (Table 2.8).

The peak abundance of *L. littorea* at the 2.0 m tidal height occurred in 1999, and the densities declined slightly since that time (Fig. 2.26c). The densities of *L. obtusata* at the Odiorne 2.0 m tidal height were lower than those of *L. littorea* and they were consistent through the sampling period (Fig 2.26c). There was a significant increase in *L. saxatilis* density at Odiorne 2.0 m from 1997 to 1998 (Table 2.8), it declined slightly for the next two years and recovered slightly in 2001 (Fig. 2.26c).

The size class distributions of *L. littorea* at the 0.5 m tidal height at Odiorne were very different in 1997 as compared to subsequent years (Fig. 2.27a). The proportion in the 0 – 10 mm and 11-20 mm size classes were lower in 1997 than in most of the subsequent years and the proportion in the 21 – 30 mm size class was significantly higher in 1997 than in 1998, 1999 and 2000 (Table 2.9). In contrast, the size class distributions of both *L. obtusata* and *L. saxatilis* were consistent at this tidal height through the sampling period (Fig. 2.27b and c).

At the 1.0 m tidal height, *L. littorea* had consistent size class distributions (Fig. 2.28a) , while *L. obtusata* and *L. saxatilis* size class distributions were comparatively less consistent (Fig. 2.28b and c). The proportion of *L. obtusata* in the 2 – 10 mm size class was significantly lower in 1997 than in 1999 (Table 2.10). No *L. saxatilis* in the smallest size class (<2 mm) have been recorded since 1998 at either the 1.0 m or 2.0 m tidal heights (Fig. 2.28c and 2.29c).

The proportion of *L. littorea* in the smallest size class at the 2.0 m tidal height was significantly lower in 1998 as compared to 2001 (Table 2.9; Fig. 2.29a) while the proportion in the 11 – 20 mm size class in 1998 was significantly higher than in 2001. In addition, the proportion of *L. littorea* in the 11 –20 mm size class significantly declined from 2000 to 2001 (Table 2.9; Fig. 2.29a). The proportion of *L. obtusata* at the 2.0 m tidal height in the middle size class was significantly lower in 1997 as compared to every subsequent year while the proportion in the largest size class was significantly higher in 1997 compared to every subsequent year (Table 2.10; Fig. 2.29b). Finally, *L. saxatilis* size class distributions were highly variable from 1998 to 2001 at the 2.0 m tidal height and there were no statistically significant differences between any of the years (Table 2.11; Fig. 2.29c).

Carcinus maenas was more abundant at Odiorne than at Ft. Stark; the overall average densities at both the 1.0 and 2.0 m tidal heights were higher at Odiorne (87 and 85/m^2 respectively) than at Ft. Stark (50 and 67/m^2). The density of *C. maenas* at both the 0.5 and 1.0 m tidal heights followed similar patterns at Odiorne; both rose from 1997 to 1999, declined in 2000 and the density in the mid zone slightly increased in 2001 while in the low zone, it continued to decline slightly (Fig. 2.30). At both the 0.5 m and 1.0 m tidal heights, the densities in 1997 were significantly lower than the 1999 densities while at the 1.0 m tidal height, the density in 1999 was significantly higher than the two subsequent years (Table 2.5). In contrast to these fluctuations, the density at the 2.0 m tidal height was fairly consistent through the five year sampling period and there were no statistically significant differences between the years (Table 2.5; Fig. 2.30). The stepwise multiple regression indicated that there was also a significant positive relationship between the number of snails and the number of *C. maenas* (p<0.001; Table 2.12) at Odiorne.

There were large changes in the size class distributions of *C. maenas* at Odiorne through the sampling period and most of the statistically significant differences occurred in the two smallest size classes. The general pattern at all three tidal heights was that the proportion in the 0 – 5 mm size class in the earlier sampling period (1997-1999) was significantly higher than the last two years of sampling (Table 2.14; Fig. 2.31a - c). Conversely, the proportion in the 6 – 10 mm size class was frequently significantly higher in 2000 and 2001 than in previous years (Table 2.14).

Hemigrapsus sanguineus was first found at Odiorne in 2000, two individuals were found in two separate quadrats at the 2.0 m tidal height (Fig. 2.32a). By 2001, a total of 13 *H. sanguineus* were found between all three tidal heights, and the highest density was at the lowest tidal height (Fig. 2.32a). Only two *H. sanguineus* were found at the 2.0 m tidal height each year, but they were much bigger than the individuals of this species that were found in the mid and lower zone (Fig. 2.32b).

Hilton Park

Algal evenness steadily declined at the 0.5 m tidal height at Hilton Park from 1999 to 2001 (Fig. 2.33). The evenness at the 1.0 m tidal height was highest in 2000, and at this time it was equal to that of the 0.5 m tidal height. Overall, evenness was lower at the 1.0 m tidal height. Again, both methods to estimate richness produced very similar results (Fig. 2.34a and b) and generally, richness was lower at Hilton Park than at the two coastal sites. There was very little change in richness at the 1.0 m tidal height through the years. The lowest richness estimates for the 0.5 m tidal height occurred in 2000 and in 2001, the richness was similar between the two tidal heights.

In contrast to the two coastal sites, *A. nodosum* was virtually absent from the low intertidal zone at Hilton Park (Fig. 2.35a). *Fucus vesiculosus* was the most abundant fucoid algae in the low zone at Hilton Park, and because canopy algae were patchy, *Mastocarpus stellatus* was also recorded in the analysis of the algal canopy (Fig. 2.35a). At the 1.0 m tidal height, *A. nodosum* was the dominant algal species, but it had relatively low cover as compared to the same tidal height at the two coastal sites (Fig. 2.35b). Algal canopy cover was lowest in 2000 at the 0.5 m tidal height but it was highest at the 1.0 m height in the same year. There were no statistically significant differences between the abundance of either *A. nodosum* or *F. vesiculosus* at either tidal height between any of the years (Table 2.3).

Pebble/shell substrates are the most common type of substrate at both tidal heights at Hilton Park (Figs. 2.36a and b) but there was a significant decrease in the abundance of this substrate type from 2000 to 2001 at the 0.5 m tidal height (Table 2.4). The abundance of cobble and mud substrates increased significantly from 1999 levels when compared to the two following years (Table 2.4) but both of these categories were a relatively minor portion of the substrates when compared to pebble/shell category (Fig 2.36a and b). In the low zone, the abundance of subcanopy algae declined sharply from 1999 to 2000 resulting in a significant difference (Table 2.4) but the abundance of subcanopy algae rose slightly in 2001. The majority of this category was composed of *M. stellatus*, but in both 1999 and 2001, *Ulva lactuca* was also common in the lower intertidal zone of Hilton Park and this species contributed to the subcanopy algae category.

The abundance of *S. balanoides* was similar between the low and mid zone throughout the sampling period (Fig. 2.37a and b) and in general these densities were similar to the overall average of the 2.0 m tidal heights at both coastal sites (ca. 3000/m^2). *Semibalanus balanoides* fluctuated in the low zone from 1999 to 2001, and it declined at the 1.0 m tidal height during this time period but the high overall variability did not result in statistically significant differences between these fluctuations (Table 2.5). The size class distributions for this species at both tidal heights revealed very few individuals were in the smallest size category throughout the sampling period (Fig. 2.38a and b). There were no statistically significant differences in the proportion of *S. balanoides* in any of the size classes between any of the years (Table 2.6).

Mytilus edulis was extremely abundant in the low zone at Hilton Park (Fig. 2.37a) in fact, much of the pebble/shell substrates at this tidal height were living *M. edulis* shells. The density of this species at the 0.5 m tidal in 1999 was significantly higher than in the two subsequent years (Table 2.5) and densities in 2001 were four times lower than they had been in 1999 (Fig. 2.37a). In contrast, the abundance of this species increased through the sampling period at the 1.0 m tidal height (Fig. 2.37b), but its overall densities were much lower than at the 0.5 m tidal height and none of the differences between the years were statistically significant (Table 2.5). In the low zone, the proportions of *M. edulis* in the 21 - 30 and 31 – 50 mm size classes were significantly higher in 1999 than in 2000, and the proportion in the largest size class was significantly higher in 2000 than in 1999 (Table 2.7; Fig. 2.39a). At the 1.0 m tidal height, most of the *M. edulis* were in the largest size categories (>31 mm) (Fig. 2.39b) and there were no statistically significant differences in size class distributions between years (Table 2.7).

The densities of *N. lapillus* and *N. testudinalis* were extremely low in the low zone at Hilton Park (Fig. 2.40a) and neither of these species were ever found at the 1.0 m tidal height. Only two *N. lapillus* were found at the 0.5 m tidal height at Hilton Park so conclusions regarding the size distributions of this species at this site are not warranted. The densities of littorinid snails were also relatively low at the Hilton Park 0.5 m tidal height, and those of *L. littorea* were comparable to those of the Ft. Stark 1.0 m tidal height (Fig. 2.41a). *Littorina littorea* densities increased slightly through the sampling period at the 0.5 m tidal height (Fig. 2.41a) while at the 1.0 m tidal height, the densities in 2000 were significantly greater than in 1999 and 2001(Table 2.8; Fig. 2.41b). *Littorina obtusata* densities fluctuated through the sampling period at the 0.5 m tidal height and there was a significant difference between the 2000 and 2001 densities (Table 2.8; Fig. 2.41a). At the 1.0 m tidal height, there appeared to be a slight trend of declining *L. obtusata* densities through the sampling period, but there was also high variability (Fig. 2.41b). Finally, *L. saxatilis* was never found at the 0.5 m tidal height (Fig. 2.41a) and only found in very low densities at the 1.0 m height (Fig. 2.41b).

There were very few *L. littorea* that fell into the largest size category (>30 mm), none were found in the low zone and in the mid zone, they were only recorded in 1999 (Fig. 2.42a and 2.43a). The *L. littorea* that were found in the low zone were mostly small snails (0-10 mm) (Fig. 2.42a). There was a significant difference between the proportion of *L. littorea* in the 11 - 20 mm size category between 2000 and 2001 at the 0.5 m tidal height (Table 2.9). At the 1.0 m tidal height, the proportion of *L. littorea* in the 0 – 10 mm size class was significantly lower in 1999 than in 2001, and in the 11 – 20 mm size class, the proportion significantly decreased from 1999 to 2000 (Table 2.9). Only two *L.*

obtusata were found at the 0.5 m tidal height in 2000, so their size class distributions were not compared statistically, while at the 1.0 m tidal height, the size class distributions were similar between 1999 and 2001 (Table 2.10; Figure 2.42b). Finally, there were no significant differences between the size class distributions of *L. saxatilis* at the 1.0 m tidal height in any year (Table 2.11; Fig. 2.42c).

The densities of *C. maenas* at Hilton Park were lower than those of the same tidal heights at the coastal sites. *Carcinus maenas* densities significantly increased from 1999 to 2001 at the 0.5 m tidal height; its density in 2001 (64/m^2) was over double that of 1999 (24/m^2) (Table 2.5; Fig. 2.44). In contrast, the density of *C. maenas* at the 1.0 m tidal height slightly fluctuated from 1999 to 2001 but there were no significant differences between 1999 and 2001 (Table 2.5; Fig. 2.44). The stepwise multiple regression indicated that the amount of fucoid algae and the number of snails were both positively related to the density of *C. maenas* ($p<0.001$; Table 2.12) but the residuals appeared to have a slight positive trend indicating that there may have been underlying variation that was not accounted for by the measured variables. The size class distributions of *C. maenas* were very consistent at each tidal height through the sampling period (Table 2.15; Fig. 2.45a and b). *Carcinus maenas* in the low zone were smaller than those in the mid zone.

Hilton Park had the highest densities of *H. sanguineus* of all three sampling locations. The second specimen of *H. sanguineus* for the state of New Hampshire was found at Hilton Park in 1999. More *H. sanguineus* have been found at the 1.0 m tidal height than at the 0.5 m tidal height (Fig. 2.46a). There were too few *H. sanguineus* found thus far to make definitive conclusions regarding temporal shifts in its size distributions (Fig. 2.46b).

Community analyses

The results from the cluster analysis at Ft. Stark and Hilton Park both showed that the community at each tidal height in each year was more similar to that in other years than to other tidal heights (Fig. 2.47a and c). At Odiorne, the average values for the community at the 2.0 m tidal height in 1997 were more similar to the average values for the community at the 1.0 m tidal height than to the 2.0 m values for other years (Fig. 2.47b). Aside from this exception, all of the average values for the community clustered out by tidal height rather than by year of sampling. When the data from all locations were analyzed simultaneously, a similar pattern prevailed. For the most part, the average values for the community at each tidal height and location combination were most similar to each other between years (Fig. 2.48). One major group that could be characterized as the higher intertidal zone group was composed of the 2.0 m tidal height at both Ft. Stark and Odiorne (except 1997) and the 1.0 m tidal height at Hilton Park. The other major group could be characterized as the coastal low to mid-intertidal zone group, it contained: the Ft. Stark and Odiorne 1.0 m tidal heights, the 0.5 m tidal heights at Ft. Stark and Hilton Park and the 1997 2.0 m tidal height at Odiorne. The average values from the 1997 Odiorne 2.0 m tidal height appeared to be anomalous when all locations were considered simultaneously, just as they had been when the Odiorne values were examined separately.

Finally, the multidimensional scaling was also used to examine the relationships between the average values for the various location, tidal height and year combinations.

In this analysis, the Odiorne 0.5 1998 samples appeared to be an outlier (Fig. 2.49a). This was likely due to the fact that only one *S. balanoides* was found in all ten quadrats for that year. The stress value of 0.13 indicated that this was a fairly good ordination of the quadrat data. When the analysis was repeated without the Odiorne 0.5 1998 samples, the distinction between both Hilton Park samples (particularly the 0.5 m tidal height) from the rest of the coastal samples became clear, but the coastal sites remained strongly intermixed (Fig. 2.49b). The stress value rose slightly for the MDS when the Odiorne 0.5 1998 samples were excluded, but the stress value was still low enough to be considered a good ordination. An ANOVA indicated that there was a significant difference in the MDS scores between the locations, tidal heights and the interaction of these two factors (Table 2.16). However, there was no significant difference in MDS scores for the year that sampling took place.

DISCUSSION

The objective of this study was to document the community structure at three rocky intertidal sites prior to the establishment of a predator, *H. sanguineus*. The fact that *H. sanguineus* was found at all three sites by the last year of the study indicates not only that the study sites provide suitable habitat for this introduced crab but also that further increases in the abundance and range of *H. sanguineus* are likely in northern New England.

Overall, the results of this community structure monitoring indicated that there were no consistent between site trends in the abundance of any of the species monitored for this study. This result implies that these data will be useful for assessing changes that may occur after *H. sanguineus* becomes abundant because these communities both have relatively stable composition and are independent of each other (following recommendations of a BACI design; Stewart-Oaten et al. [1986]). The one exception to this observation was the sharp decline in *S. balanoides* at the 2.0 m tidal height that occurred in 1999 at both Ft. Stark and Odiorne.

The community structure monitoring was performed at physically defined tidal heights in order to insure that the results were comparable both between study sites and over a long time scale. For example, intertidal ecologists often subjectively define upper, mid and lower intertidal zones based on the abundance of species that are characteristic of each of these zones. Naturally, these subjective definitions vary between researchers thereby making generalizations difficult. In addition, the distribution and abundance of these characteristic species can shift over time because of changing physical and biological conditions (Ballantine, 1961). By using physically defined tidal heights, I avoided some of these potential problems encountered by other ecologists, however, the study sites varied in other attributes. The most obvious difference between the study sites is that Hilton Park is an estuarine tidal rapids while Ft. Stark and Odiorne are both coastal. The aspect of the sites also varied which affects both desiccation stress and exposure to storms (most large storms in this region come from the northeast). The Odiorne site faced northeast, the Ft. Stark site was northwest facing and the Hilton Park site faced southeast. These differences in the orientation of my study sites may have accounted for the fact that *A. nodosum* dominated up to the 2.0 m tidal height at Odiorne but at Ft. Stark, this tidal height was a mixture of *F. spiralis* and *A. nodosum*. When the whole community was considered simultaneously, the cluster analysis showed that the highest tidal heights at each site (2.0 at Odiorne and Ft. Stark and 1.0 at Hilton Park) were most similar to each other, along with the 0.5 m tidal height at Odiorne. However, within this group, the 0.5 m Odiorne cluster was most dissimilar from the three other groups.

The distributions of several organisms, especially, *N. testudinalis* and *N. lapillus* appeared to have been strongly affected by tidal height. *Notoacmea testudinalis* was never found at the 2.0 m tidal height and *N. lapillus* was only found there once. In addition, the red alga, *M. stellatus* was never encountered at the 2.0 m tidal height. The relative abundance of *M. edulis* decreases with increasing tidal height at all three sites but at the estuarine site, it is highest at the 0.5 m tidal height while peak densities are found at the intermediate tidal height at the two coastal locations.

Hemigrapsus sanguineus has variously been reported to be both an upper intertidal species (Fukui, 1988; Takada and Kituchi, 1991; Takada, 1999) and a lower intertidal species (highest densities between the low water marks)(Siagusa and Kawagoye, 1997) in Japan. In its invaded range, various researchers have found the highest densities of *H. sanguineus* in the lower intertidal zone (Long Island Sound, Lohrer and Whitlatch, 1997; southeastern Massachusetts: Lesdesma and O'Connor, 2001). Although the densities are comparatively much lower at my study sites, I found *H. sanguineus* in the upper or mid zone first at every site and the densities are highest in the upper and mid zone. The conflicting observations regarding the tidal height distribution of this species may result from size specific habitat utilization, competition for shelter with other species or a combination of both factors. Fukui (1988) stacked cobble and boulders across the width of the intertidal zone in Japan and found that in the summer, higher densities of juvenile (8 mm CW) *H. sanguineus* were found in the upper intertidal zone. At his study sites, *H. sanguineus* co-existed with up to 7 other grapsid crab species and its presence in the high intertidal zone may be the result of competitive interactions. Because *C. maenas* is the only other crab species commonly found in the rocky intertidal zone in its invaded range, the competitive interactions between the two species are presumably less intense for *H. sanguineus* than in its native range. It is possible that when populations of *H. sanguineus* are very low, as they currently are in New Hampshire, the crabs initially colonize the upper intertidal zone. The majority of the *H. sanguineus* that I have found are juveniles (<10 mm CW), and these individuals may migrate lower in the intertidal zone as they grow larger, much like the subtidal migration *C. maenas* undergo when they reach 30-35 mm CW (Edwards, 1958; Warman et al., 1993).

In an early investigation into the factors responsible for the structure of the mid to high New England rocky intertidal community, Menge (1976) judged *Nucella (Thais) lapillus* to be to be the only important predator in the mid to high intertidal zone based on its density. The highest density of *C. maenas* that he found was only $4/m^2$ at Canoe Beach Cove, MA. In contrast, the average density (over all study sites and years) of *C. maenas* was over fifteen times greater in this study than in Menge's study. The large discrepancies in density estimates for the two studies is intriguing and could be due to several factors such as inherent differences in habitat quality or regional increases in *C. maenas* populations coincident with increasing water temperatures in the last several decades (Glude, 1955). However, the most likely reason for the disparity in density estimates was probably due to the fact that I looked under cobble and sifted through gravel and soft substrates while Menge apparently only counted *C. maenas* that were directly encountered under the algal canopy. The differences in the search techniques could largely account for the differences in densities, especially since the vast majority (>85%) of the *C. maenas* that I found were seeking refuge under rocks (rather than just under the algal canopy) or were buried in the substrate.

The most important factor determining the density of intertidal crabs may be the availability of shelter. In a previous study, I found a significant relationship between the density of *C. maenas* and the amount of substrate that was categorized as large rock, cobble, or pebble/shell (all were *a priori* judged to provide suitable shelter for crabs) at Ft. Stark ($r^2 = 0.51$, $p<0.05$; Tyrrell, 1999). Lesdesma and O'Connor (2001) also found a significant relationship between the density of *H. sanguineus* and the amount of shelter providing rocks ($r^2 = 0.53$, $p<0.05$) in southeastern Massachusetts. Lohrer et al. (2000) studied the vertical zonation and habitat complexity of *H. sanguineus* and other crabs in Japan. They found that while *H. sanguineus* had higher densities in the upper intertidal zone prior to manipulation of shelter providing rocks, this species also responded positively to addition of rocks, especially in the upper intertidal zone (Lohrer et al., 2000). Takada (1999) also found that *H. sanguineus* responded positively to the addition of cobble for shelter, as well as to the addition of artifical shades. Surprisingly, the multiple regressions between the density of *C. maenas* and various physical and biological factors in this study only revealed a significant relationship between the abundance of these shelter-providing substrates and the density of *C. maenas* at the Ft. Stark site.

One of the species that may not have been adequately sampled in this study was *Mytilus edulis*. It is difficult to quantify both the number and size distributions of *M. edulis* without physically removing the animals from the substrate. In particular, juvenile *M. edulis* are often nestled at the base of adults and are therefore obscured from overhead view. It is likely that my data on size distributions of *M. edulis* is therefore heavily biased toward larger individuals. Because the goal of this study was long term monitoring, I did not remove *M. edulis* in order to remove this bias.

The statistical analyses of density and size distributions of the most abundant animals at the study sites often revealed statistically significant differences between the first year of sampling (1997 at the coastal sites and 1999 at the estuarine site) and subsequent years. These results are most likely due to my enhanced search image and increasing familiarity with the behavior of the organisms and with the community in general after the first year of sampling. Minimizing variability due to sampling technique or observer is critical in a monitoring program, and the high proportion of statistically significant differences between my first year of sampling and subsequent years highlights the importance of having a single, well trained observer rather than several novice observers in a monitoring effort. Despite the statistically significant differences between the 1997 values and those of subsequent years for some groups of organisms, the overall community structure was relatively stable. The results from both the cluster analysis and the ANOVA of MDS scores support this assertion. The average values for the community at each tidal height for each year clustered together (except for the 1997 Odiorne 0.5 m values) and the ANOVA of MDS scores indicated that the year of sampling was the only factor that did not have a significant influence on MDS scores.

Both methods indicate that the background temporal variability in community structure was relatively low, thus the impacts of high densities of *H. sanguineus* may be detectable once this crab reaches high densities in these communities.

Differences in sampling dates at each site between years also poses a potential problem for the interpretation of temporal changes in abundance. For example, concurrent recruitment studies of *C. maenas* indicate that there is a strong peak in recruitment of this species that starts at the end of July and continues through September. The higher density of *C. maenas* at Odiorne versus Ft. Stark may be due to the fact that the Odiorne sites were sampled later than the Ft. Stark sites. The sampling dates at both Odiorne and Hilton Park were relatively consistent through the years, while the sampling dates at Ft. Stark were much later in 1997 and 1998 than in the three following years. Because of the shift in sampling period at Ft. Stark, the analysis of temporal shifts in species' abundance should be interpreted with this potential confounding factor in mind, particularly for the smallest size classes of animals and for algal species with short life spans.

Overall, the species composition and relative abundance was more similar between the two coastal sites than between either coastal site and the estuarine site. The Hilton Park site is a tidal rapids, and the high current speeds at this site may restrict the abundance of some species that cannot tolerate these conditions. In addition, the estuarine site is likely to experience highly variable salinities as compared to the coastal sites. It is interesting, and perhaps surprising, that this estuarine rapids site has the highest density of *H. sanguineus* of my three sites. If the range expansion of *H. sanguineus* is taking place mainly via larval dispersal from the south (where *H.*

sanguineus already has substantial populations), then it seems more likely that the coastal sites, particularly Odiorne, would have the highest densities of this new invader. However, the Hilton Park site is very near an electrical power plant that often has large ships docked nearby. It is possible that ballast water from these ships was the vector that was initially responsible for the appearance of *H. sanguineus* at Hilton Park. In addition, the electrical plant may have a warm water discharge that affects the thermal conditions in adjacent communities. Although the exact mechanism(s) by which *H. sanguineus* first appeared in northern New England are not clear, the likelihood that this species will continue to expand its range and abundance in northern New England is high. Several specimens of *H. sanguineus* have been reported for various locations in Maine, including Casco Bay (Richardson, 2001).

All of the major algal and animal species that were quantified in this study are potential prey for *H. sanguineus*. In particular, *H. sanguineus* was shown to cause significant declines in *A. nodosum*, *F. vesiculosus*, *F. spiralis* and *M. stellatus* in laboratory feeding rate experiments (Tyrrell and Harris, 2001). Although it was originally reported to be primarily herbivorous (Depledge, 1984), *H. sanguineus* readily consumes a variety of animal prey items and all of the animal species quantified in this study are potential prey items for *H. sanguineus* (for molluscs: Tyrrell, 1999; Tyrrell and Harris, 2001; for *S. balanoides*, Chapters IV and V). In particular, the high feeding rate of *H. sanguineus* on *S. balanoides* may lead to severely reduced abundance of this species as *H. sanguineus* increases its population density at these study sites and in northern New England in general. Interestingly, the site that has the highest density of *H. sanguineus*, the Hilton Park 1.0 m site, has had a decline in the density of *S. balanoides* from 1999 to 2001. Further monitoring will be required to determine whether the trend of declining *S. balanoides* with increasing *H. sanguineus* continues at this and other sites.

Recently, there has been much research interest generated into the biology and impacts of *H. sanguineus*. This species has reached very high densities in Long Island Sound (ca. 70/m^2, Lohrer, 2000) and it even appears that *H. sanguineus* could be replacing *C. maenas* in the rocky intertidal zone. Lohrer (2000) found that adult *H. sanguineus* selectively consume newly recruited *C. maenas* over conspecific recruits. At various locations in Long Island Sound, there has been a decline in the relative abundance of *C. maenas* as *H. sanguineus* has increased (Lohrer, 2000). If this trend continues in northern New England, the rocky intertidal zone could be dominated by a different introduced crustacean predator that has a higher feeding rate (Chapters IV and V; DeGraaf and Tyrrell, in prep) than the previously introduced crab species. The implications of the increase in abundance of intertidal crabs and the potential replacement of *C. maenas* by *H. sanguineus* were illustrated by Tyrrell and Harris (2001). Because both species are generalized predators, it is unlikely that any prey species would be driven to local extinction with the initial increase in the abundance of *H. sanguineus*. However, because *H. sanguineus* has more herbivorous tendencies than *C. maenas* and because of its higher feeding rate, it is likely that the per capita impact of the crab guild could be greater if *H. sanguineus* eventually replaces *C. maenas*. In addition, a decrease in the abundance of algae could be expected because of the differences in the feeding habits of the two crab species (*C. maenas* appears to be less omnivorous than *H. sanguineus*, for *C. maenas*, Ropes, 1968, P.A. Madigan, unpub. data; for *H. sanguineus*, Tyrrell, 1999). The indirect impacts of an increase in *H. sanguineus* on the rest of the community could be substantial, including potential increased desiccation stress and potential competition for food with gastropods (Tyrrell and Harris, 2001).

In conclusion, this pre-*Hemigrapsus sanguineus* community structure monitoring data were primarily intended to be used as a baseline for comparison after the crab becomes abundant in this region. It seems likely that this 'new' crab invader will continue to increase in northern New England. If so, this data will be valuable for marine ecologists to compare the changes in the abundance of both potential prey of *H. sanguineus* (algae, mollusks, barnacles, juvenile *C. maenas*) and potential competitors (adult *C. maenas*). Long term community monitoring data is unusual, particularly in the marine environment, because it is both difficult and expensive to obtain. However, this type of data is also invaluable to discern the impacts of introduced species and in this case, it is likely that "after" comparisons can be made within a short time frame.

Table 2.3 Results of ANOVA (F) or Kruskall Wallis (KW) and post hoc tests (Tukey's for ANOVA, Dunn's for KW) of the comparison of percent cover of each canopy algal species in each year of sampling. The results from each species at each tidal height were tested separately. *=$p<0.05$, **=$p<0.01$, ***=$p<0.001$.

Location	Tidal height	*Ascophyllum nodosum*	*Fucus vesiculosus*	*Fucus spiralis*
Ft. Stark	0.5 m	F=1.9240 p=0.1228	F=2.9614 **p=0.0296** 98>01*	N/A
	1.0 m	KW=0.1539 p=0.9603	KW=0.2580 p=0.9032	N/A
	2.0 m	F=0.3783 p=0.8229	KW=13.660 **p=0.0085** 98>99* 98>01*	F=1.1947 p=0.3262
Odiorne	0.5 m	F=2.9637 **p=0.0295** all p>0.05	F=1.7113 p=0.1641	N/A
	1.0 m	F=2.5637 **p=0.0507** 97<01*	KW=4.4306 p=0.3509	N/A
	2.0 m	F=0.1982 p=0.9380	KW=4.8828 p=0.2995	N/A
Hilton Park	0.5 m	N/A	F=2.7288 p=0.0833	N/A
	1.0 m	F=1.1798 p=0.3227	F=1.9858 p=0.1568	N/A

Table 2.4 Results of ANOVA (F) or Kruskall Wallis (KW) and post hoc tests (Tukey's for ANOVA, Dunn's for KW) of the comparison of percent cover of each substrate type or subcanopy algae in each year of sampling. The results from each category at each tidal height were tested separately. RB=Rock bench, LR=Large rock, CB=Cobble, PS=Pebble/shell, *=p<0.05, **=p<0.01, ***=p<0.001.

Location	Tidal height	Rock bench	Large rock	Cobble	Pebble/shell	Mud/sand	Subcanopy algae	post hoc
Ft. Stark	0.5 m	KW=6.8545 p=0.1438	F=1.7250 p=0.1616	F=1.0316 p=0.4017	F=1.2030 p=0.3231	F=3.8411 **p=0.0092**	KW=2.2770 p=0.6850	mud 97<99* 97<00* 97<01**
	1.0 m	F=0.5120 p=0.7272	KW=2.3668 p=0.6686	F=0.9069 p=0.4681	F=0.4321 p=0.7847	KW=2.5658 p=0.6329	F=0.5507 p=0.6995	
	2.0 m	KW=4.1915 **p=0.0058**	KW=14.206 **p=0.0067**	F=2.3603 p=0.0679	F=1.7084 p=0.1652	KW=6.6366 p=0.1564		RB 97<99* 97<01** LR 97>99** 97>00*
Odiorne	0.5 m		F=5.5231 **p=0.0035**	F=1.8960 p=0.1495	F=1.2450 p=0.3092	KW=4.2087 p=0.2398	KW=0.0666 p=0.9955	LR 99>00* 99>01**
	1.0 m	KW=3.2674 p=0.3522	F=0.1917 p=0.9013	F=0.2726 p=0.8447	F=0.6999 p=0.5584	F=0.8729 p=0.4647	KW=2.7664 p=0.4291	
	2.0 m	KW=9.4725 **p=0.0236**	F=0.6124 p=0.6114	F=1.4635 p=0.2408	F=2.9527 **p=0.0455**	KW=3.000 p=0.3916	KW=3.000 p=0.3916	RB 98>01* PS 98<01*
Hilton Park	0.5 m	F=1.3641 p=0.2717	KW=4.1379 p=0.1263	F=5.2901 **p=0.0115**	F=4.4978 **p=0.0206**	F=9.5468 **p=0.0007**	KW=14.012 **p=0.0009**	CB 99<00* 99<01* PS 00>01* mud 99<00** 99<01*** algae 99>00***
	1.0 m	F=0.9466 p=0.4006	F=0.7649 p=0.4752	F=0.4564 p=0.6383	F=0.5995 p=0.5562	F=0.1078 p=0.7465	F=2.2500 p=0.1248	

Table 2.5 Results of ANOVA (F) or Kruskall Wallis (KW) and post hoc tests (Tukey's for ANOVA, Dunn's for KW) of the comparison of density of each species in each year of sampling. The results from each species at each tidal height were tested separately. *=p<0.05, **=p<0.01, ***=p<0.001.

Location	Tidal height	*Semibalanus balanoides*	*Mytilus edulis*	*Carcinus maenas*
Ft. Stark	0.5 m	F=2.5153 **p=0.0545** 98>99 *	F=0.8667 p=0.4907	F=11.440 **p<0.0001** 97<99 *** 97<00 ** 97<01 *** 98<99 **
	1.0 m	F=2.0708 p=0.1005	F=1.1525 p=0.3444	F=6.2883 **p=0.0004** 97<98 ** 97<99 *** 97<00 * 97<01 **
	2.0 m	F=4.5438 **p=0.0036** 99<00** 00>01 *	N/A	F=1.4200 p=0.2428
Odiorne	0.5 m	KW=35.384 **p<0.0001** 97<00** 98<99* 98<00*** 98<01***	N/A	F=4.2189 **p=0.0055** 97<99 **
	1.0 m	F=1.6148 p=0.1866	F=0.4085 p=0.8016	F=4.8671 **p=0.0023** 97<99 ** 99>00 * 99>01 **
	2.0 m	F=3.3124 **p=0.0184** 97>99 *	KW=16.054 **p=0.0029** 97>98* 97>99* 97>01*	F=0.8636 p=0.4931
Hilton Park	0.5 m	F=1.8898 p=0.1713	F=14.362 **p<0.0001** 99>00 ** 99>01 ***	F=3.4840 **p=0.0451** 99<01 *
	1.0 m	F=0.9538 p=0.3979	F=0.1007 p=.9045	F=2.1932 p=0.1310

Table 2.6 Results of ANOVA (F) or Kruskall Wallis (KW) and post hoc tests (Tukey's for ANOVA, Dunn's for KW) of the comparison of size classes of *Semibalanus balanoides* in each year of sampling. SB= *Semibalanus balanoides*. *=p<0.05, **=p<0.01, ***=p<0.001.

Location	Tidal height	SB<2	SB 2-5	SB>5
Ft. Stark	0.5 m	F=3.9921 **p=0.0081** 98>00 *	F=2.5898 **p=0.0511** all p>0.05	KW=4.2593 p=0.3721
	1.0 m	F=0.2879 p=0.8842	F=0.5179 p=0.7229	KW=3.8975 p=0.4201
	2.0 m	KW=13.167 **p=0.0105** 98<00 * 99<00 *	F=3.4214 **p=0.0191** all p>0.05	KW=17.136 **p=0.0018** 98>00 * 98>01 * 99>00 *
Odiorne	0.5 m	KW=10.601 **p=0.0141** 97>99 * 97>00 *	F=10.639 **p<0.0001** 97<99 *** 97<00 *** 97<01 ***	KW=9.7229 **p=0.0446** all p>0.05
	1.0 m	KW=10.139 **p=0.0382** all p>0.05	F=0.1930 p=0.9004	KW=9.7229 **p=0.0446** all p>0.05
	2.0 m	F=2.0894 p=0.0997	F=0.8877 p=0.4799	KW=4.3060 p=0.3662
Hilton Park	0.5 m	KW=3.5154 p=0.1724	F=1.2316 p=0.3083	F=1.0289 p=0.3715
	1.0 m	KW=3.6127 p=0.1643	F=0.5190 p=0.6014	KW=1.8394 p=0.3986

Table 2.7 Results of ANOVA (F) or Kruskall Wallis (KW) and post hoc tests (Tukey's for ANOVA, Dunn's for KW) of the comparison of size classes of *Mytilus edulis* in each year of sampling. ME=*Mytilus edulis*. *=p<0.05, **=p<0.01, ***=p<0.001.

Location	Tidal height	ME 0-10	ME 11-20	ME 21-30	ME 31-50	ME >50
Ft. Stark	0.5 m	KW=2.3695 p=0.6682	KW=10.345 **p=0.0350** all p>0.05	KW=10.025 **p=0.0400** all p>0.05	KW=17.391 **p=0.0016** 97>01 * 98>01 *	F=7.1743 p=0.0005 97<99 * 97<00 ** 98<99 * 98<00 * 98<01 *
	1.0 m	KW=5.2057 p=0.2668	KW=6.6792 p=0.1538	KW=9.2935 **p=0.0542** 98>00 *	F=4.0184 **p=0.0092** 98>00 * 99>00 *	KW=13.772 **p=0.0081** 98<00 **
	2.0 m	N/A	N/A	N/A	N/A	N/A
Odiorne	0.5 m	N/A	N/A	N/A	N/A	N/A
	1.0 m	N/A	KW=6.6667 p=0.1546	KW=4.8236 p=0.3059	F=1.5932 p=0.2192	F=0.3354 p=0.8505
	2.0 m	N/A	N/A	N/A	N/A	N/A
Hilton Park	0.5 m	N/A	N/A	KW=11.586 **p=0.0030** 99>00 **	KW=11.077 **p=0.0039** 99>00 **	KW=12.914 **p=0.0016** 99<00 **
	1.0 m	N/A	N/A	KW=3.000 p=0.2231	KW=1.7781 p=0.4110	KW=1.5349 p=0.4642

Table 2.8 Results of ANOVA (F) or Kruskall Wallis (KW) and post hoc tests (Tukey's for ANOVA, Dunn's for KW) of the comparison of density of each littorinid species in each year of sampling. The results from each littorinid species at each tidal height were tested separately. *=p<0.05, **=p<0.01, ***=p<0.001.

Location	Tidal height	*Littorina littorea*	*Littorina obtusata*	*Littorina saxatilis*
Ft. Stark	0.5 m	F=2.8081 **p=0.0365** 97< 98 *	F=1.8999 p=0.1269	N/A
	1.0 m	F=1.6485 p=0.1787	F=6.9332 **p=0.0002** 97<99 *** 97<00 *** 97<01 *	KW=2.5658 p<0.6329
	2.0 m	F=0.7339 p=0.5737	F=8.6344 **p<0.0001** 97<98 ** 97<99 *** 97<00 *** 97<01 **	F=0.9532 p=0.4424
Odiorne	0.5 m	F=13.435 **p<0.0001** 97<98 *** 97<99 ** 97<00 *** 97<01 ***	F=3.5694 **p=0.0130** 97<99 * 98<99 *	F=5.3001 **p=0.0014** 97<00 * 97<01 * 98<00 * 98<01 *
	1.0 m	F=0.7580 p=0.5580	F=11.937 **p<0.0001** 97<99 *** 97<00 *** 97<01 *** 98<99 ** 98<00 **	F=1.4944 p=0.2195
	2.0 m	F=1.4371 p=0.2373	F=2.429 p=0.0563	F=2.5317 **p=0.0533** 97<98 *
Hilton Park	0.5 m	F=1.2040 p=0.3156	F=5.3677 **p=0.0109** 00<01 **	N/A
	1.0 m	F=4.7359 **p=0.0173** 99<00 * 00>01 *	F=0.4427 p=0.6469	F=0.0929 p=0.9115

Table 2.9 Results of ANOVA (F) or Kruskall Wallis (KW) and post hoc tests (Tukey's for ANOVA, Dunn's for KW) of the comparison of size classes of *Littorina littorea* in each year of sampling. LL=*L. littorea*= *=$p<0.05$, **=$p<0.01$, ***=$p<0.001$.

Location	Tidal height	LL 0-10	LL 11-20	LL 21-30	LL >30
Ft. Stark	0.5 m	F=2.8225 **p=0.0358** 97<99*	F=0.6530 p=0.6278	F=1.4713 p=0.2267	KW=3.9714 p=0.4099
	1.0 m	KW=3.3140 p=0.5067	KW=2.556 p=0.6347	KW=2.7808 p=0.5951	KW=14.575 **p=0.0057** 97<99* 97<00* 97<01*
	2.0 m	KW=7.3861 p=0.1168	KW=3.9044 p=0.4184	KW=6.7760 p=0.1482	KW=28.619 **p<0.0001** 97>98*** 97>99*** 97>00*** 97>01***
Odiorne	0.5 m	F=4.8939 **p=0.0023** 97<98* 97<99** 97<00*	F=4.8637 **p=0.0024** 97<98* 97<00** 97<01*	KW=16.982 **p=0.0019** 97>98* 97>99* 97>00**	N/A
	1.0 m	F=1.4321 p=0.2385	F=0.1850 p=0.9450	F=0.9237 p=0.4584	N/A
	2.0 m	F=2.6841 **p=0.0436** 98<01*	F=3.9357 **p=0.0081** 98>01* 00>01*	KW=3.3962 p=0.4938	N/A
Hilton Park	0.5 m	F=2.4132 p=0.1086	F=4.1680 **p=0.0265** 00>01*	KW=3.8854 p=0.1433	N/A
	1.0 m	F=4.6214 **p=0.0188** 99<01*	F=12.394 **p=0.0002** 99>00**	F=2.4317 p=0.1069	N/A

Table 2.10 Results of ANOVA (F) or Kruskall Wallis (KW) and post hoc tests (Tukey's for ANOVA, Dunn's for KW) of the comparison of size classes of *Littorina obtusata* in each year of sampling. LO=*Littorina obtusata*. *=p<0.05, **=p<0.01, ***=p<0.001.

Location	Tidal height	LO <2	LO 2-10	LO>10
Ft. Stark	0.5 m	KW=5.4428 p=0.2448	F=8.5069 **p<0.0001** 97<99** 97<00*** 98<99* 98<00* 98<01*	F=16.503 **p<0.0001** 97<98*** 97<99** 97<01* 98>99*** 98>00*** 98>01**
	1.0 m	KW=4.6058 p=0.3302	F=24.146 **p<0.0001** 97<99** 97<00*** 97<01**	KW=7.1263 p=0.1294
	2.0 m	KW=1.5353 p=0.8204	KW=26.007 **p<0.0001** 97<99** 97<01*** 98>99* 98>01**	KW=18.582 **p=0.0089** 98>99* 98>01**
Odiorne	0.5 m	KW=3.2970 p=0.5094	F=1.4801 p=0.2274	F=0.4192 p=0.7938
	1.0 m	KW=9.8160 **p=0.0436** all p>0.05	F=4.7286 **p=0.0029** 97<99***	F=1.6251 p=0.1849
	2.0 m	KW=4.5895 p=0.3321	F=7.2652 **p=0.0001** 97<98** 97<99*** 97<00** 97<01***	F=6.0941 **p=0.0006** 97>98* 97>99** 97>00* 97>01***
Hilton Park	0.5 m	N/A	N/A	N/A
	1.0 m	KW=3.8197 p=0.1481	F=0.0279 p=0.9861	KW=0.0027 p=0.9987

Table 2.11 Results of ANOVA (F) or Kruskall Wallis (KW) and post hoc tests (Tukey's for ANOVA, Dunn's for KW) of the comparison of size classes of *Littorina saxatilis* in each year of sampling. LS=*Littorina saxatilis*. *=p<0.05, **=p<0.01, ***=p<0.001.

Location	Tidal height	LS <2	LS 2-10	LS>10
Ft. Stark	0.5 m	N/A	N/A	N/A
	1.0 m	N/A	N/A	N/A
	2.0 m	KW=13.270 **p=0.0100** 97>98* 97>99* 97>00* 97>01*	KW=7.8790 p=0.0961	KW=5.7822 p=0.2160
Odiorne	0.5 m	N/A	KW=6.5323 p=0.1628	KW=1.8841 p=0.7571
	1.0 m	KW=3.400 p=0.4932	KW=6.5323 p=0.1628	KW=9.7336 **p=0.0452** all p>0.05
	2.0 m	KW=2.500 p=0.6446	KW=7.3377 p=0.1191	KW=5.9430 p=0.2034
Hilton Park	0.5 m	N/A	N/A	N/A
	1.0 m	N/A	KW=5.1852 p=0.0638	KW=5.1852 p=0.0638

Table 2.12: Significant regressions of various physical and biological parameters versus density of *C. maenas* at each of the three New Hampshire study sites.

Location	Adj. multiple r^2	Shelter (+)	Canopy algae (+)	Barnacles (-)	Gastropods (+)
Ft. Stark	0.30	p=0.008	-	p=0.001	p<0.001
Odiorne	0.19	-	-	-	p<0.001
Hilton Park	0.38	-	p<0.001	-	p<0.001

Table 2.13 Results of ANOVA (F) or Kruskall Wallis (KW) and post hoc tests (Tukey's for ANOVA, Dunn's for KW) of the comparison of size classes of *Carcinus maenas* in each year of sampling.

Location	Tidal height	0 - 5	6 - 10	11 - 15	16 -20	21-25	>25
Ft. Stark	0.5 m	KW=5.2444 p=0.2631	F=9.1969 **p<0.0001** 97<98 *** 97<99 ** 97<00 ** 97<01 ***	F=1.5105 p=0.2512	KW=6.8264 p=0.1453	KW=0.9429 p=0.9183	KW=7.6384 p=0.1058
	1.0 m	KW=2.4895 p=0.6465	F=4.2744 **p=0.0054** 97<98 * 97<99 ** 97<01 *	KW=1.8156 p=0.7696	KW=7.8350 p=0.0978	KW=4.5451 p=0.3372	KW=2.4295 p=0.6573
	2.0 m	KW=19.727 **p=0.0006** 97>98 * 97>99 ** 97>00 ** 97>01 *	F=45.991 **p<0.0001** 97<98 ** 97<99 *** 97<00 *** 97<01 ***	KW=1.7380 p=0.7838	KW=6.9172 p=0.1403	KW=3.0161 p=0.5551	KW=1.8884 p=0.7563

Table 2.14 Results of ANOVA (F) or Kruskall Wallis (KW) and post hoc tests (Tukey's for ANOVA, Dunn's for KW) of the comparison of size classes of *Carcinus maenas* in each year of sampling.

Location	Tidal height	0 - 5	6 - 10	11 - 15	16 - 20	21-25	>25
Odiorne	0.5 m	F=34.532 **p<0.0001** 97>98 ** 97>00 *** 97>01 *** 98>00 *** 98>01 *** 99>00 *** 99>01 ***	F=27.264 **p<0.0001** 97<98 ** 97<00 *** 97<01 *** 98<00 *** 98<01 *** 99<00 *** 99<01 ***	F=0.7817 p=0.5430	KW=9.2063 **p=0.0561** all p>0.05	KW=10.627 **p=0.0311** 97<01 *	KW=16.045 **p=0.0030** all p>0.05
	1.0 m	F=39.438 **p<0.0001** 97>98 * 97>00 *** 97>01 *** 98>00 *** 98>01 *** 99>00 *** 99>01 ***	F=24.801 **p<0.0001** 97<00 *** 97<01 *** 98<00 *** 98<01 ** 99<00 *** 99<01 ***	KW=5.9446 p=0.2033	KW=13.388 **p=0.0095** 97<01 * 98<01 *	KW=7.2173 p=0.1248	KW=4.6020 p=0.3306
	2.0 m	KW=40.000 **p<0.0001** 97>98 ** 97>00 *** 97>01 *** 99>00 * 99>01 **	F=30.898 **p<0.0001** 97<98 *** 97<99 *** 97<00 *** 97<01 *** 99<00 *** 99<01 **	F=3.7086 **p<0.0108** 97<98 *	KW=9.3935 **p=0.0520** all p>0.05	KW= 2.5785 p=0.6306	KW=2.2479 p=0.6903

Table 2.15 Results of ANOVA (F) or Kruskall Wallis (KW) and post hoc tests (Tukey's for ANOVA, Dunn's for KW) of the comparison of size classes of *Carcinus maenas* in each year of sampling.

Location	Tidal height	0 - 5	6 - 10	11 - 15	16 -20	21-25	>25
Hilton Park	0.5 m	F=0.3878 p=0.6822	F=0.4444 p=0.6458	KW=1.5735 p=0.4553	KW=0.5560 p=0.7573	KW=2.0000 p=0.3679	KW=1.0379 p=0.5951
	1.0 m	F=1.7653 p=0.1903	F=0.4893 p=0.6184	KW=4.2191 p=0.1213	KW=1.6283 p=0.4430	KW=1.0379 p=0.5951	KW=3.9917 p=0.1359

Table 2.16. ANOVA of axis scores from nonmetric multidimensional scaling (MDS) and the year, location, tidal height and the interaction of location and tidal height for quantitative community analysis prior to the establishment of *Hemigrapsus sanguineus*. Values in bold indicate statistical significance.

MDS axis score 1	F-ratio	df	p
Location	115.929	2	**<0.001**
Tidal height	46.259	1	**<0.001**
Year	0.598	2	0.569
Location*tidal height	58.141	2	**<0.001**
MDS axis score 2			
Location	21.726	2	**<0.001**
Tidal height	7.136	1	**0.023**
Year	1.175	2	0.348
Location*tidal height	32.769	2	**<0.001**

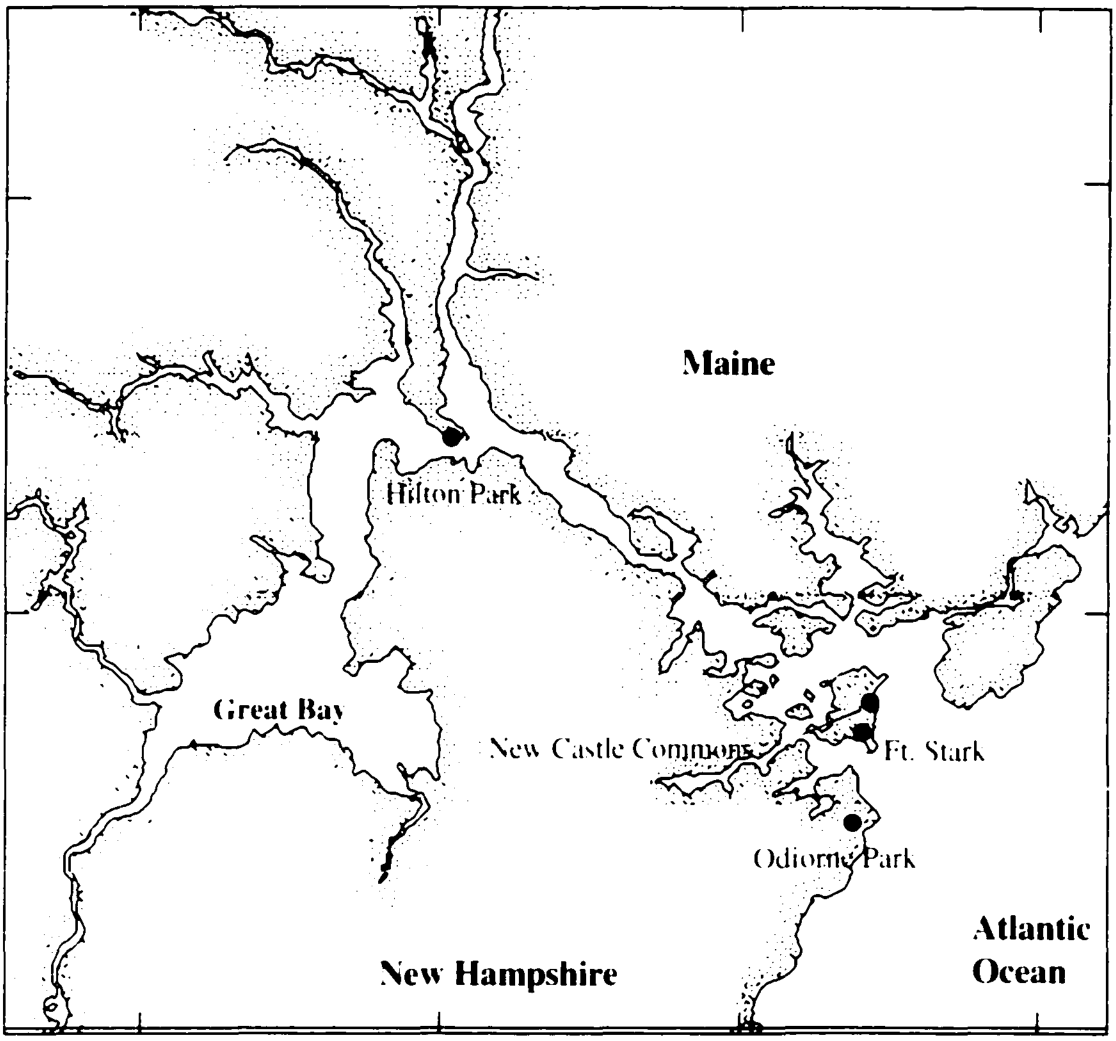


Figure 2.1 Map of New Hampshire coast and Great Bay estuary showing study locations for community structure monitoring prior to the establishment of *H. sanguineus*.

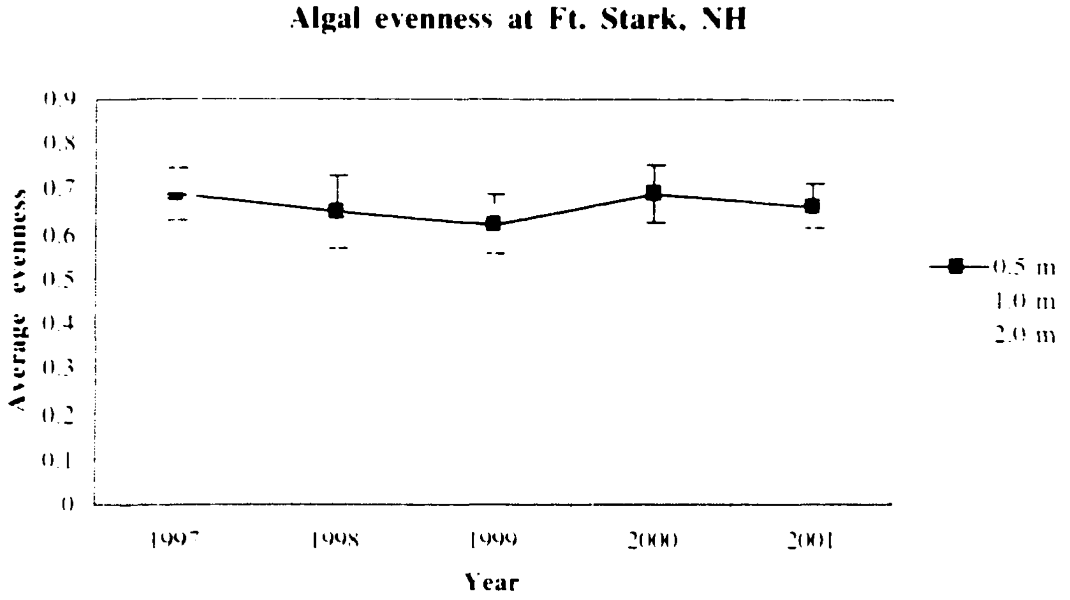


Figure 2.2 Average algal evenness and standard error for different tidal heights at Ft. Stark, NH from 1997 to 2001 calculated using Pielou's J index for equitability.

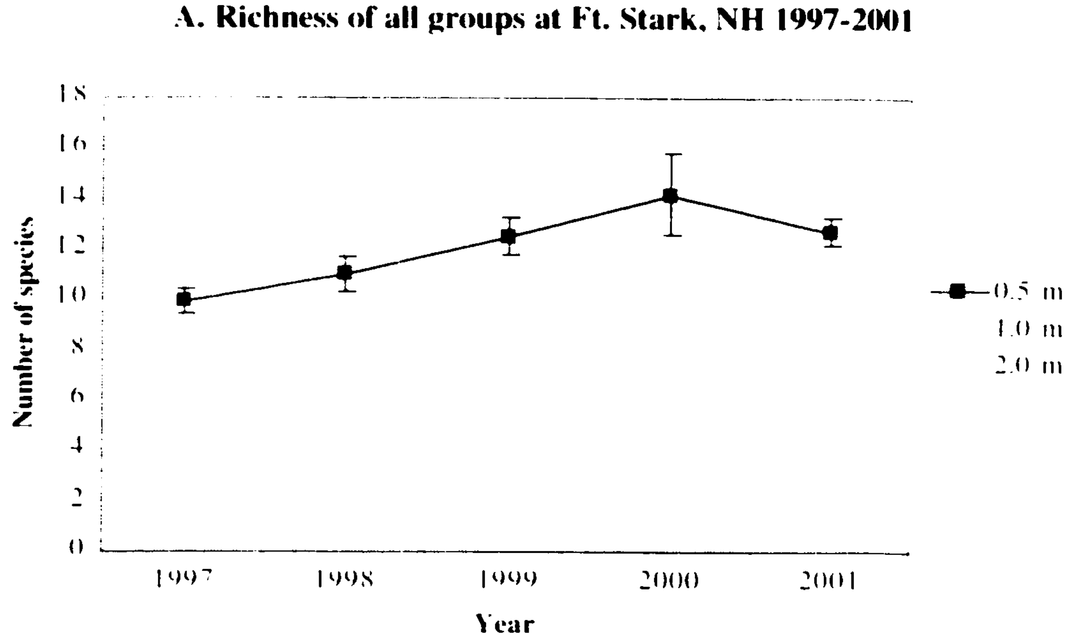


Figure 2.3a Average richness and standard error for different tidal heights at Ft. Stark, NH from 1997 to 2001 calculated by including groups of species in the richness estimate.

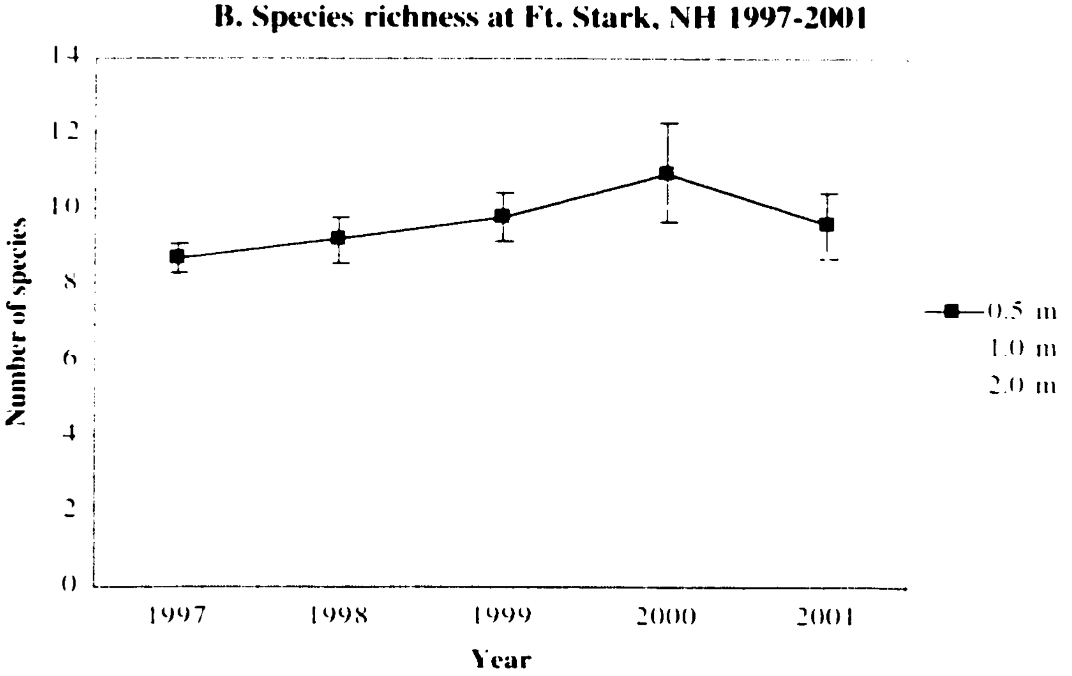


Figure 2.3b. Average richness and standard error for different tidal heights at Ft. Stark, NH from 1997 to 2001 calculated only including organisms identified to species in the estimate.

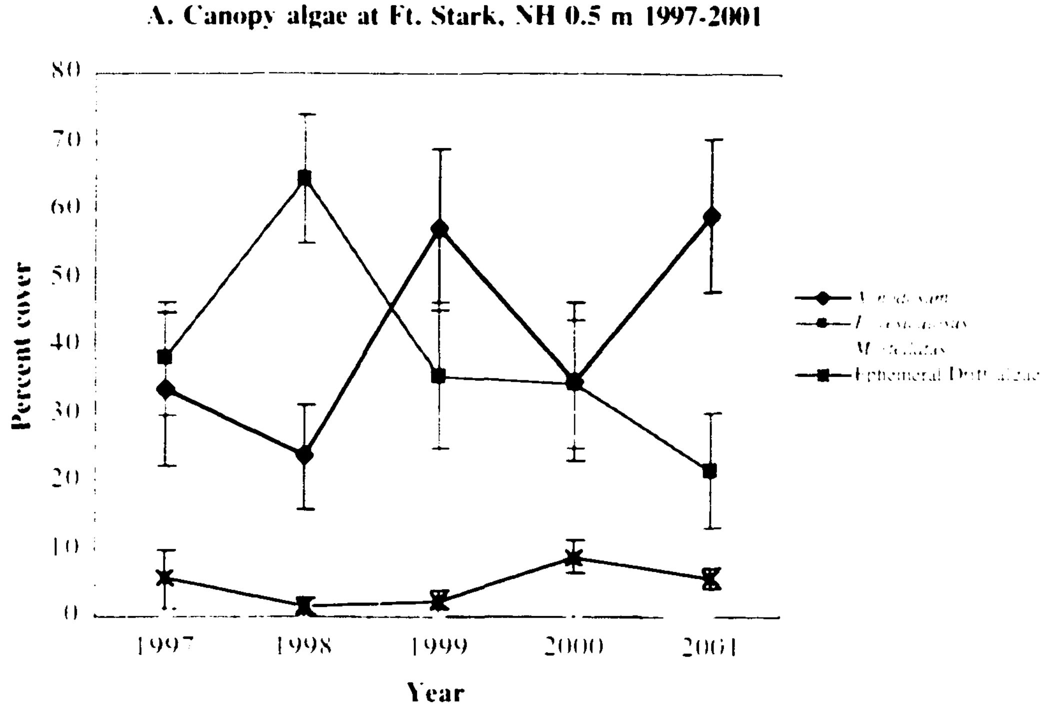


Figure 2.4a Average percent cover and standard error of algae observed in the canopy analysis at 0.5 m above MLLW (mean lower low water) at Ft. Stark, NH from 1997 - 2001. Cover types represent major algal canopy species; drift and ephemeral algae were not identified to species because of their highly variable composition and abundance.

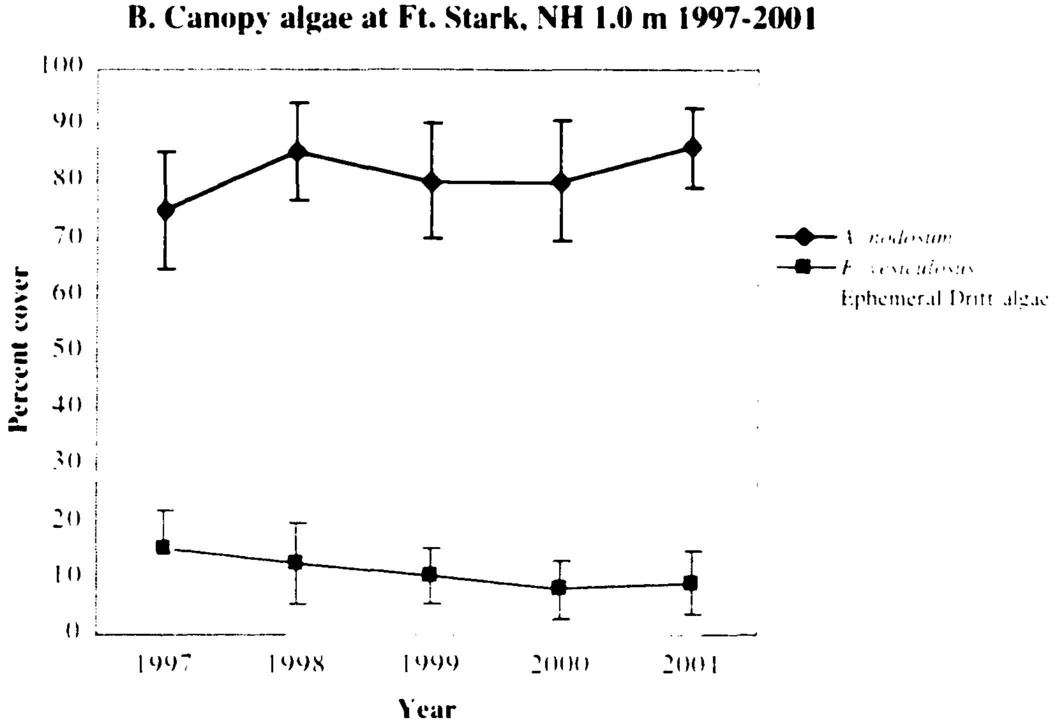


Figure 2.4b Average percent cover and standard error of algae observed in the canopy analysis at 1.0 m above MLLW at Ft. Stark, NH from 1997 - 2001. Cover types represent major algal canopy species; drift and ephemeral algae were not identified to species because of their highly variable composition and abundance.

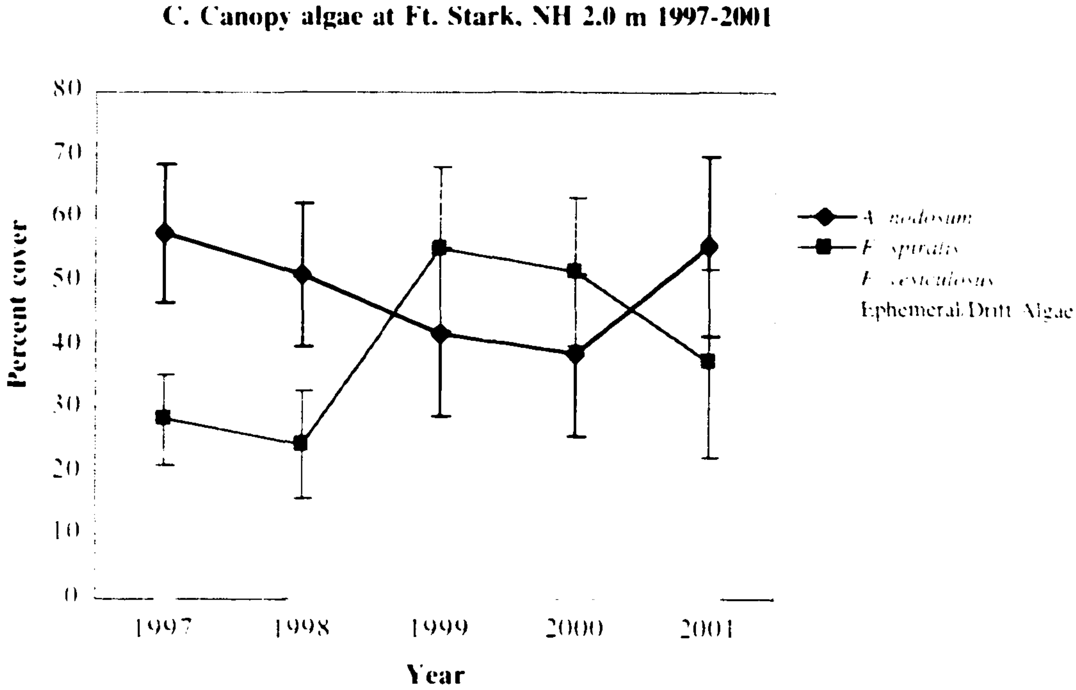


Figure 2.4c Average percent cover and standard error of algae observed in the canopy analysis at 2.0 m above MLLW at Ft. Stark, NH from 1997 - 2001. Cover types represent major algal canopy species; drift and ephemeral algae were not identified to species because of their highly variable composition and abundance.

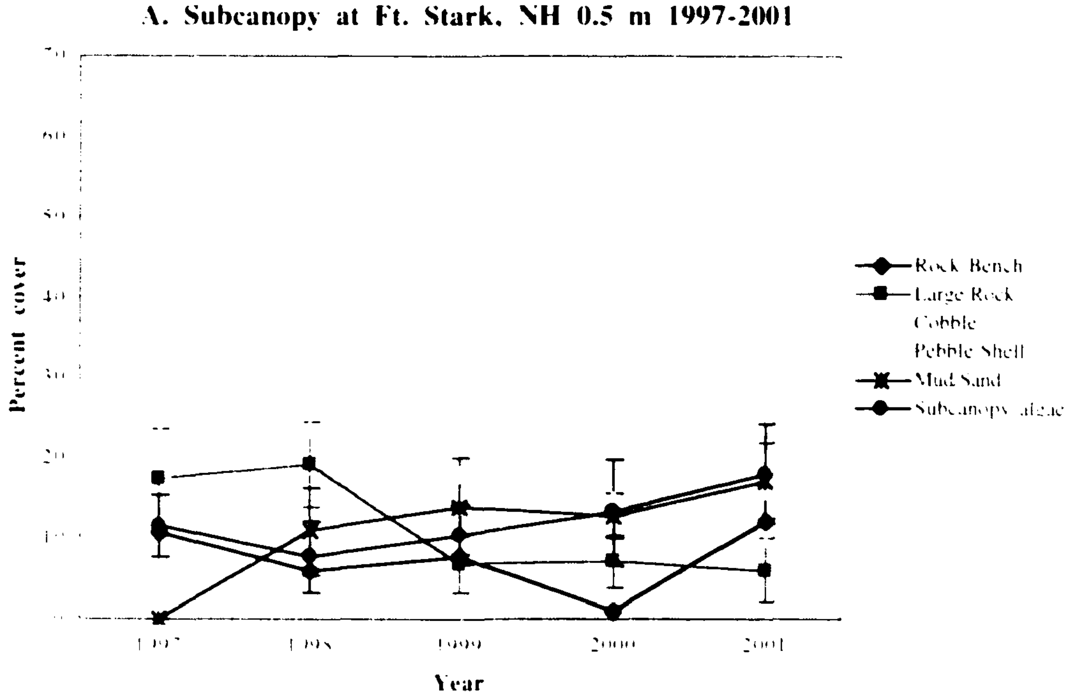


Figure 2.5a Average percent cover and standard error of substrates and subcanopy algae observed in subcanopy analysis at 0.5 m above MLLW (mean lower low water) at Ft. Stark, NH from 1997 - 2001. The majority of the subcanopy algae category was *M. stellatus*.

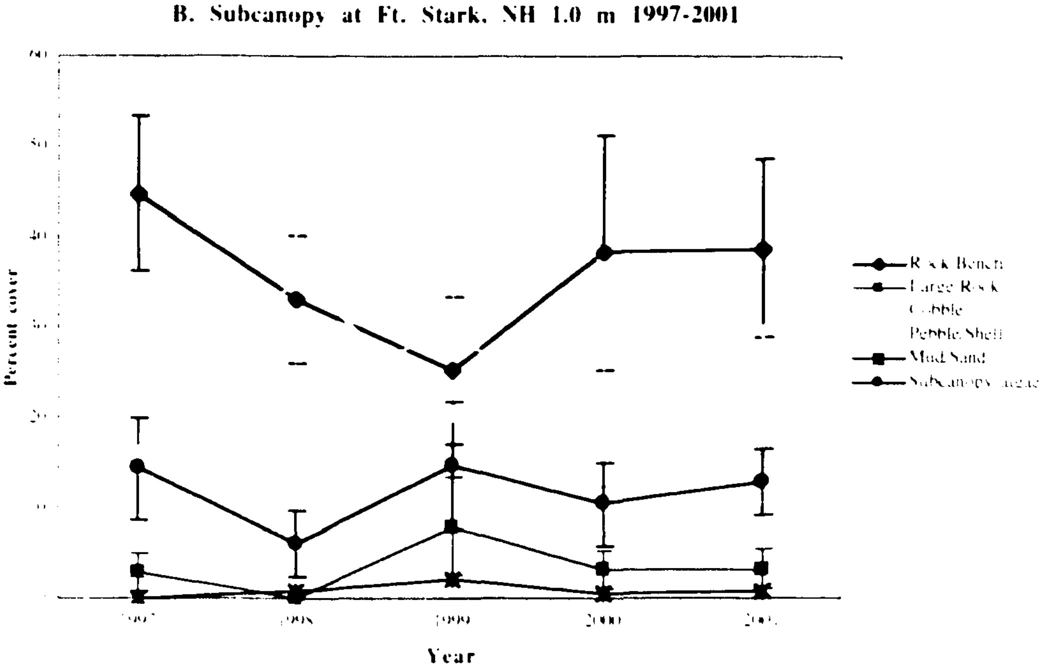

B. Subcanopy at Ft. Stark, NH 1.0 m 1997-2001

Figure 2.5b Average percent cover and standard error of substrates and subcanopy algae observed in subcanopy analysis at 1.0 m above MLLW at Ft. Stark, NH from 1997 - 2001. The majority of the subcanopy algae category was *M. stellatus* and crustose coralline algae.

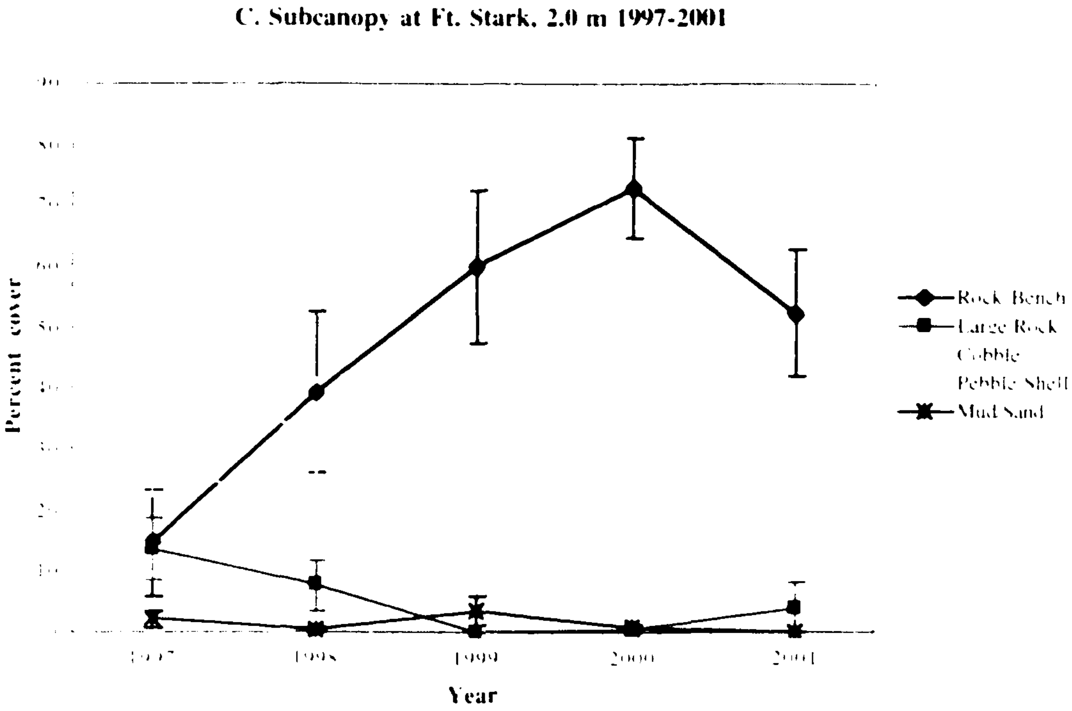


Figure 2.5c Average percent cover and standard error of substrates observed in subcanopy analysis at 2.0 m above MLLW at Ft. Stark, NH from 1997 - 2001.

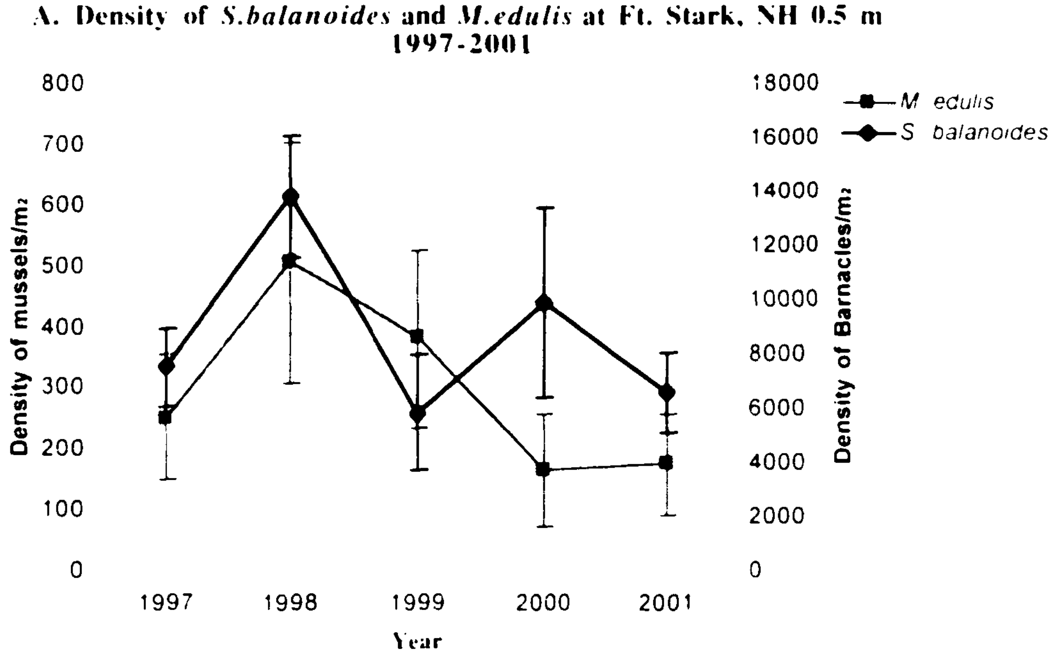
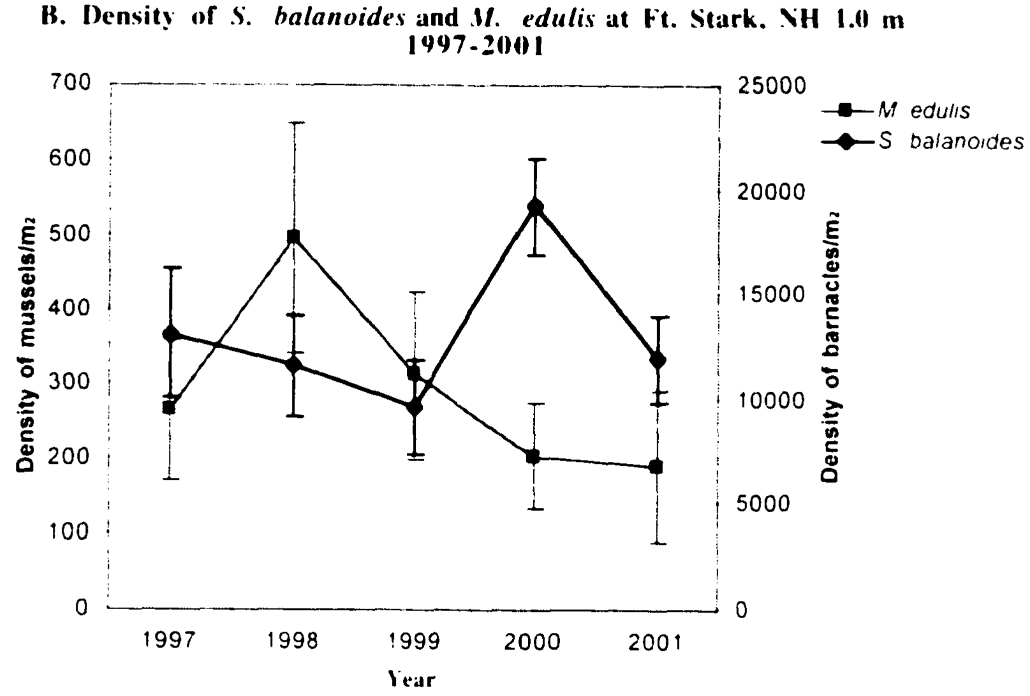
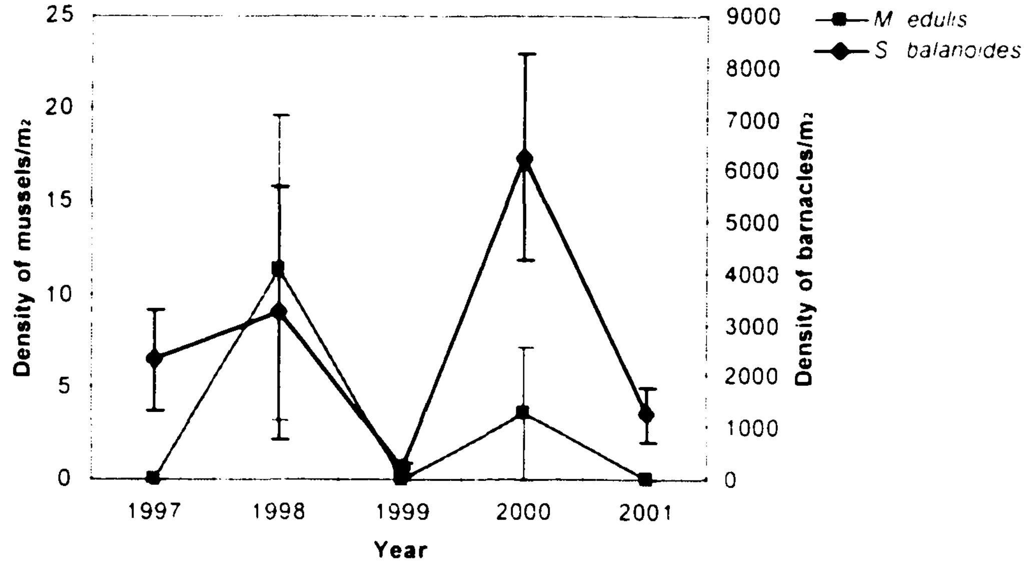


Figure 2.6a Average density/m² and standard error of *M. edulis* and *S. balanoides* at 0.5 m above MLLW (mean lower low water) at Ft. Stark, NH from 1997 - 2001.



B. Density of *S. balanoides* and *M. edulis* at Ft. Stark, NH 1.0 m 1997-2001

Figure 2.6b Average density/m^2 and standard error of *M. edulis* and *S. balanoides* at 1.0 m above MLLW at Ft. Stark, NH from 1997 - 2001.



C. Density of *S. balanoides* and *M. edulis* at Ft. Stark, NH 2.0 m 1997-2001

Figure 2.6c Average density/m² and standard error of *M. edulis* and *S. balanoides* at 2.0 m above MLLW at Ft. Stark, NH from 1997 - 2001.

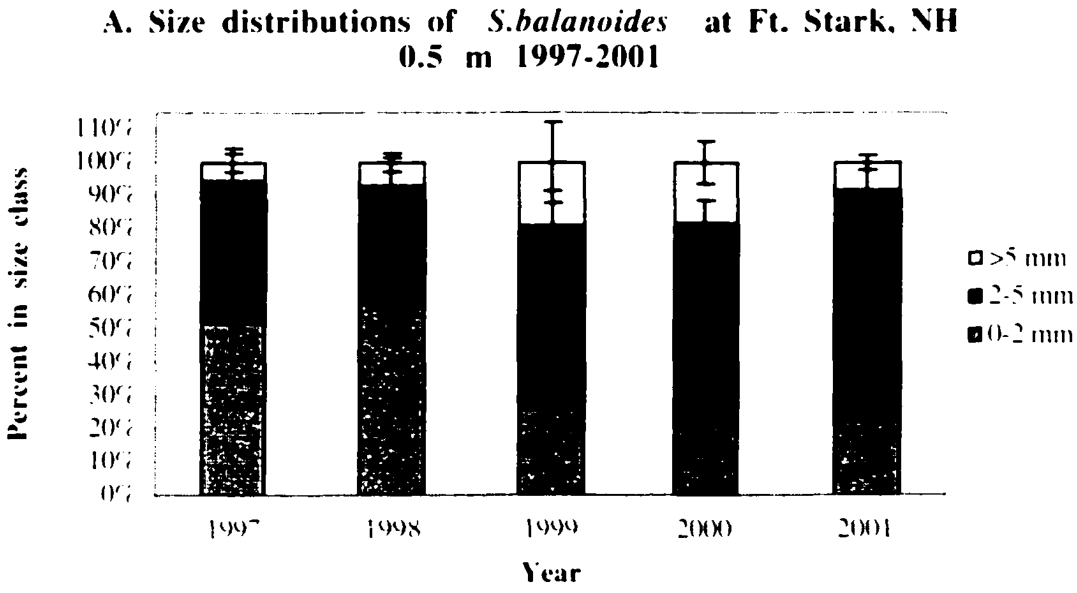

A. Size distributions of *S. balanoides* at Ft. Stark, NH 0.5 m 1997-2001

Figure 2.7a Estimated size class distribution of *S. balanoides* at 0.5 m above MLLW (mean lower low water) at Ft. Stark, NH from 1997 - 2001.

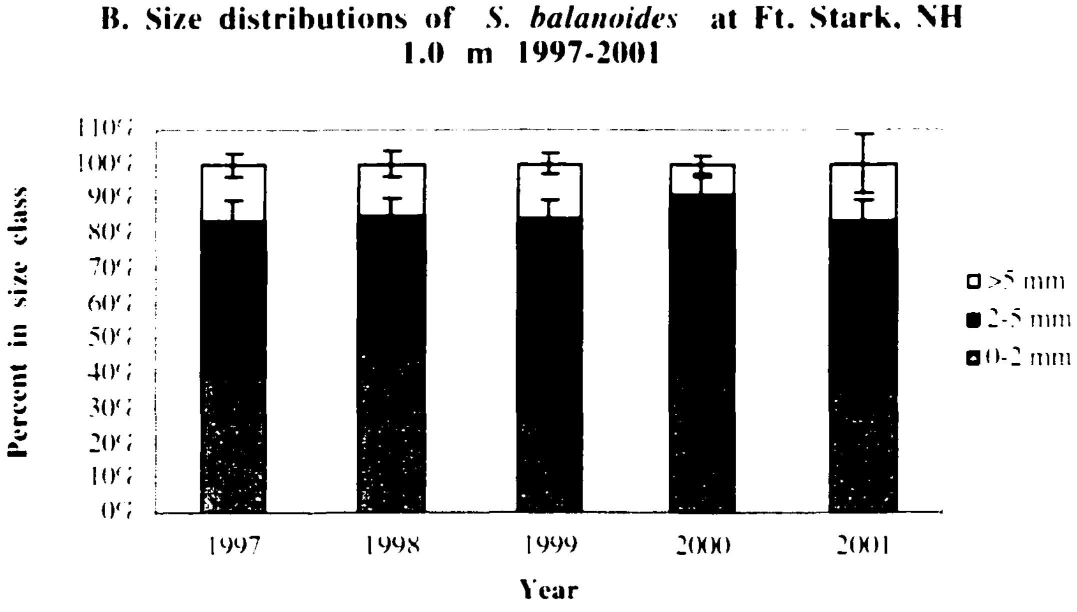
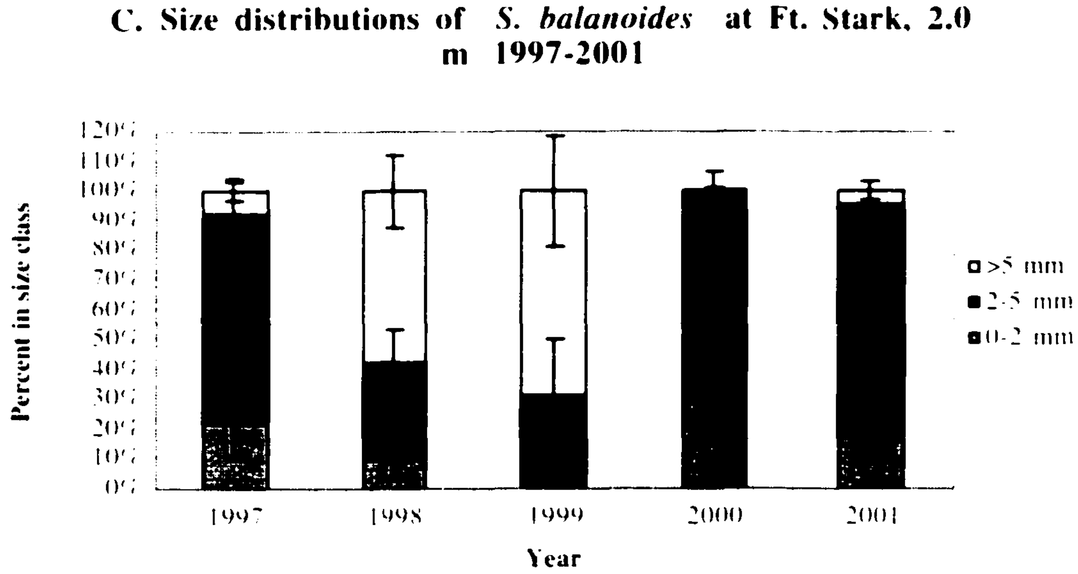

B. Size distributions of *S. balanoides* at Ft. Stark, NH 1.0 m 1997-2001

Figure 2.7b Estimated size class distribution of *S. balanoides* at 1.0 m above MLLW at Ft. Stark, NH from 1997 - 2001.



C. Size distributions of *S. balanoides* at Ft. Stark, 2.0 m 1997-2001

Figure 2.7c Estimated size class distribution of *S. balanoides* at 2.0 m above MLLW at Ft. Stark, NH from 1997 - 2001.

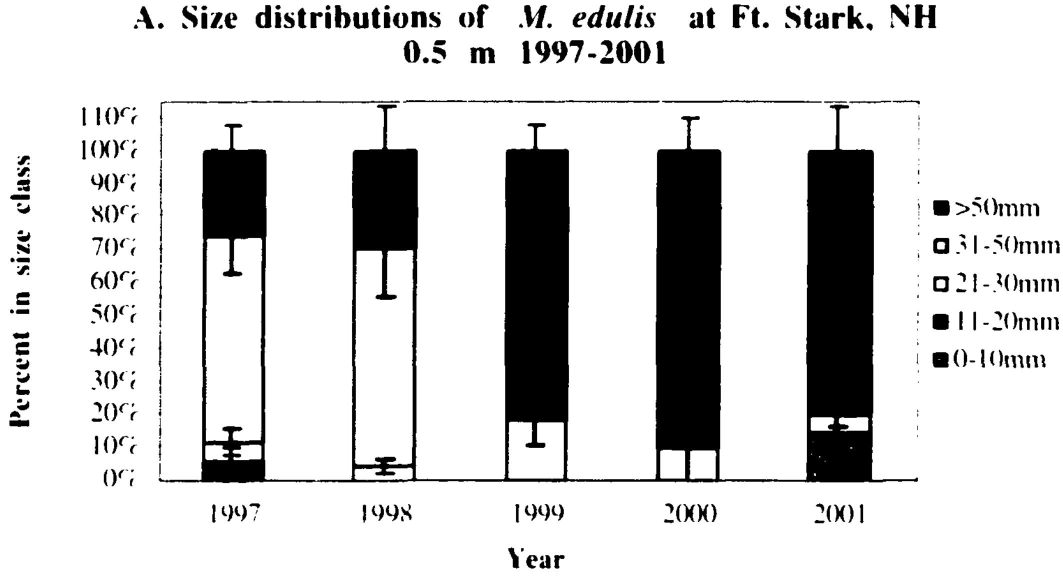

A. Size distributions of *M. edulis* at Ft. Stark, NH
0.5 m 1997-2001

Figure 2.8a Estimated size class distribution of *M. edulis* at 0.5 m above MLLW (mean lower low water) at Ft. Stark, NH from 1997 - 2001.

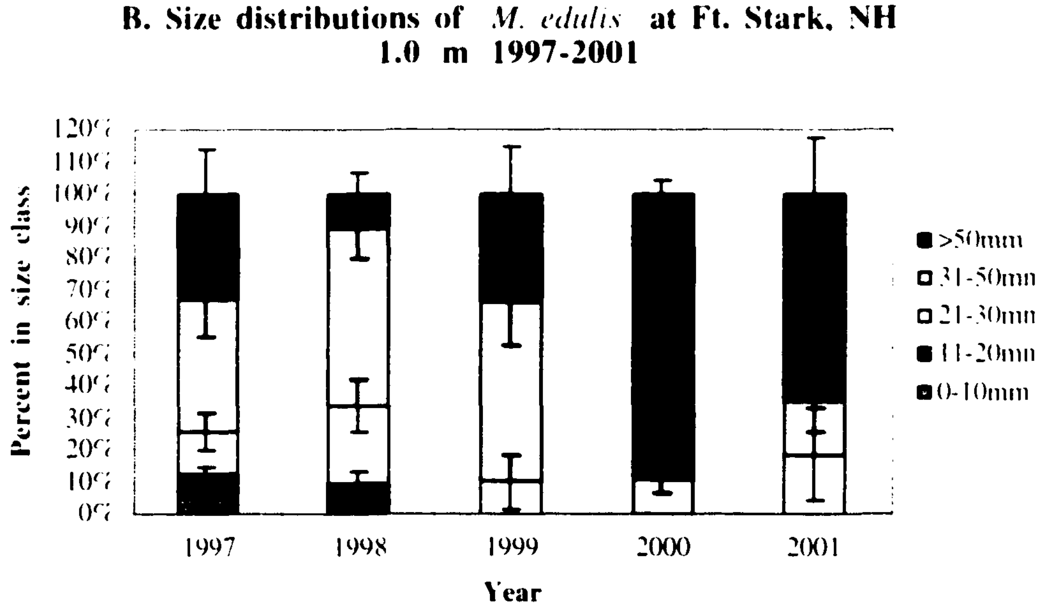
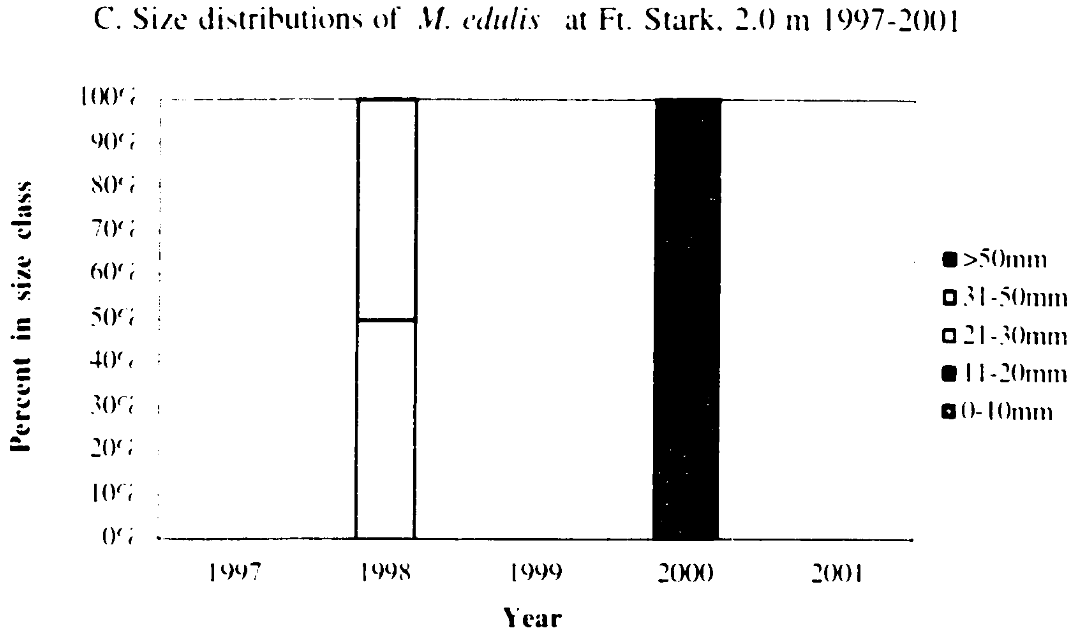

B. Size distributions of *M. edulis* at Ft. Stark, NH
1.0 m 1997-2001

Figure 2.8b Estimated size class distribution of *M. edulis* at 1.0 m above MLLW at Ft. Stark, NH from 1997 - 2001.



C. Size distributions of *M. edulis* at Ft. Stark, 2.0 m 1997-2001

Figure 2.8c Estimated size class distribution of *M. edulis* at 2.0 m above MLLW at Ft. Stark, NH from 1997 - 2001. No *M. edulis* were present at this tidal height in 1997, 1999 and 2001.

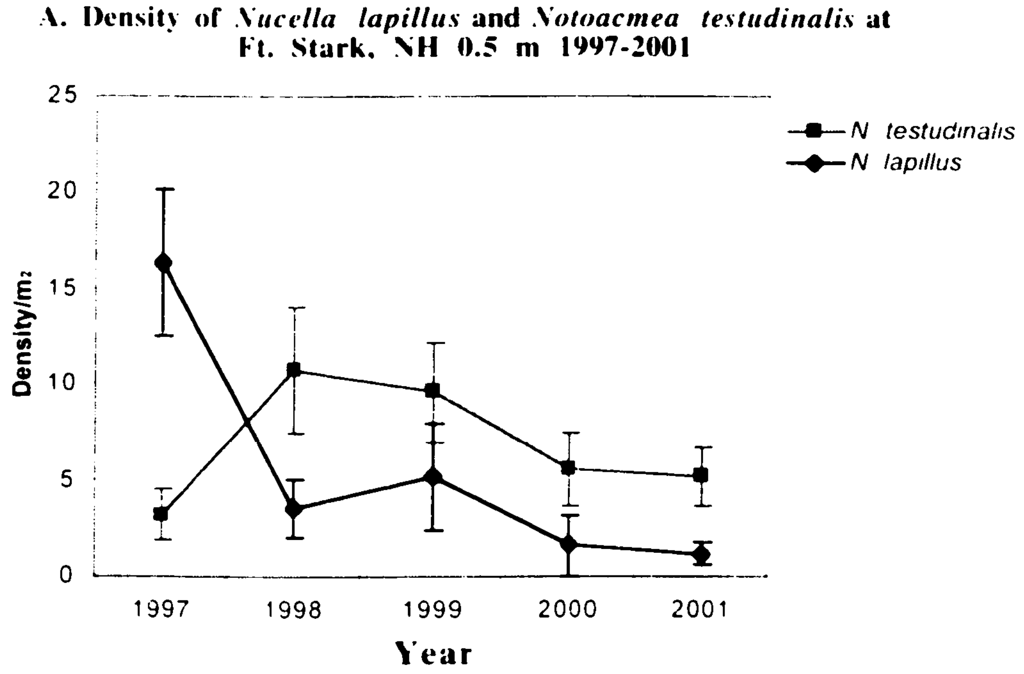


Figure 2.9a Average density/m^2 and standard error of *N. lapillus* and *N. testudinalis* at 0.5 m above MLLW (mean lower low water) at Ft. Stark, NH from 1997 - 2001.

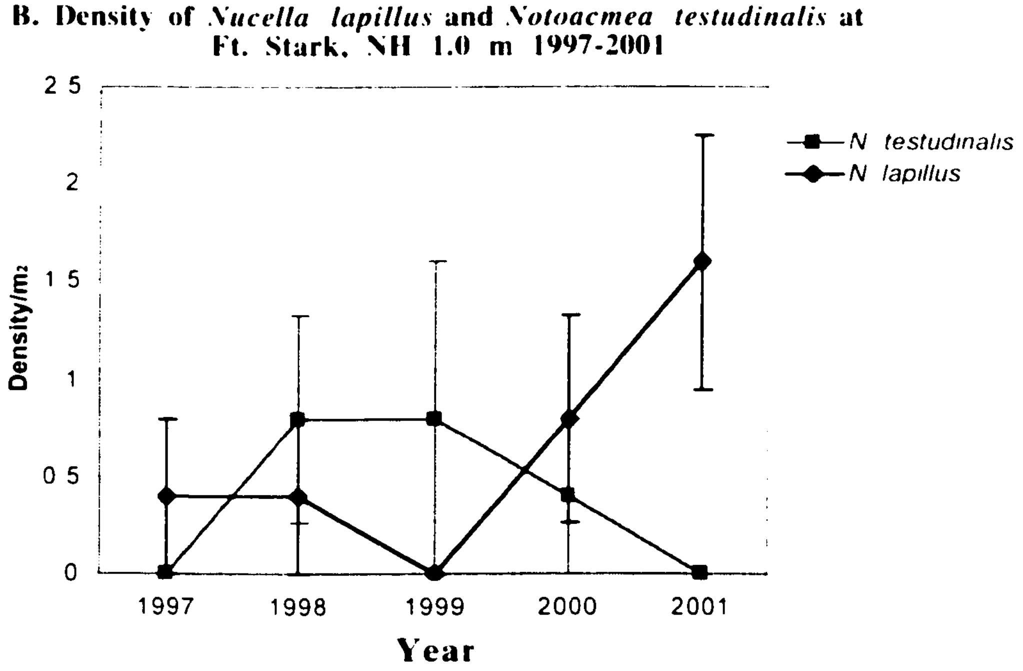


Figure 2.9b Average density/m^2 and standard error of *N. lapillus* and *N. testudinalis* at 1.0 m above MLLW at Ft. Stark, NH from 1997 - 2001.

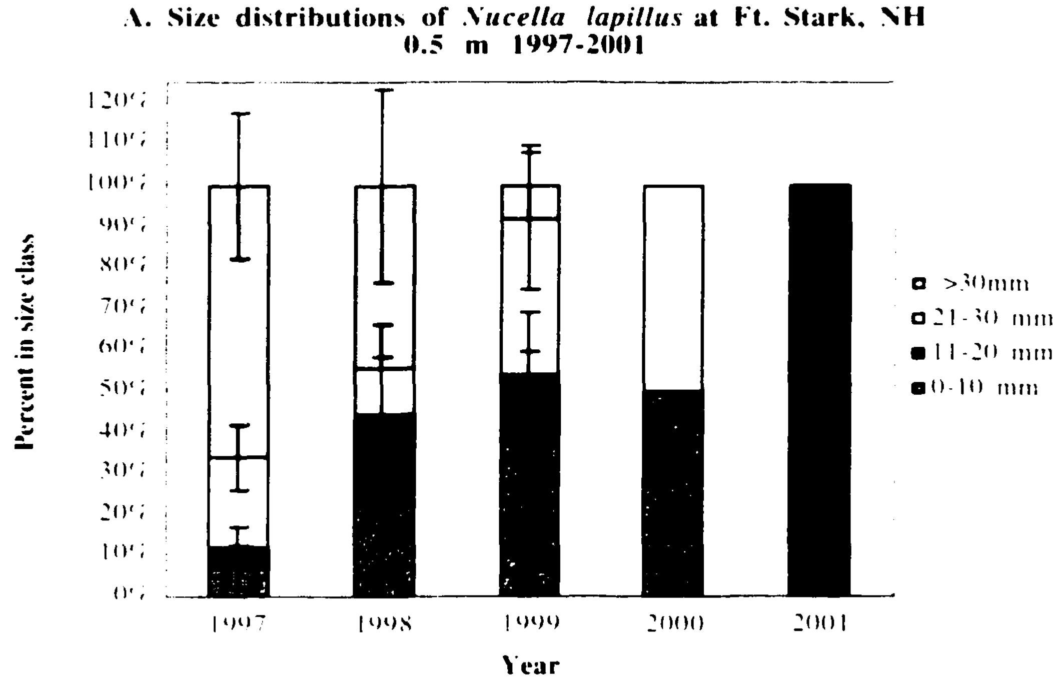


Figure 2.10a Average size distributions and standard error of *N. lapillus* at 0.5 m above MLLW (mean lower low water) at Ft. Stark, NH from 1997 - 2001.

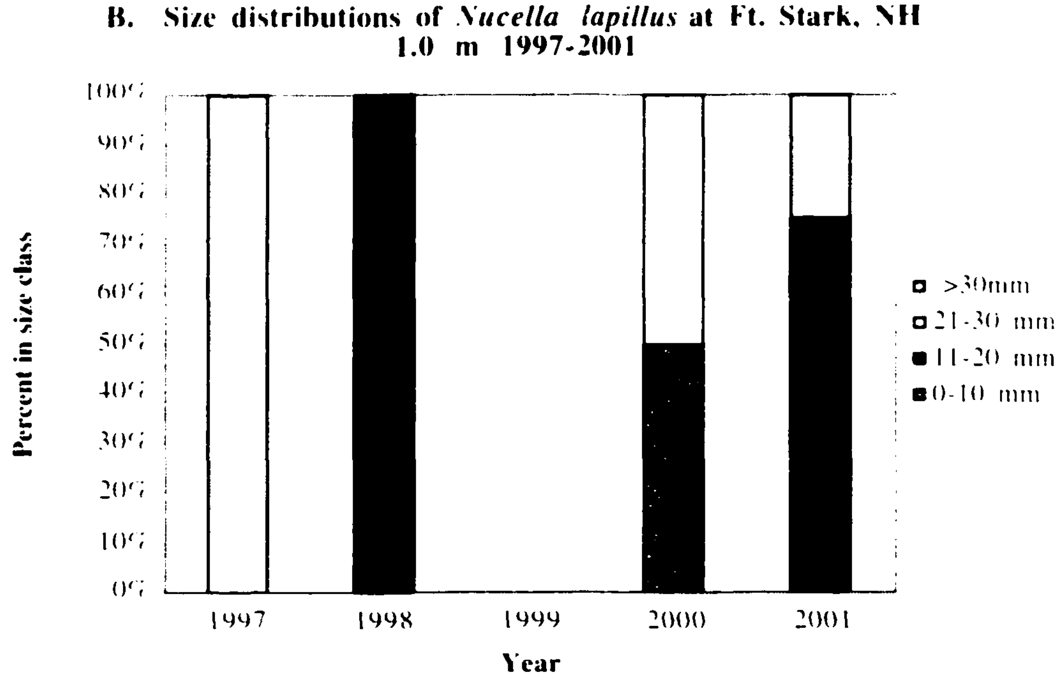


Figure 2.10b Average size distributions and standard error of *N. lapillus* at 1.0 m above MLLW at Ft. Stark, NH from 1997 - 2001.

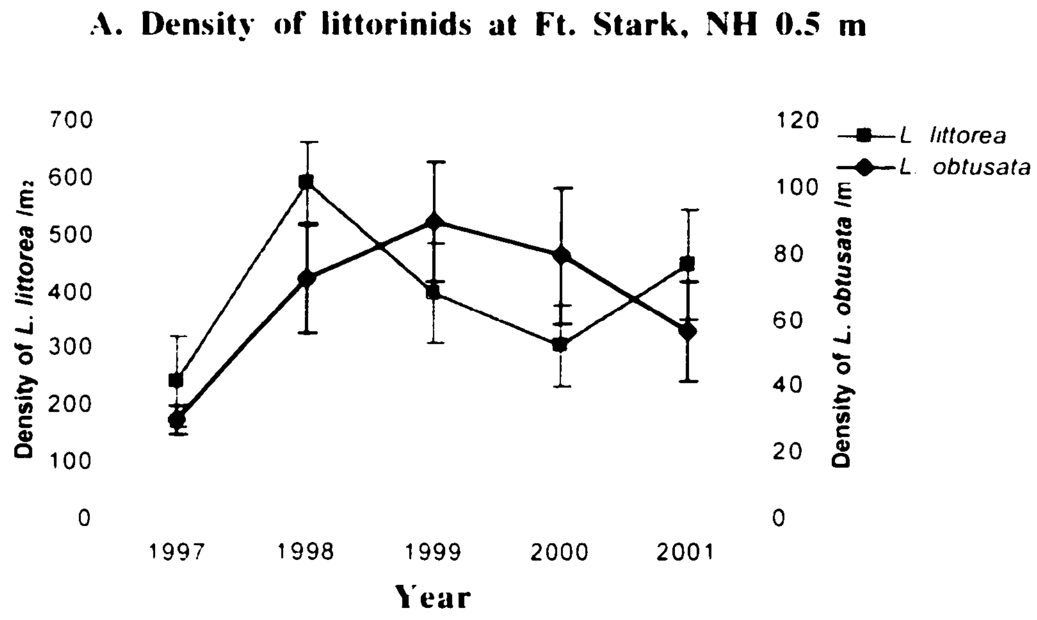

A. Density of littorinids at Ft. Stark, NH 0.5 m

Figure 2.11a Average density/m² and standard error of Littorinid snails at 0.5 m above MLLW (mean lower low water) at Ft. Stark, NH from 1997 - 2001.

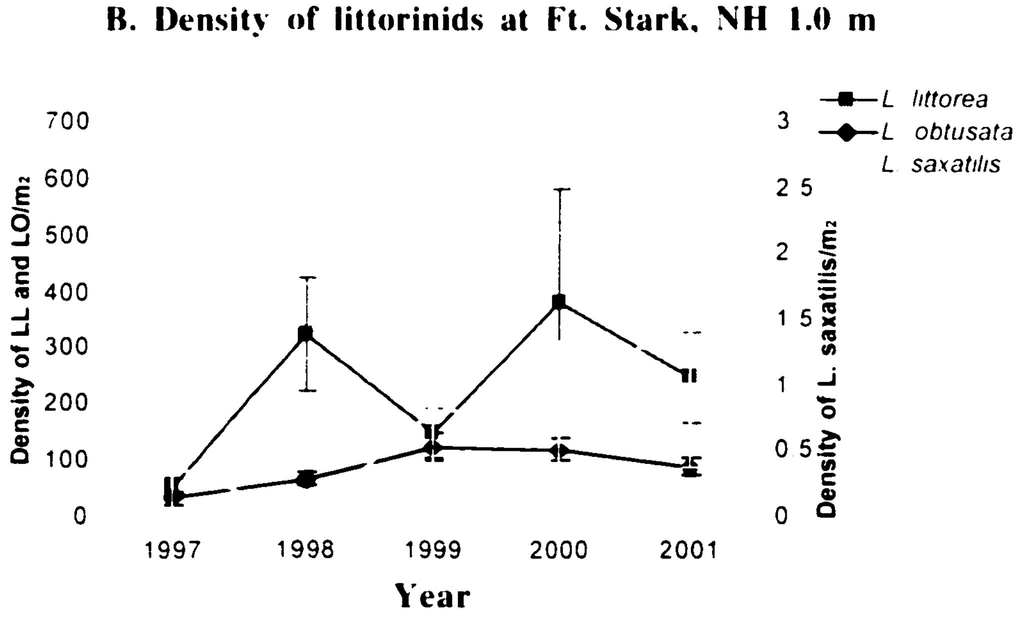
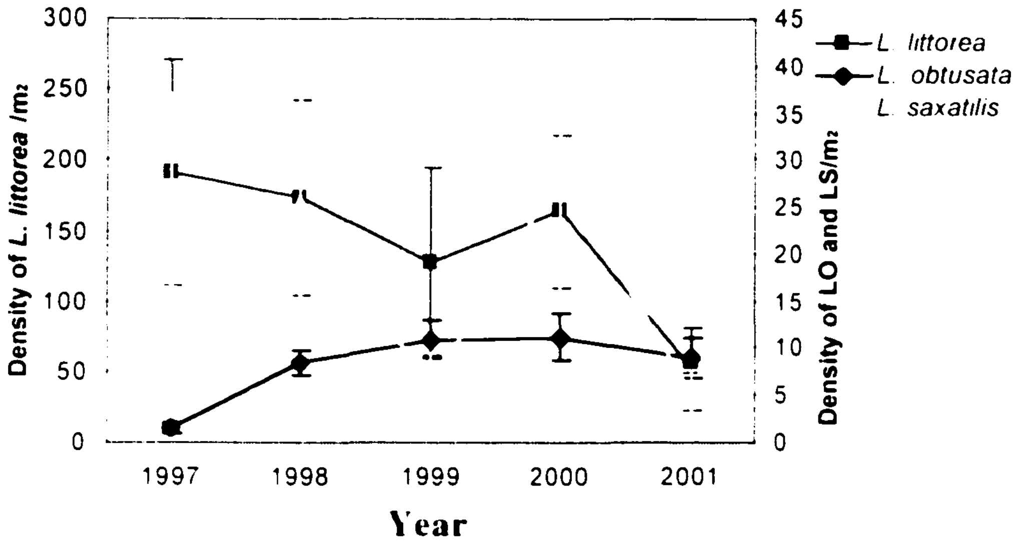

B. Density of littorinids at Ft. Stark, NH 1.0 m

Figure 2.11b Average density/m² and standard error of Littorinid snails at 1.0 m above MLLW at Ft. Stark, NH from 1997 - 2001. LL is *Littorina littorea* and LO is *L. obtusata*.



C. Density of littorinids at Ft. Stark, NH 2.0 m

Fig. 2.11c Average density/m² and standard error of Littorinid snails at 2.0 m above MLLW at Ft. Stark, NH from 1997 - 2001. LS is *Littorina saxatilis* and LO is *L. obtusata*.

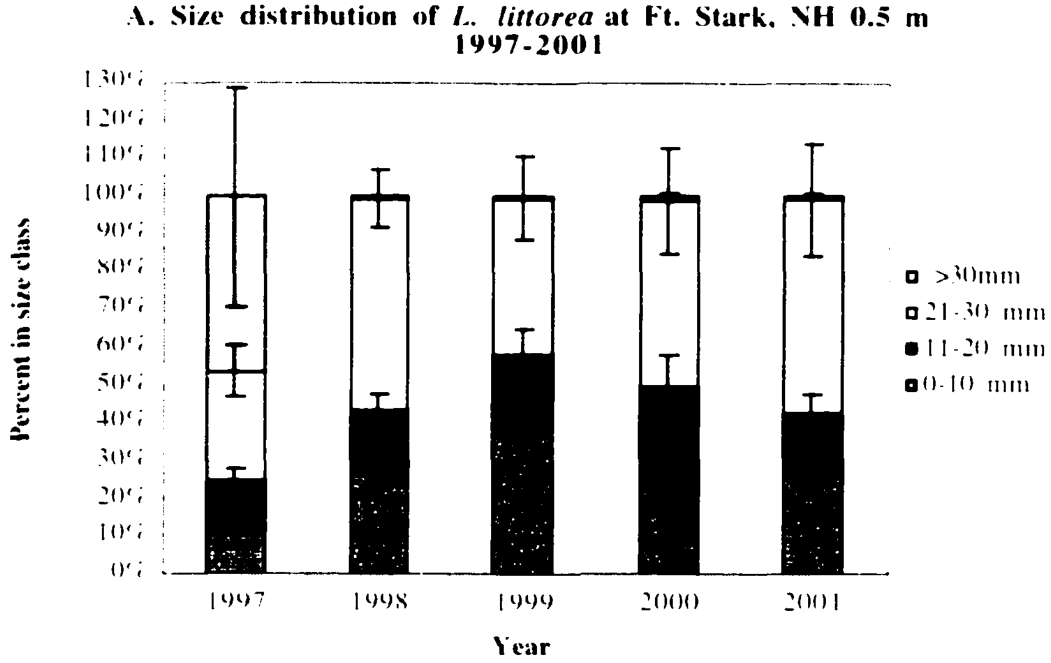


Figure 2.12a Average size distributions and standard error of *L. littorea* at 0.5 m above MLLW (mean lower low water) at Ft. Stark, NH from 1997 - 2001.

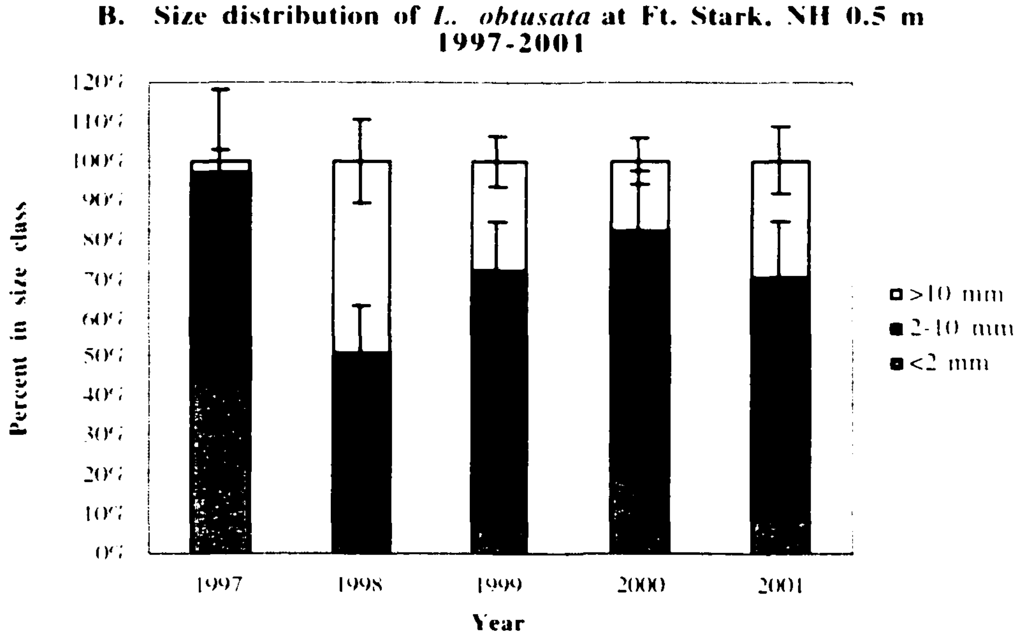


Figure 2.12b Average size distributions and standard error of *L. obtusata* at 0.5 m above MLLW at Ft. Stark, NH from 1997 - 2001.

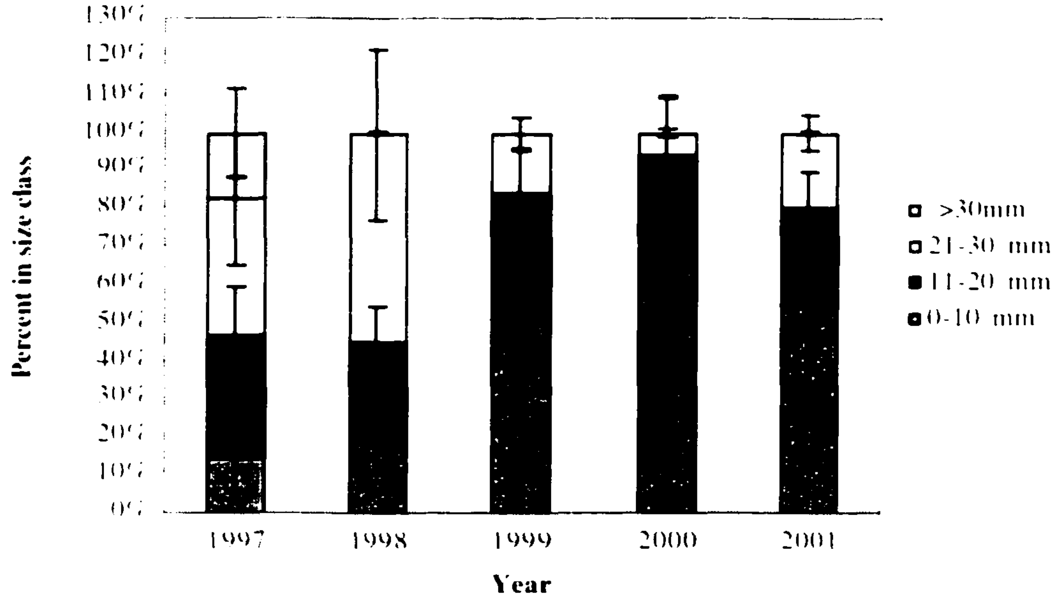

A. Size distributions of *L. littorea* at Ft. Stark, NH 1.0 m 1997-2001

Figure 2.13a Average size distributions and standard error of *L. littorea* at 1.0 m above MLLW (mean lower low water) at Ft. Stark, NH from 1997 - 2001.

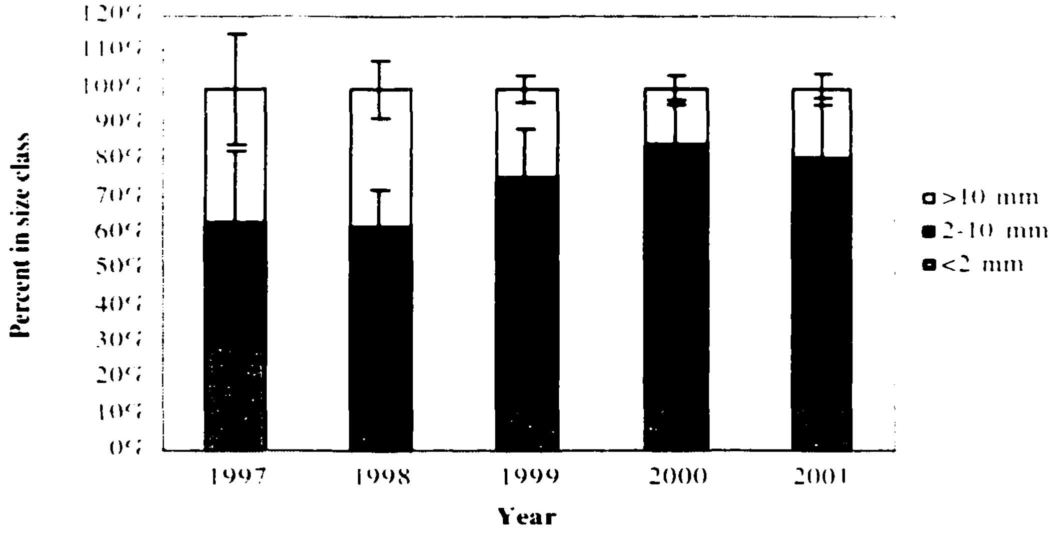

B. Size distributions of *L. obtusata* at Ft. Stark, NH 1.0 m 1997-2001

Figure 2.13b Average size distributions and standard error of *L. obtusata* at 1.0 m above MLLW at Ft. Stark, NH from 1997 - 2001.

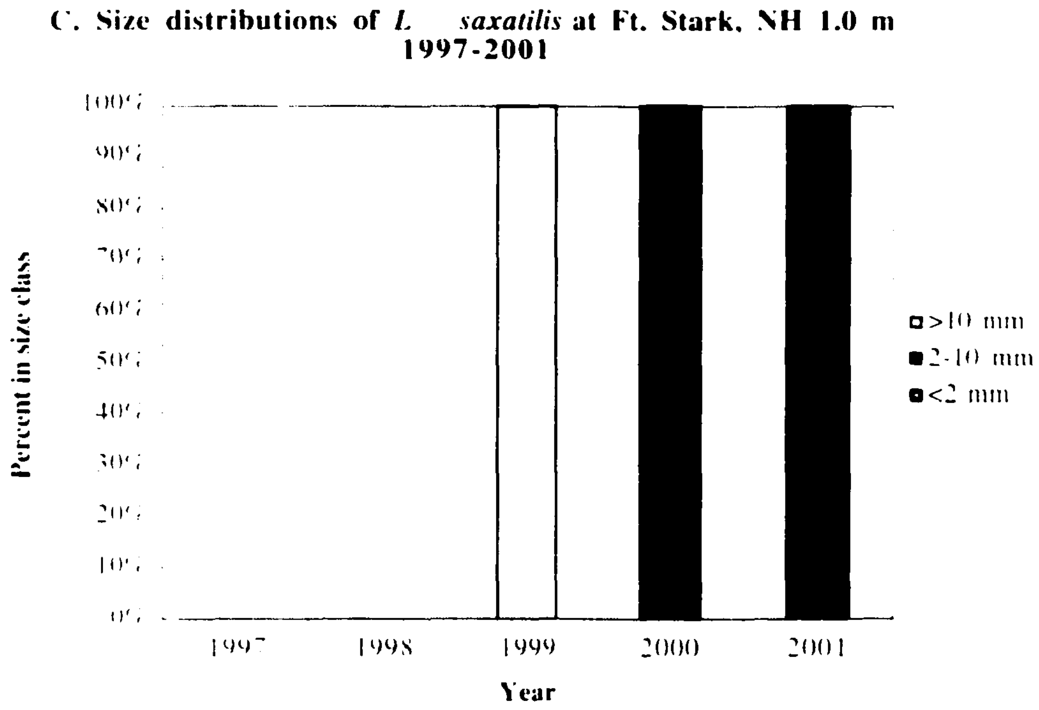
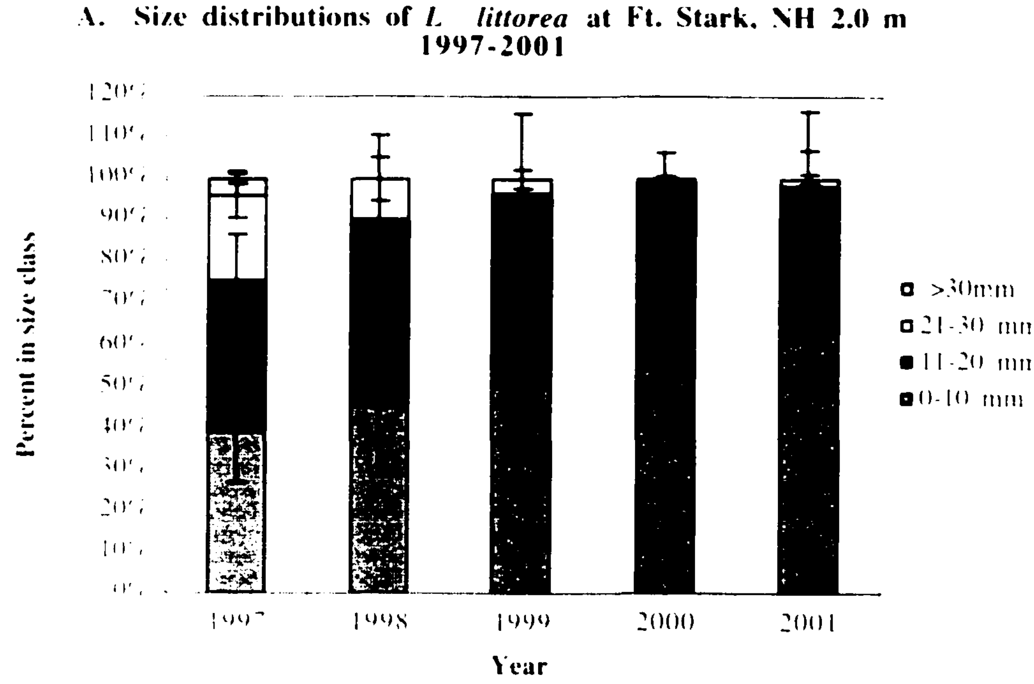
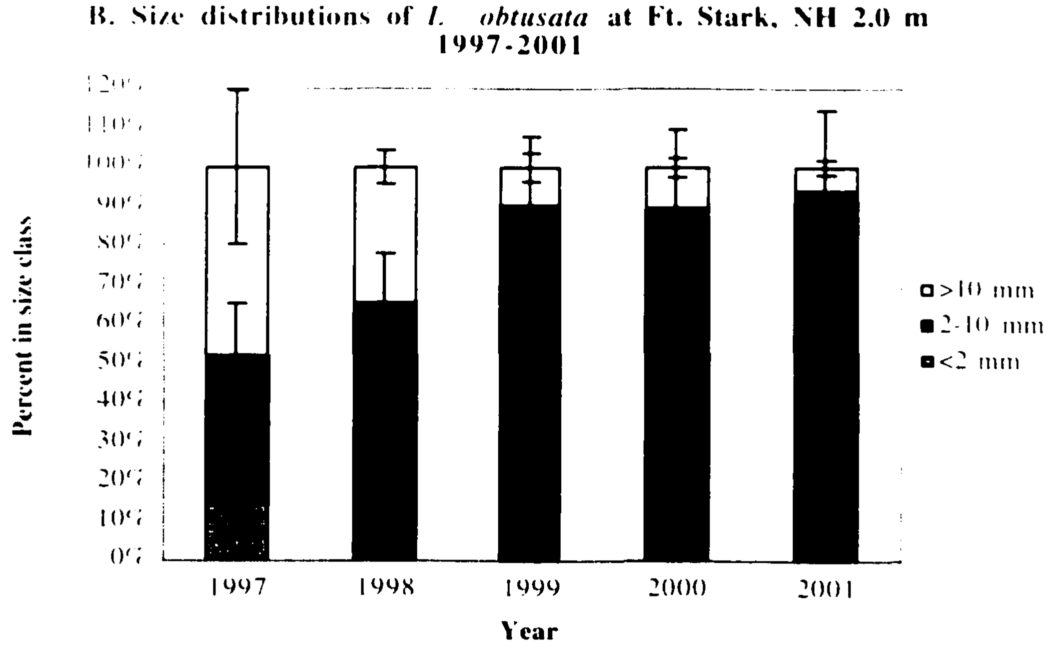


Figure 2.13c Average size distributions and standard error of *L. saxatilis* at 1.0 m above MLLW at Ft. Stark, NH from 1997 - 2001. There were no *L. saxatilis* present at this tidal height in 1998.



A. Size distributions of *L. littorea* at Ft. Stark, NH 2.0 m 1997-2001

Figure 2.14a Average size distributions and standard error of *L. littorea* at 2.0 m above MLLW (mean lower low water) at Ft. Stark, NH from 1997 - 2001.



B. Size distributions of *L. obtusata* at Ft. Stark, NH 2.0 m 1997-2001

Figure 2.14b Average size distributions and standard error of *L. obtusata* at 2.0 m above MLLW at Ft. Stark, NH from 1997 - 2001.

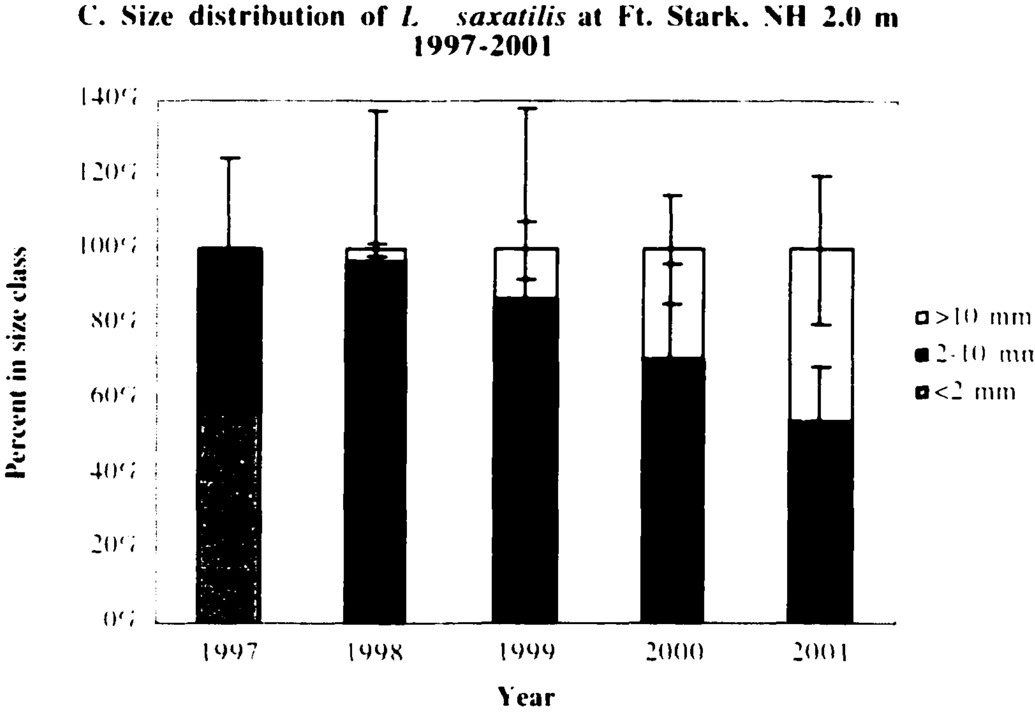


Figure 2.14c Average size distributions and standard error of *L. saxatilis* at 2.0 m above MLLW at Ft. Stark, NH from 1997 - 2001.

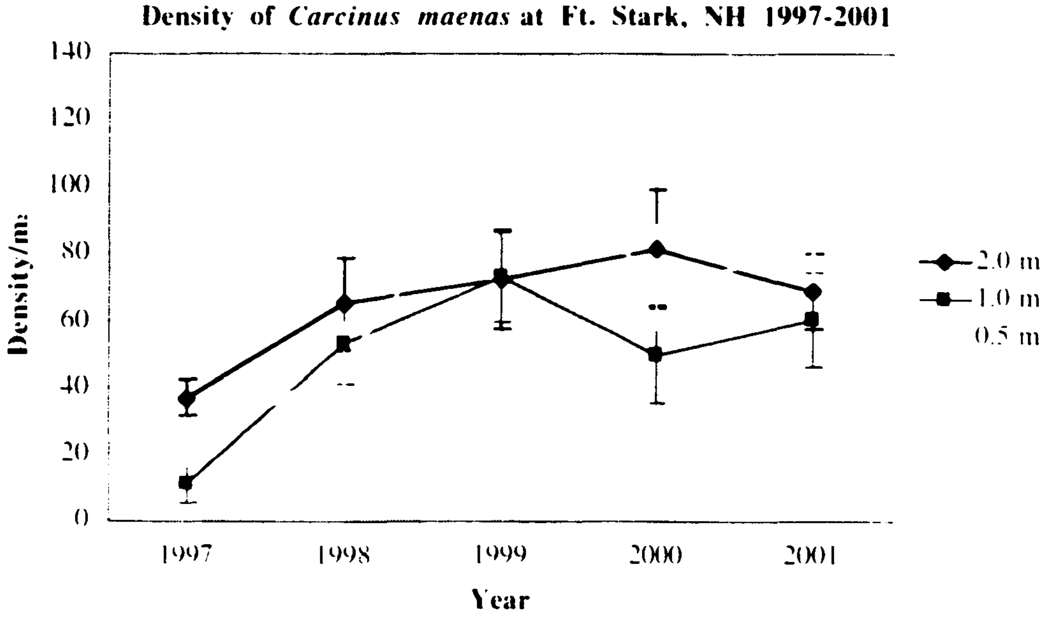
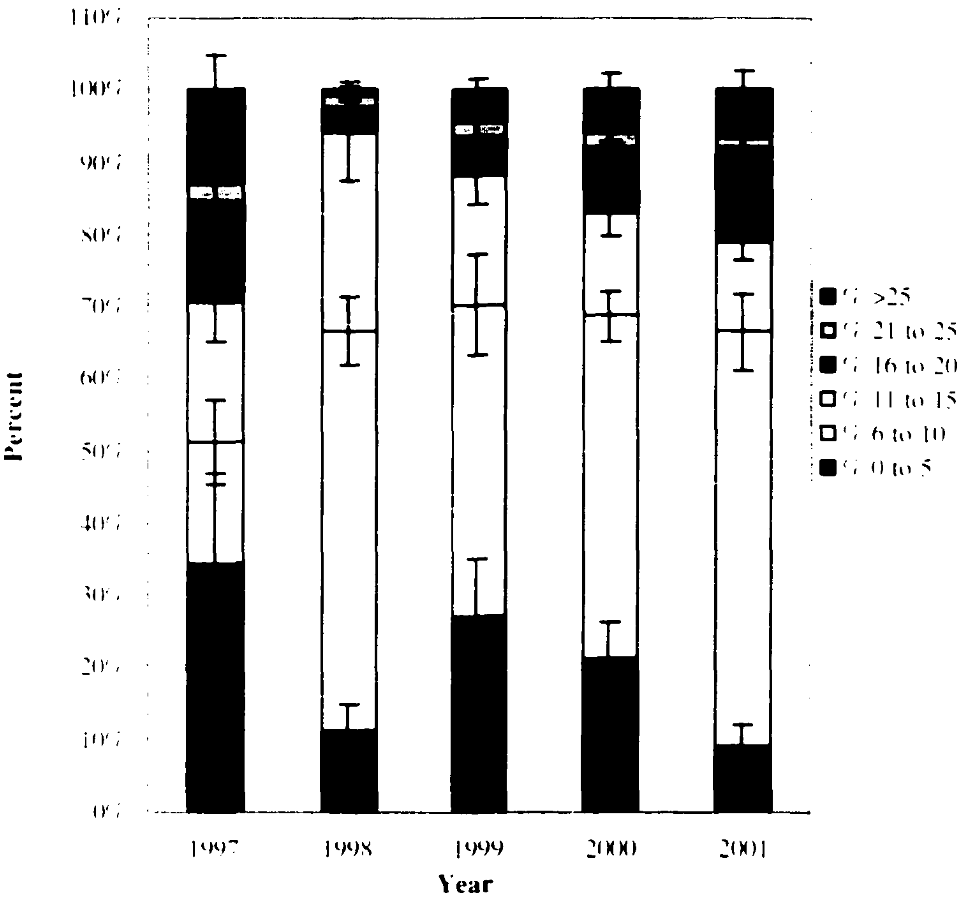


Figure 2.15 Average density/m^2 and standard error of *C. maenas* at Ft. Stark, NH from 1997 - 2001.



A. Size distributions of *Carcinus maenas* at Ft. Stark, NH 0.5 m 1997-2001

Figure 2.16a Average size distributions and standard error of *C. maenas* at 0.5 m above MLLW (mean lower low water) at Ft. Stark, NH from 1997 - 2001.

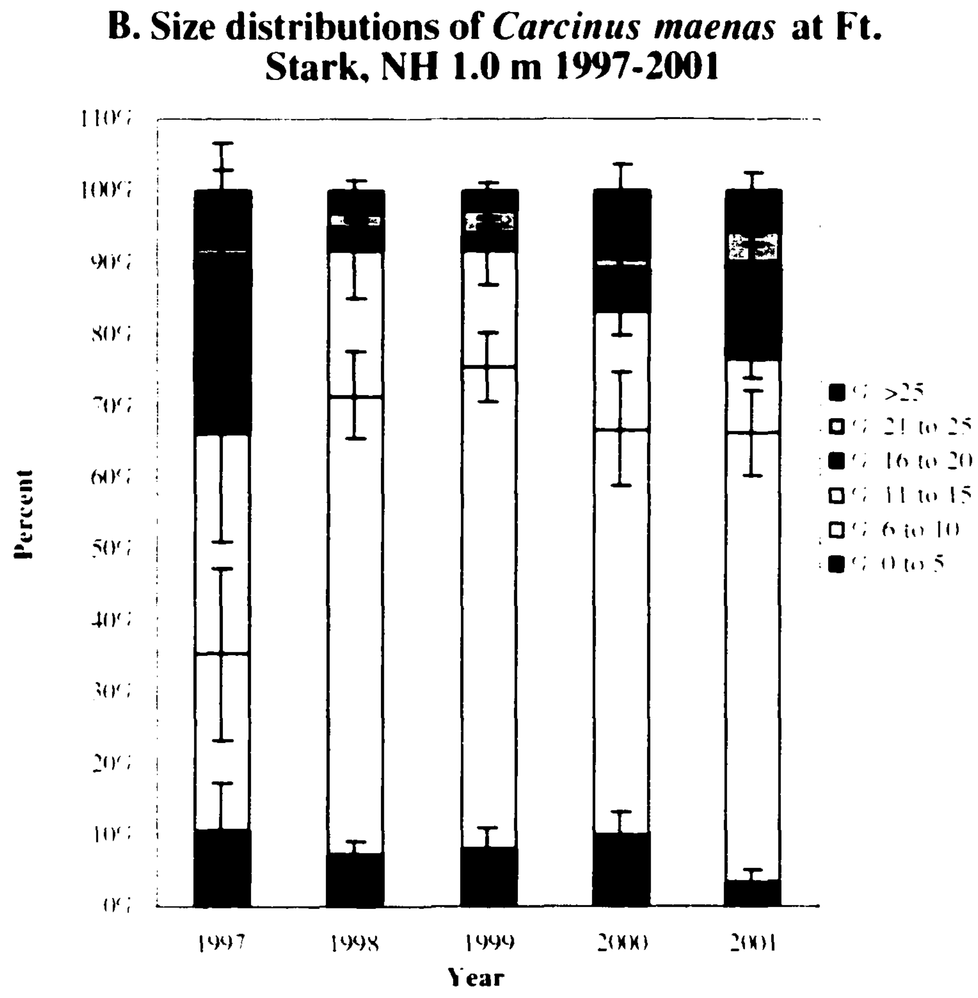

B. Size distributions of *Carcinus maenas* at Ft. Stark, NH 1.0 m 1997-2001

Figure 2.16b Average size distributions and standard error of *C. maenas* at 1.0 m above MLLW (mean lower low water) at Ft. Stark, NH from 1997 - 2001.

C. Size distributions of *Carcinus maenas* at Ft. Stark, NH 2.0 m 1997-2001

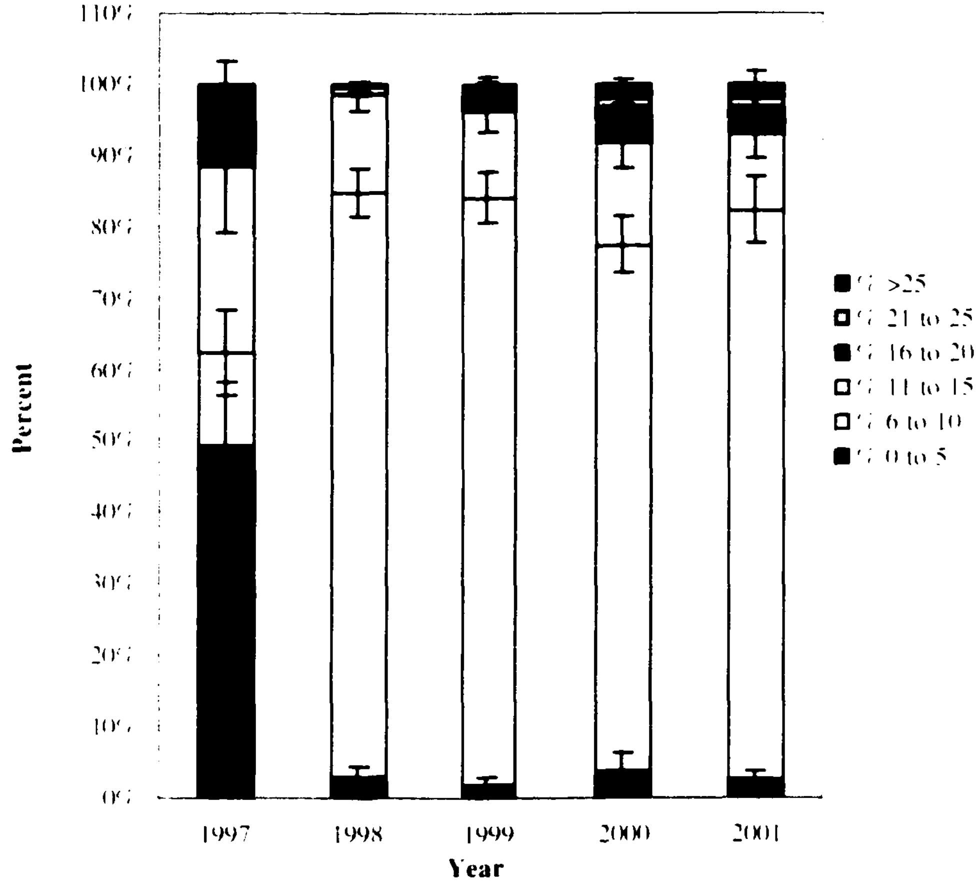


Figure 2.16c Average size distributions and standard error of *C. maenas* at 2.0 m above MLLW (mean lower low water) at Ft. Stark, NH from 1997 - 2001.

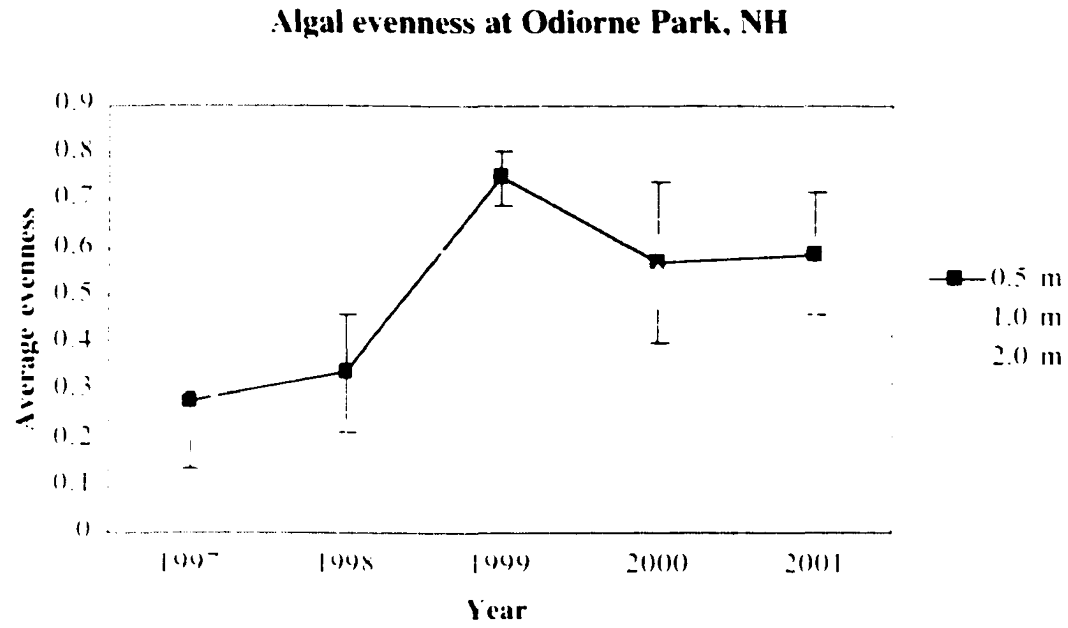


Figure 2.17 Average algal evenness and standard error at different tidal heights at Odiorne Park, NH from 1997 to 2001 calculated using Pielou's J index for equitability.

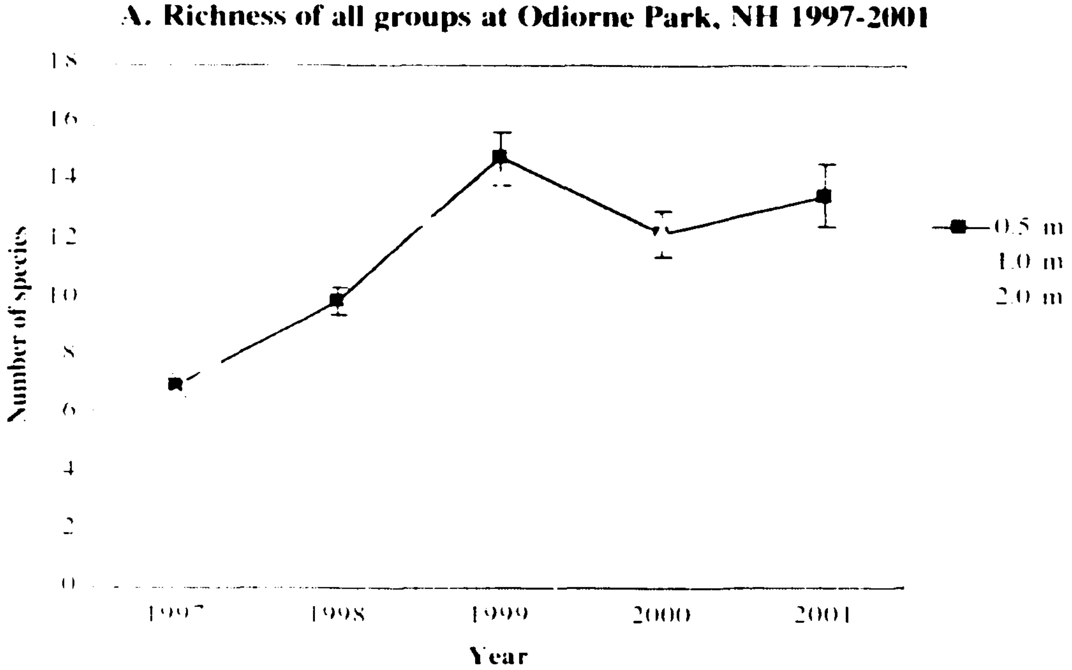


Figure 2.18a. Average richness and standard error at different tidal heights at Odiorne Park, NH from 1997 to 2001 calculated by including groups of species in the richness estimate.

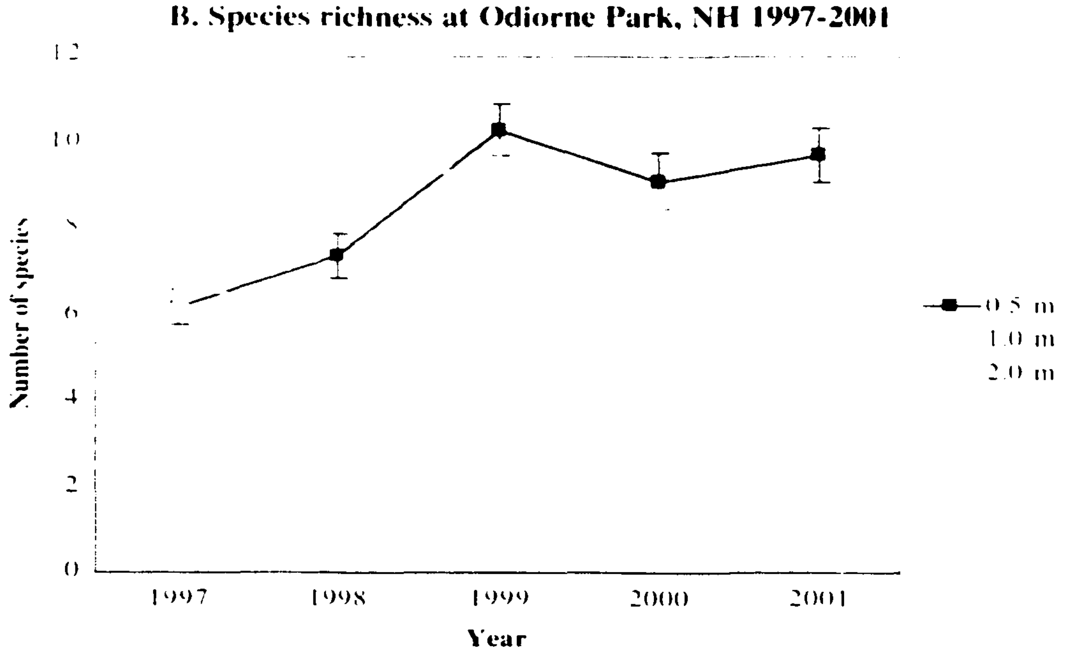


Figure 2.18b. Average species richness and standard error at different tidal heights at Odiorne Park, NH from 1997 to 2001 calculated only including organisms identified to species in the estimate.

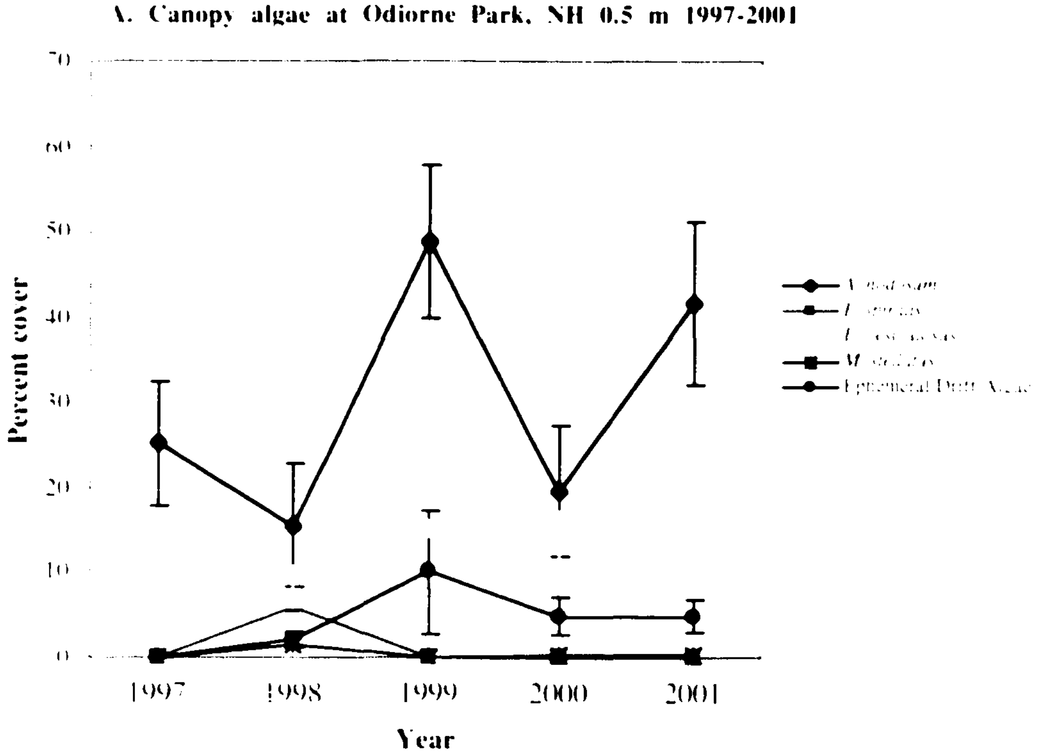


Figure 2.19a Average percent cover and standard error of algae observed in the canopy analysis at 0.5 m above MLLW (mean lower low water) at Odiorne Park, NH from 1997-2001. Cover types represent major algal canopy species; drift and ephemeral algae were not identified to species because of their highly variable composition and abundance.

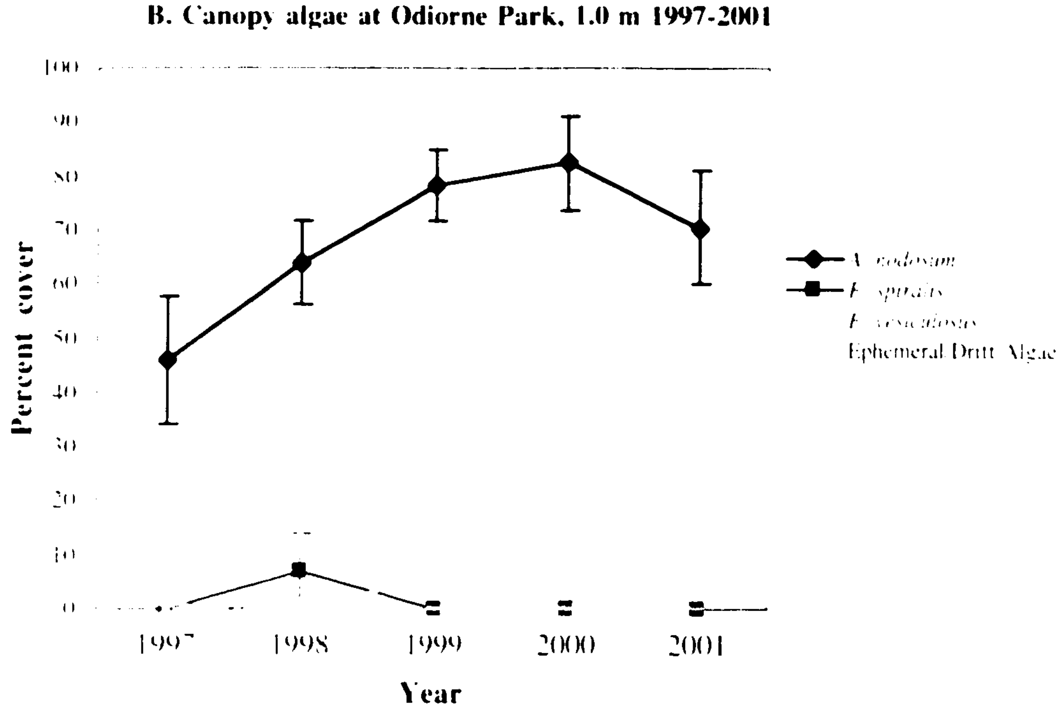


Figure 2.19b Average percent cover and standard error of algae observed in the canopy analysis at 1.0 m above MLLW at Odiorne Park, NH from 1997 – 2001. Cover types represent major algal canopy species; drift and ephemeral algae were not identified to species because of their highly variable composition and abundance.

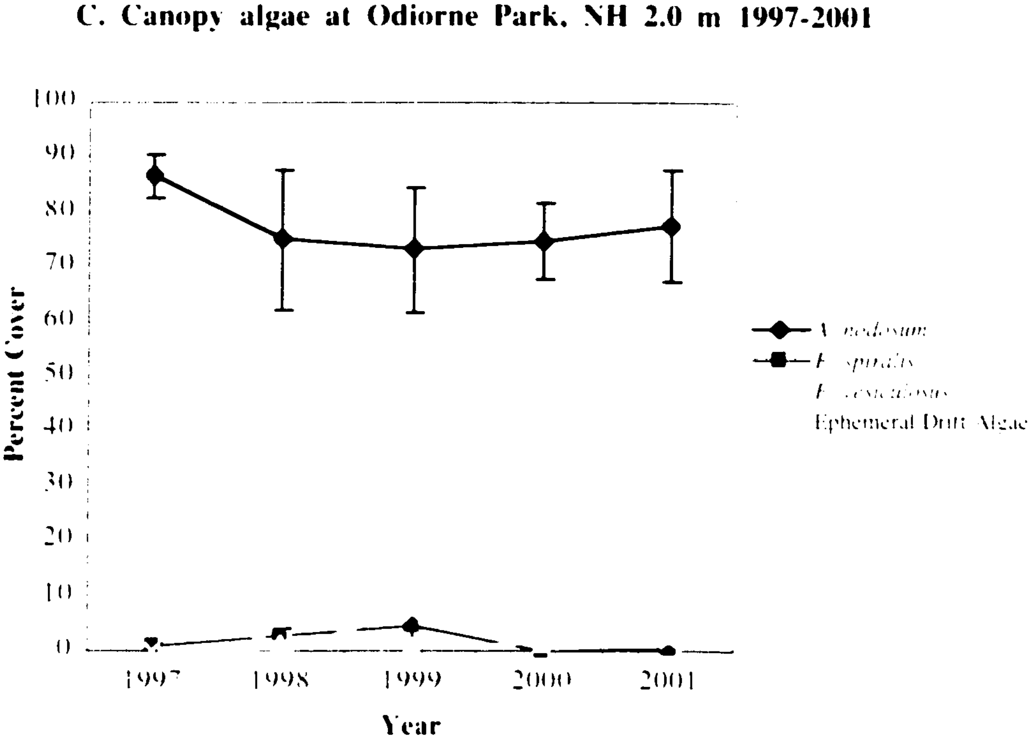


Figure 2.19c Average percent cover and standard error of algae observed in the canopy analysis at 2.0 m above MLLW at Odiorne Park, NH from 1997 - 2001. Cover types represent major algal canopy species; drift and ephemeral algae were not identified to species because of their highly variable composition and abundance.

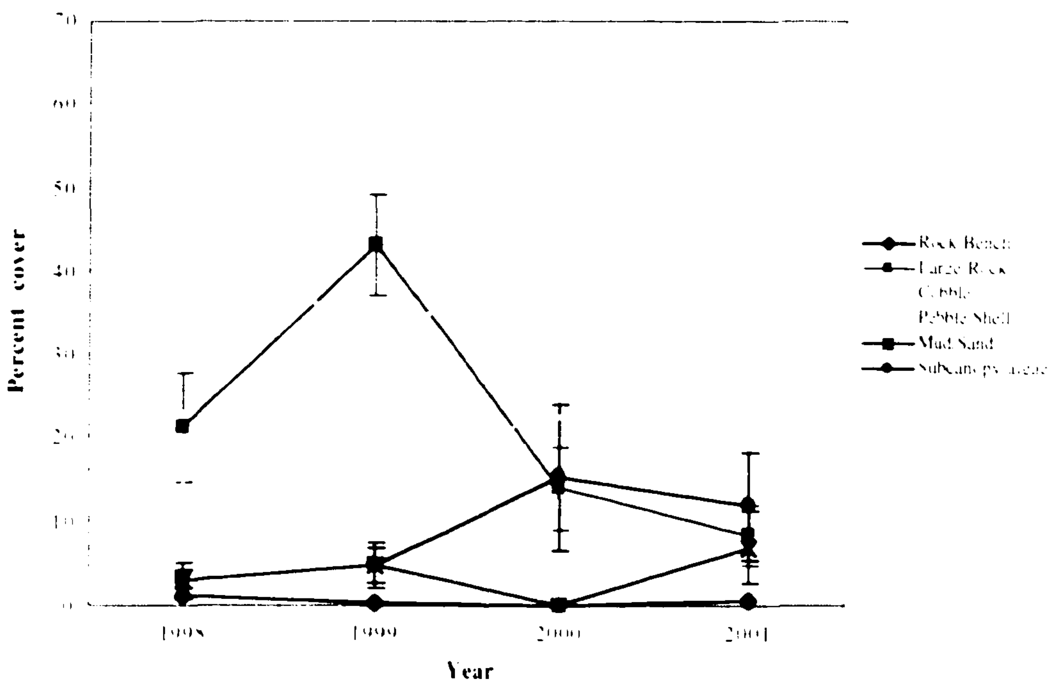

A. Subcanopy at Odiorne Park, NH 0.5 m 1998-2001

Figure 2.20a Average percent cover and standard error of substrates and subcanopy algae observed in subcanopy analysis at 0.5 m above MLLW (mean lower low water) at Odiorne Park, NH from 1997 - 2001. The majority of the subcanopy algae category was *M. stellatus* with some crustose coralline algae.

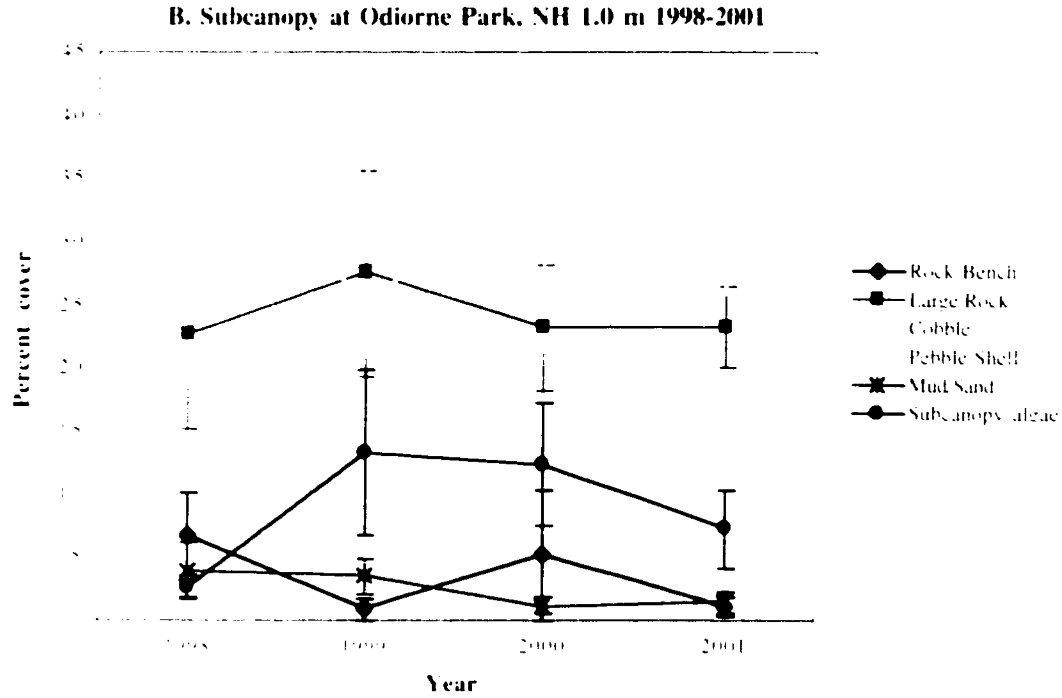

B. Subcanopy at Odiorne Park, NH 1.0 m 1998-2001

Figure 2.20b Average percent cover and standard error of substrates and subcanopy algae observed in subcanopy analysis at 1.0 m above MLLW at Odiorne Park, NH from 1997 - 2001. The majority of the subcanopy algae category was *M. stellatus* with some crustose coralline algae.

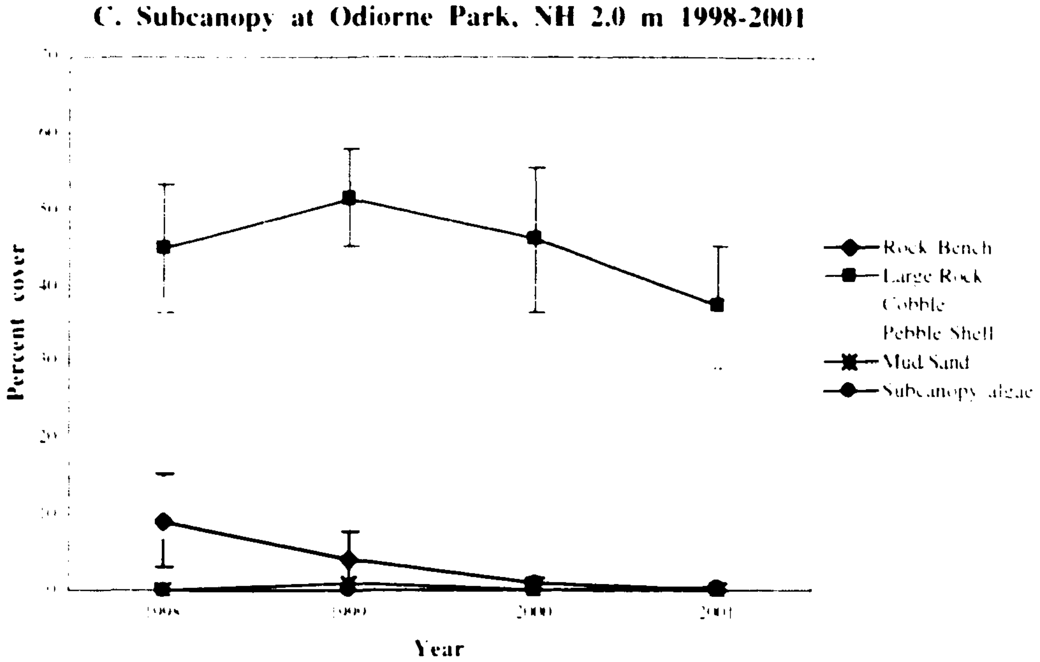
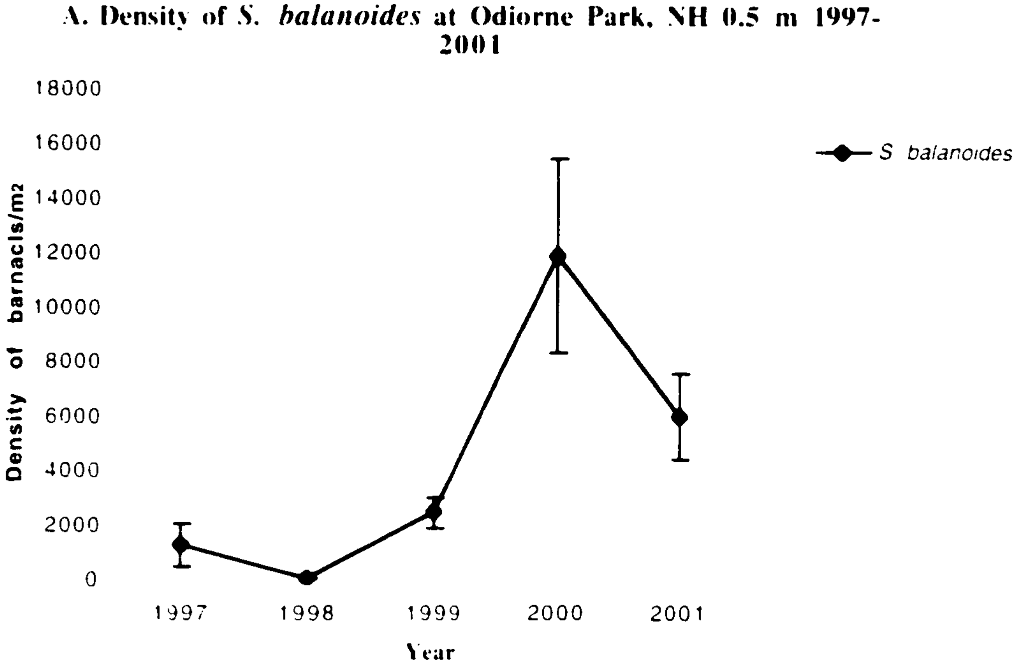


Figure 2.20c Average percent cover and standard error of substrates and subcanopy algae observed in subcanopy analysis at 2.0 m above MLLW at Odiorne Park, NH from 1997 - 2001. The subcanopy algae category was crustose coralline algae.



A. Density of *S. balanoides* at Odiorne Park, NH 0.5 m 1997-2001

Figure 2.21a Average density/m^2 and standard error of *S. balanoides* at 0.5 m above MLLW (mean lower low water) at Odiorne Park, NH from 1997 - 2001. There were never any *M. edulis* found at this tidal height throughout the sampling period.

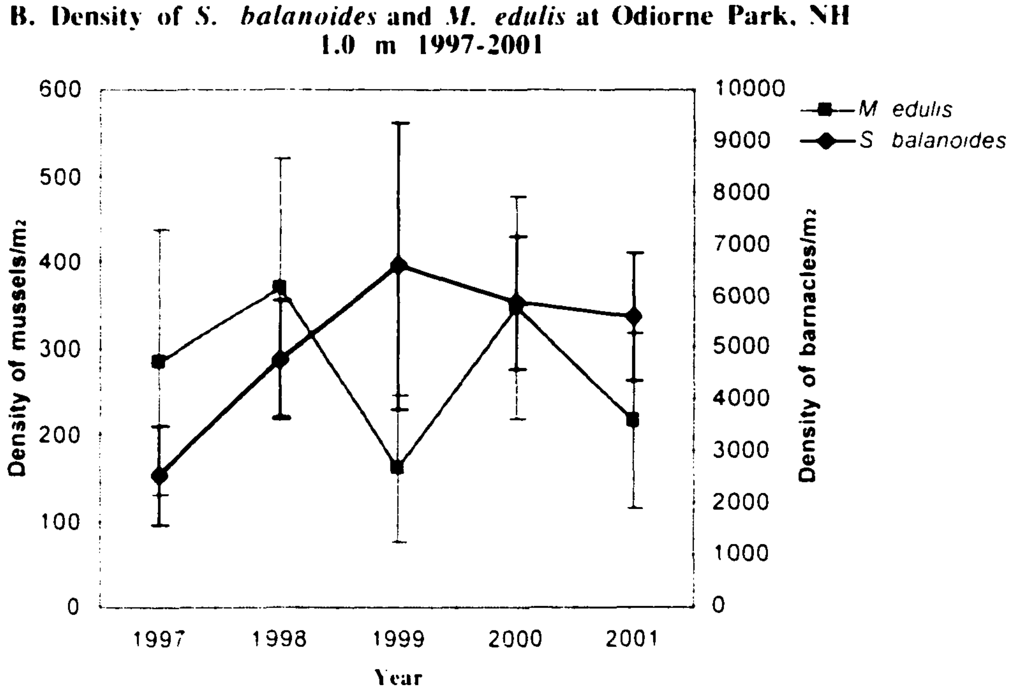
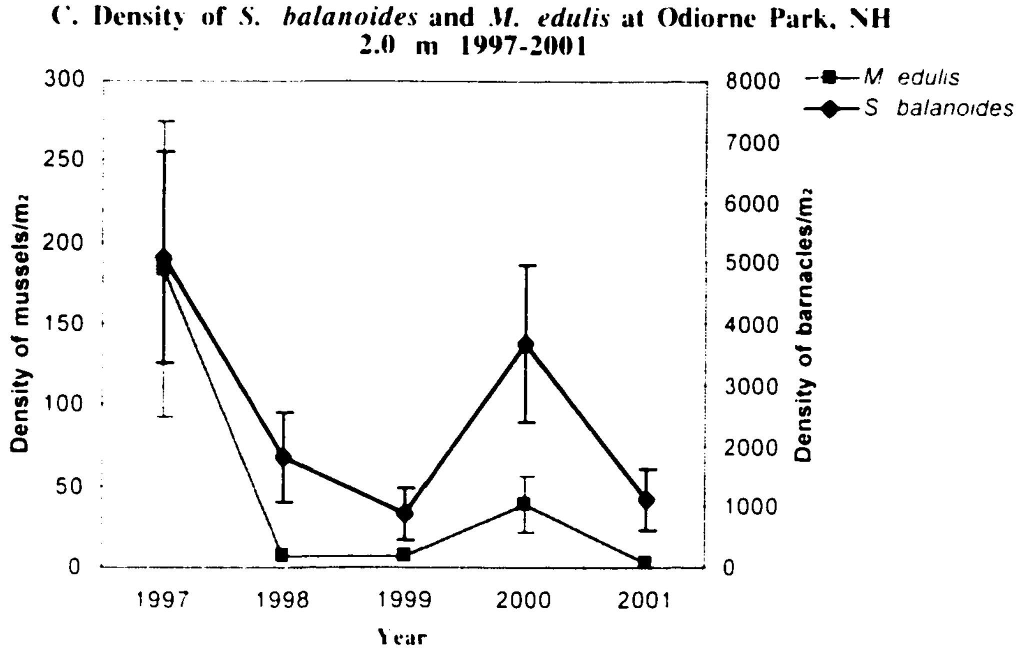


Figure 2.21b Average density/m^2 and standard error of *M. edulis* and *S. balanoides* at 1.0 m above MLLW at Odiorne Park, NH from 1997 - 2001.



C. Density of *S. balanoides* and *M. edulis* at Odiorne Park, NH 2.0 m 1997-2001

Figure 2.21c Average density/m² and standard error of *M. edulis* and *S. balanoides* at 2.0 m above MLLW at Odiorne Park, NH from 1997 - 2001.

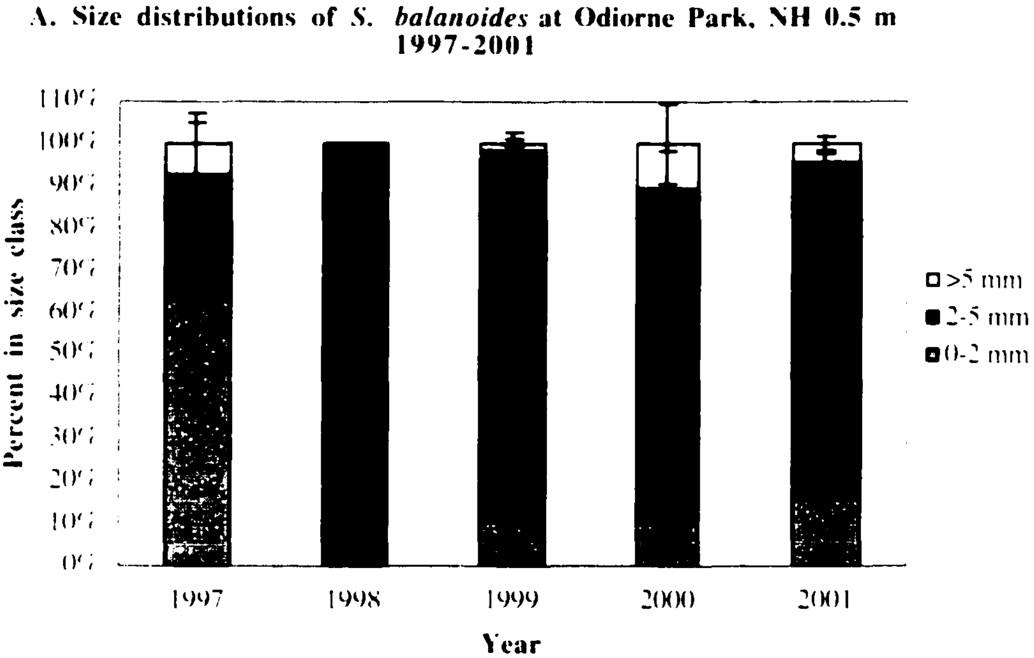


Figure 2.22a Estimated size class distribution of *S. balanoides* at 0.5 m above MLLW (mean lower low water) at Odiorne Park, NH from 1997 - 2001.

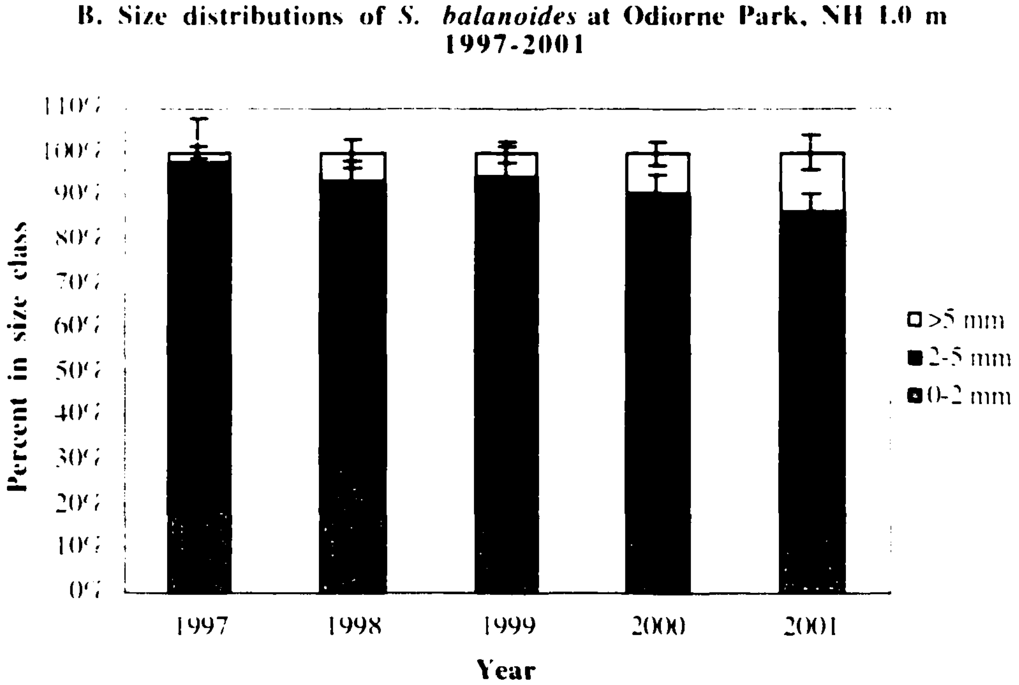


Figure 2.22b Estimated size class distribution of *S. balanoides* at 1.0 m above MLLW at Odiorne Park, NH from 1997 - 2001.

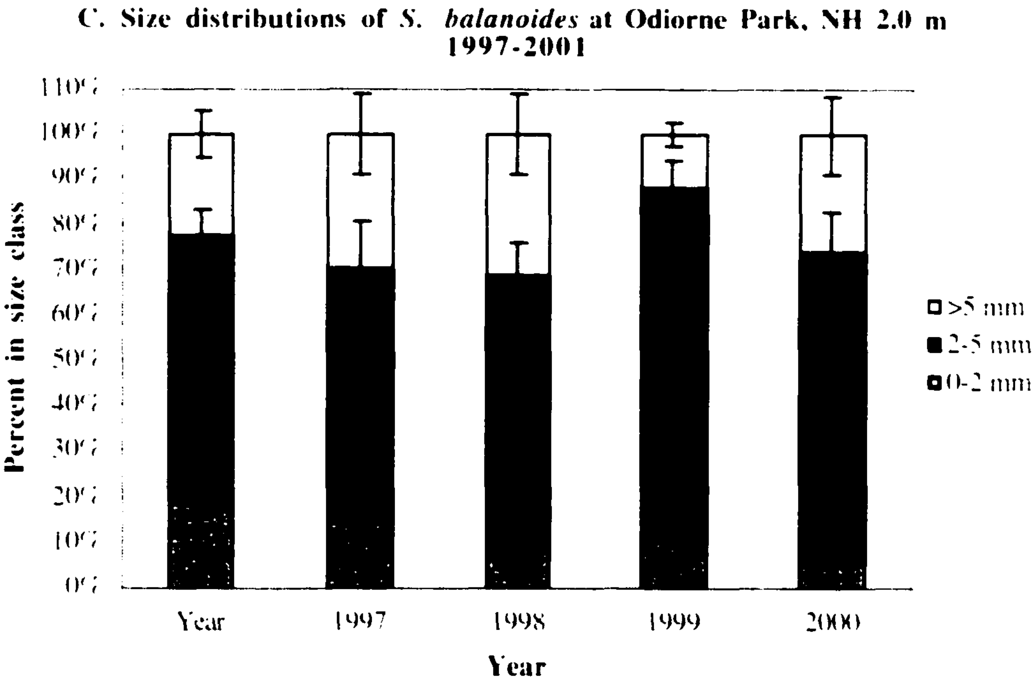

C. Size distributions of *S. balanoides* at Odiorne Park, NH 2.0 m 1997-2001

Figure 2.22c Estimated size class distribution of *S. balanoides* at 2.0 m above MLLW at Odiorne Park, NH from 1997 - 2001.

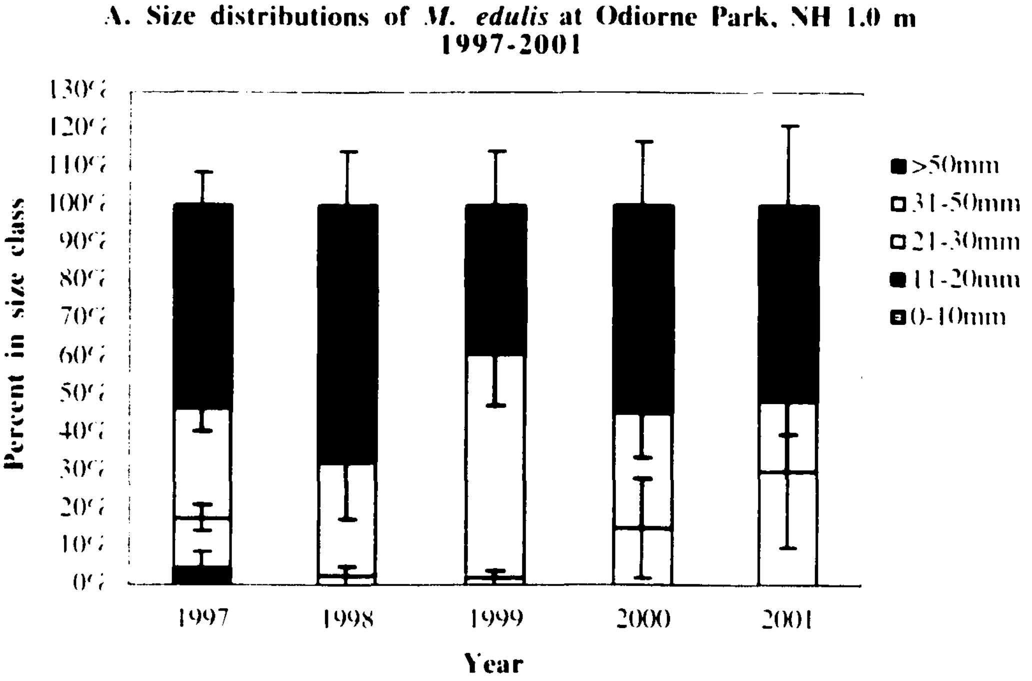


Figure 2.23a Estimated size class distribution of *M. edulis* at 1.0 m above MLLW (mean lower low water) at Odiorne Park, NH from 1997 - 2001.

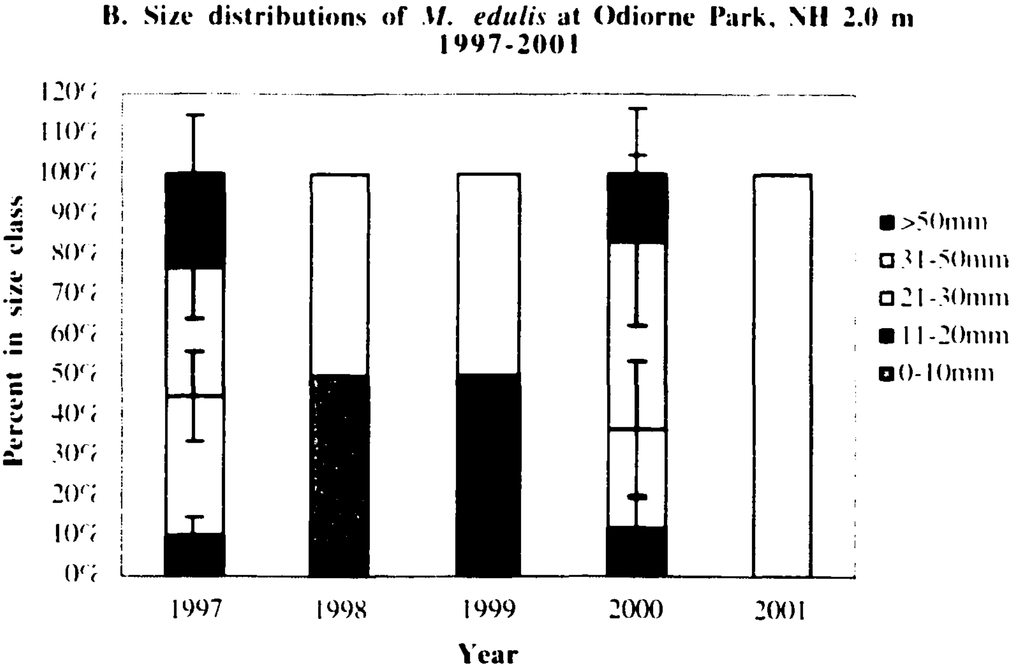
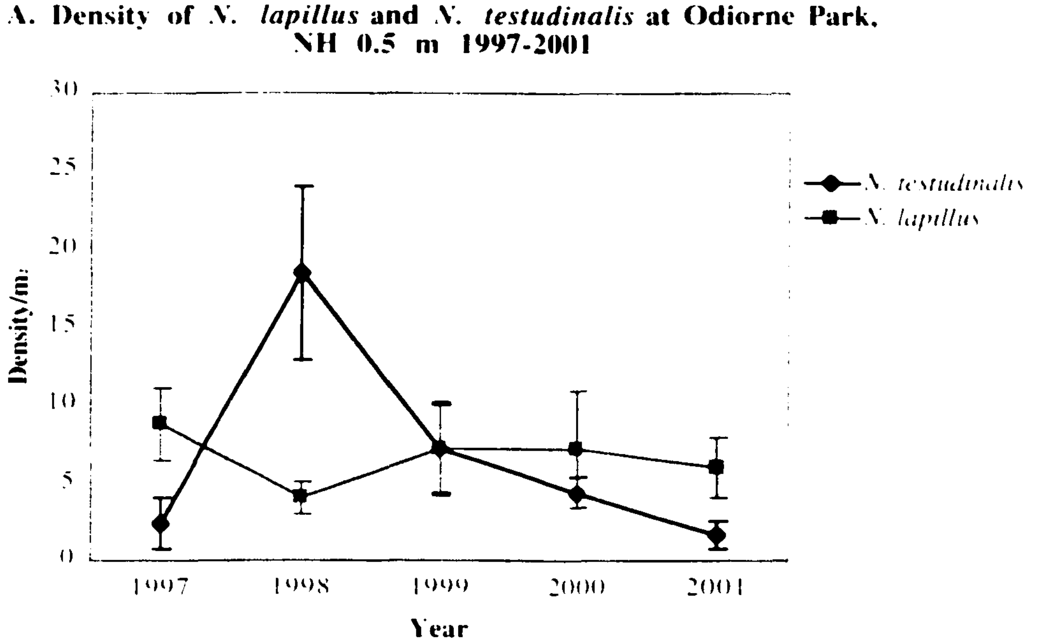
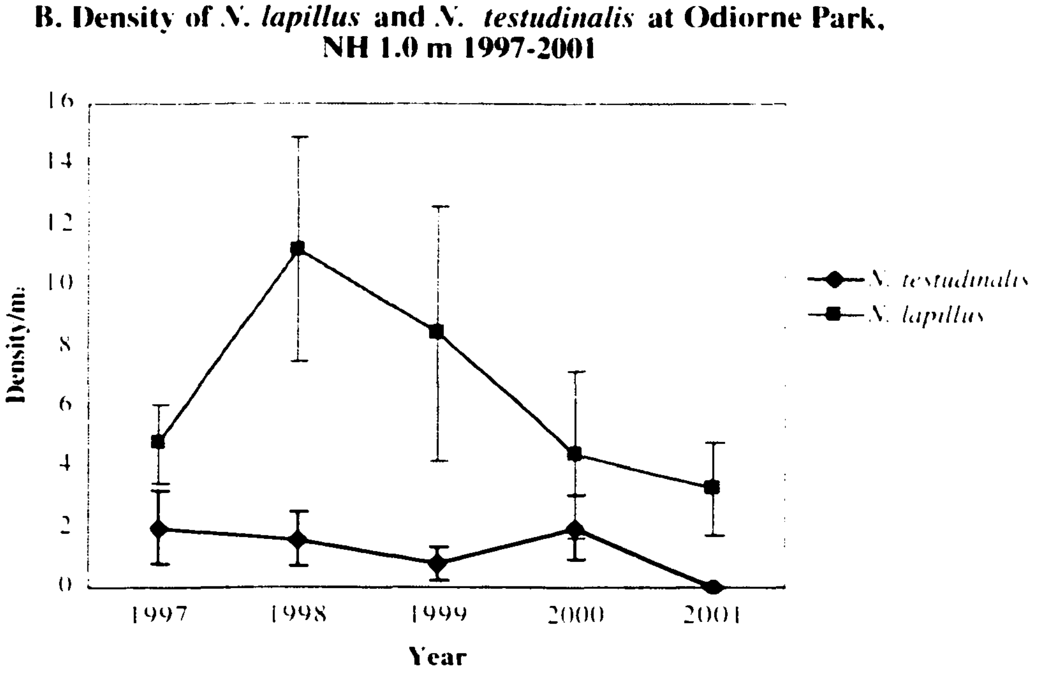


Figure 2.23b Estimated size class distribution of *M. edulis* at 2.0 m above MLLW at Odiorne Park, NH from 1997 - 2001.



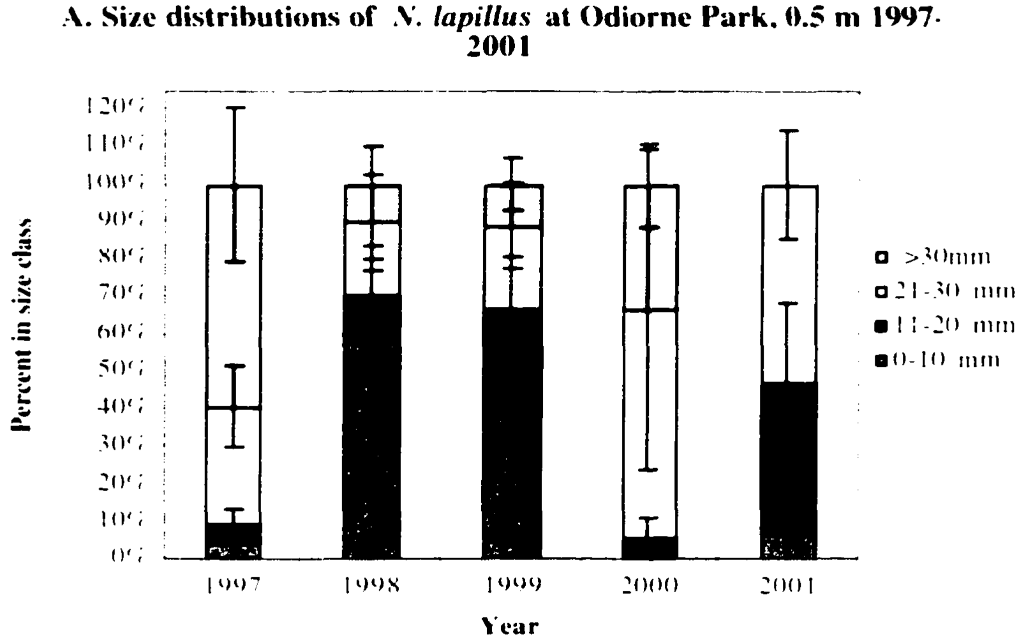
A. Density of *N. lapillus* and *N. testudinalis* at Odiorne Park, NH 0.5 m 1997-2001

Figure 2.24a Average density/m^2 and standard error of *N. lapillus* and *N. testudinalis* at 0.5 m above MLLW (mean lower low water) at Odiorne Park, NH from 1997 - 2001.



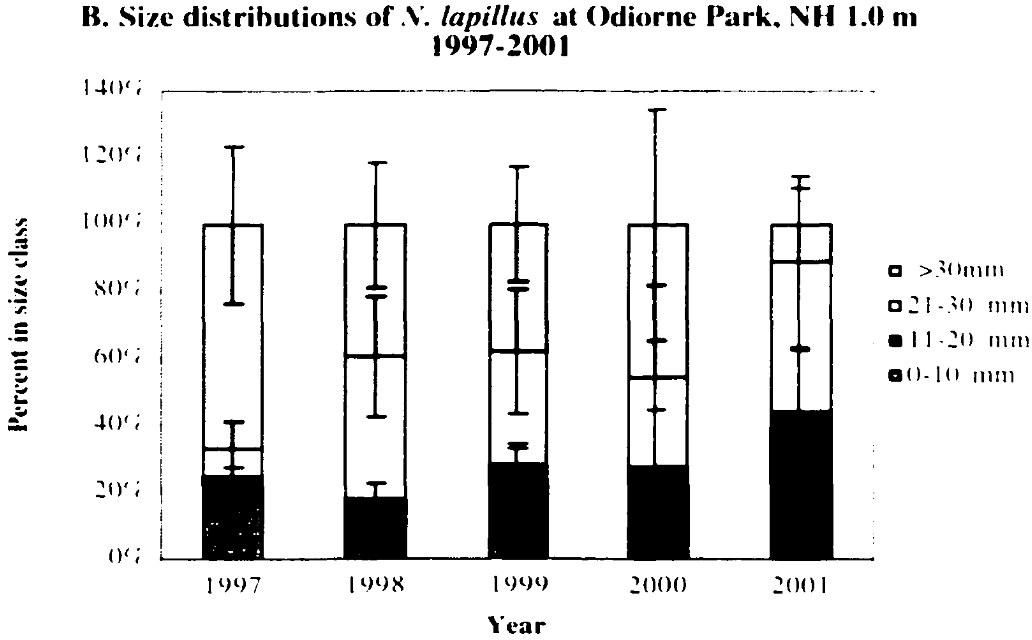
B. Density of *N. lapillus* and *N. testudinalis* at Odiorne Park, NH 1.0 m 1997-2001

Figure 2.24b Average density/m^2 and standard error of *N. lapillus* and *N. testudinalis* at 1.0 m above MLLW at Odiorne Park, NH from 1997 - 2001.



A. Size distributions of *N. lapillus* at Odiorne Park, 0.5 m 1997-2001

Figure 2.25a Average size distributions and standard error of *N. lapillus* at 0.5 m above MLLW (mean lower low water) at Odiorne Park, NH from 1997 - 2001.



B. Size distributions of *N. lapillus* at Odiorne Park, NH 1.0 m 1997-2001

Figure 2.25b Average size distributions and standard error of *N. lapillus* at 1.0 m above MLLW at Odiorne Park, NH from 1997 - 2001.

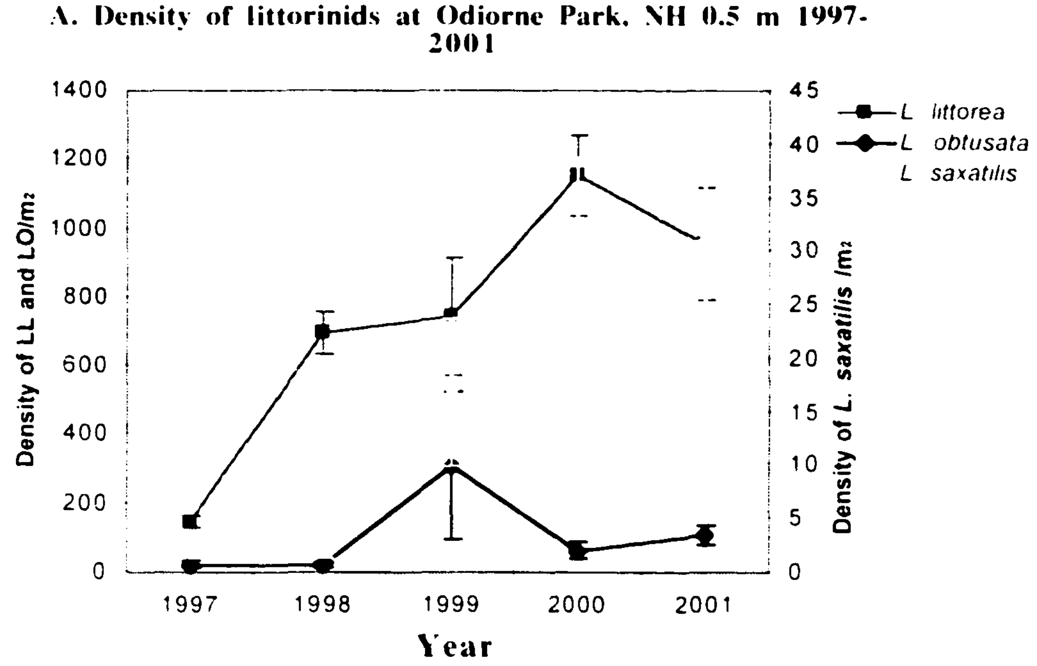

A. Density of littorinids at Odiorne Park, NH 0.5 m 1997-2001

Figure 2.26a Average density/m^2 and standard error of Littorinid snails at 0.5 m above MLLW (mean lower low water) at Odiorne Park, NH from 1997 - 2001. LL is *Littorina littorea* and LO is *L. obtusata*.

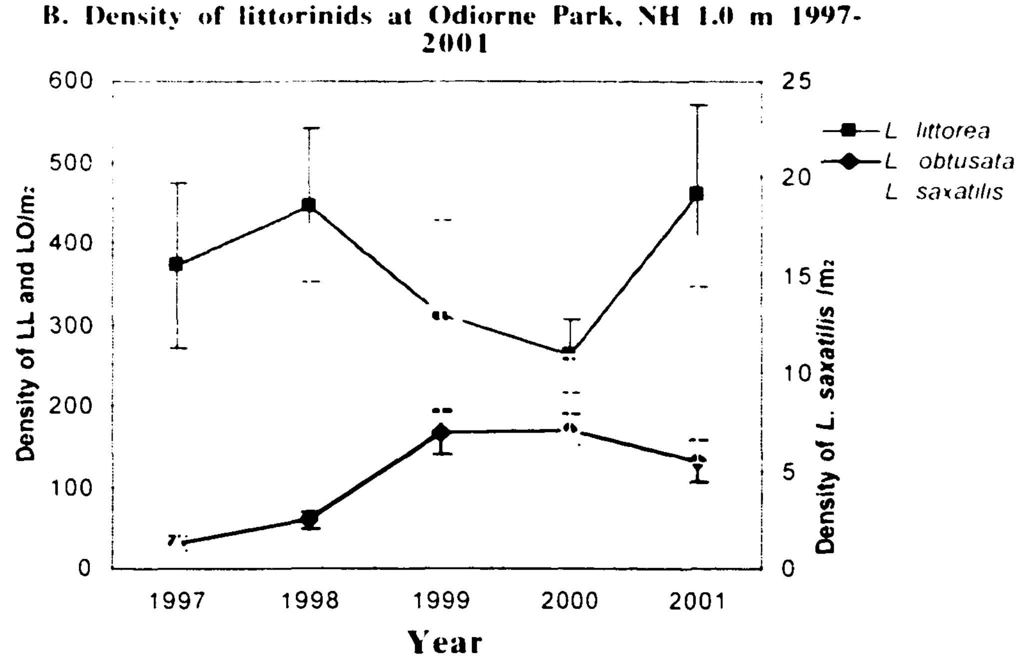

B. Density of littorinids at Odiorne Park, NH 1.0 m 1997-2001

Figure 2.26b Average density/m^2 and standard error of Littorinid snails at 1.0 m above MLLW at Odiorne Park, NH from 1997 - 2001. LL is *Littorina littorea* and LO is *L. obtusata*.

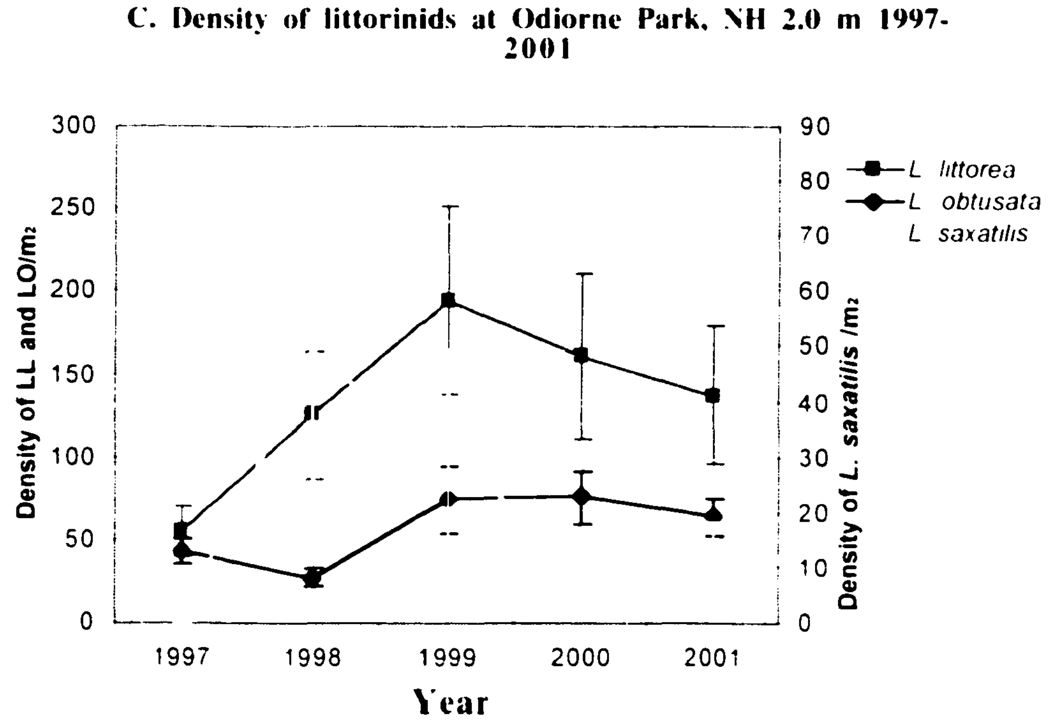


Figure 2.26c Average density/m² and standard error of Littorinid snails at 2.0 m above MLLW at Odiorne Park, NH from 1997 - 2001. LL is *Littorina littorea* and LO is *L. obtusata*.

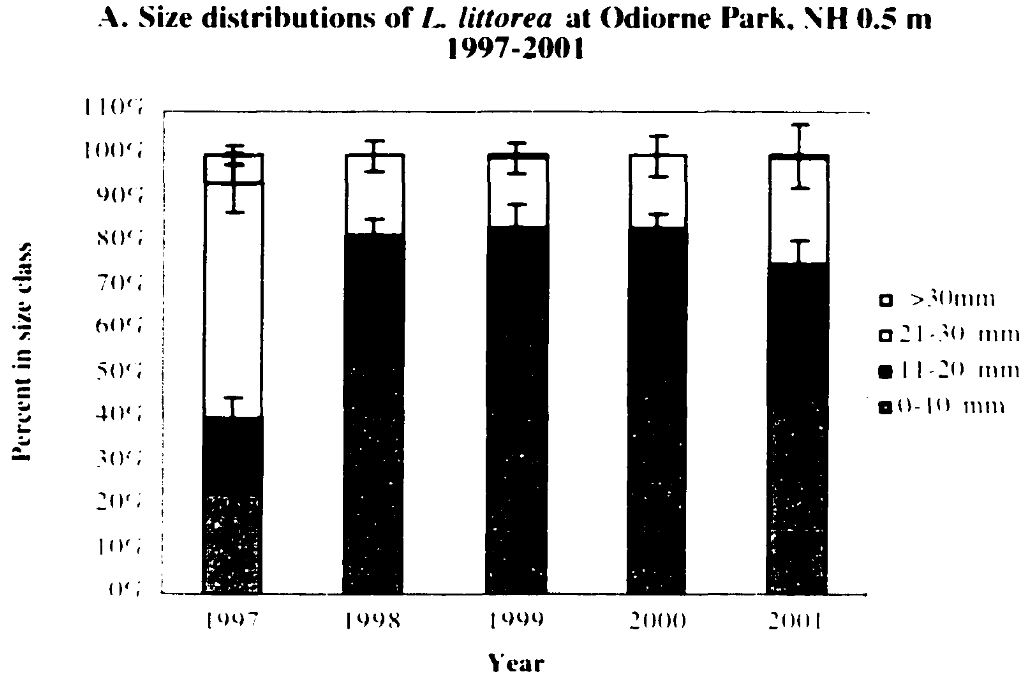

A. Size distributions of *L. littorea* at Odiorne Park, NH 0.5 m 1997-2001

Figure 2.27a Average size distributions and standard error of *L. littorea* at 0.5 m above MLLW (mean lower low water) at Odiorne Park, NH from 1997 - 2001.

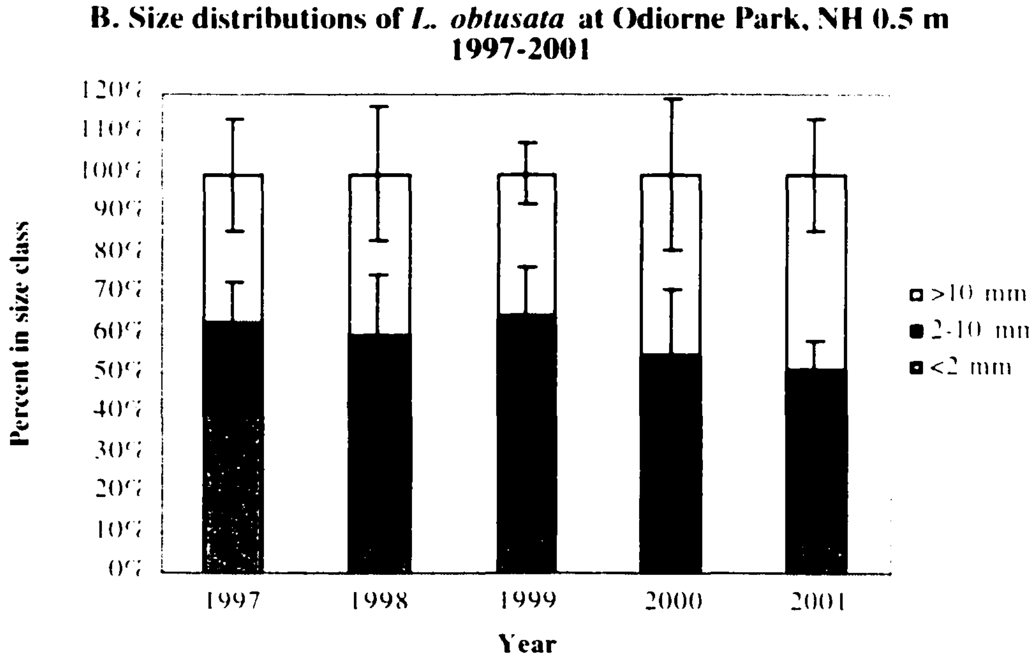

B. Size distributions of *L. obtusata* at Odiorne Park, NH 0.5 m 1997-2001

Figure 2.27b Average size distributions and standard error of *L. obtusata* at 0.5 m above MLLW at Odiorne Park, NH from 1997 - 2001.

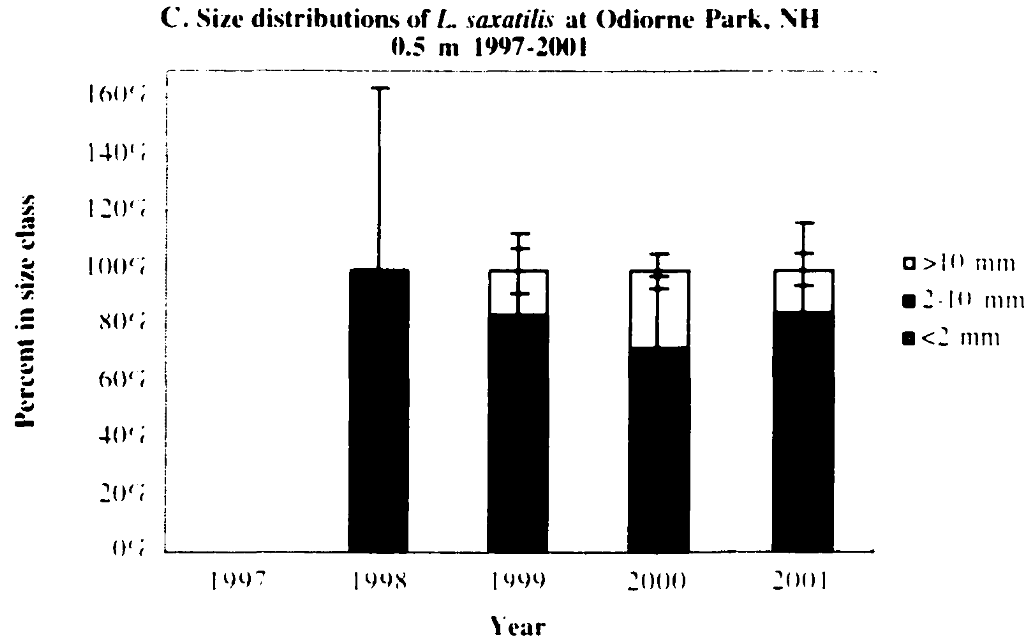


Figure 2.27c Average size distributions and standard error of *L. saxatilis* at 0.5 m above MLLW at Odiorne Park, NH from 1997 - 2001. There were no *L. saxatilis* found at this tidal height in 1997.

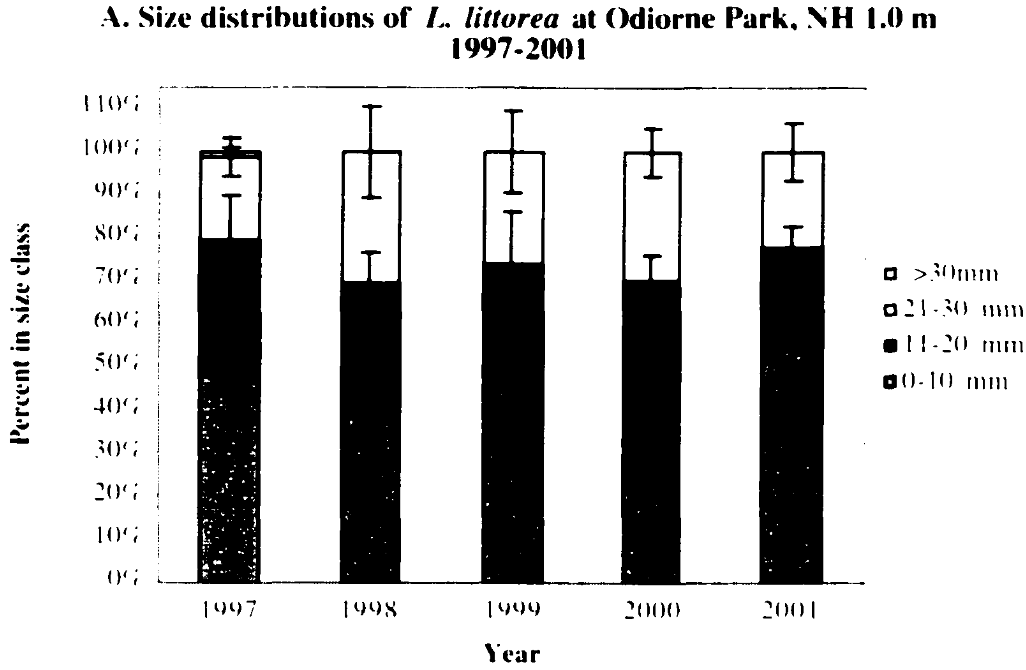

A. Size distributions of *L. littorea* at Odiorne Park, NH 1.0 m 1997-2001

Figure 2.28a Average size distributions and standard error of *L. littorea* at 1.0 m above MLLW (mean lower low water) at Odiorne Park, NH from 1997 - 2001.

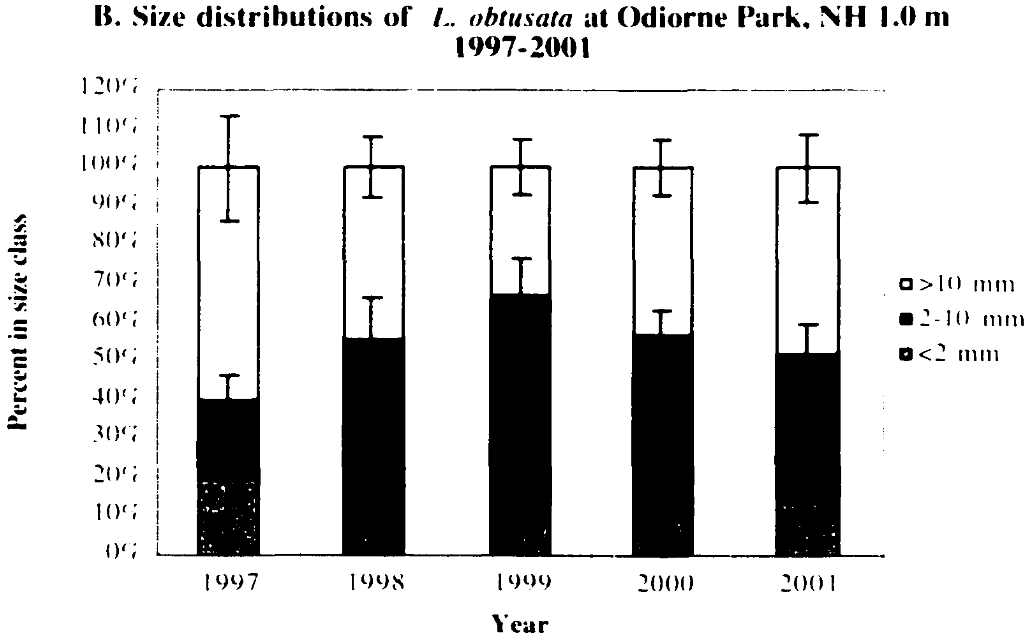

B. Size distributions of *L. obtusata* at Odiorne Park, NH 1.0 m 1997-2001

Figure 2.28b Average size distributions and standard error of *L. obtusata* at 1.0 m above MLLW at Odiorne Park, NH from 1997 - 2001.

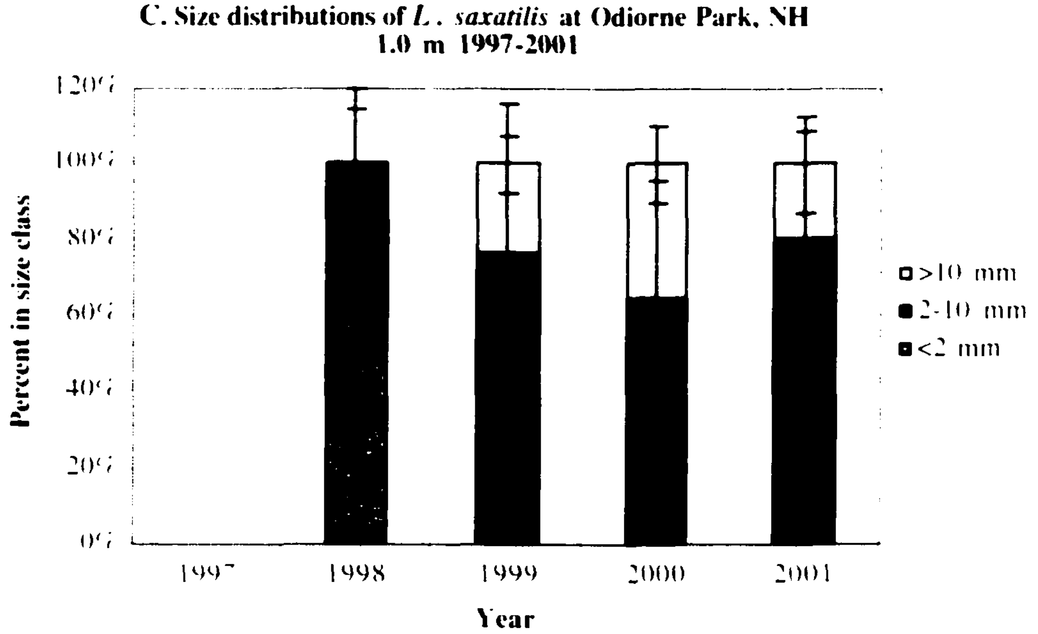


Figure 2.28c Average size distributions and standard error of *L. saxatilis* at 1.0 m above MLLW at Odiorne Park NH from 1997 - 2001. There were no *L. saxatilis* present at this tidal height in 1997.

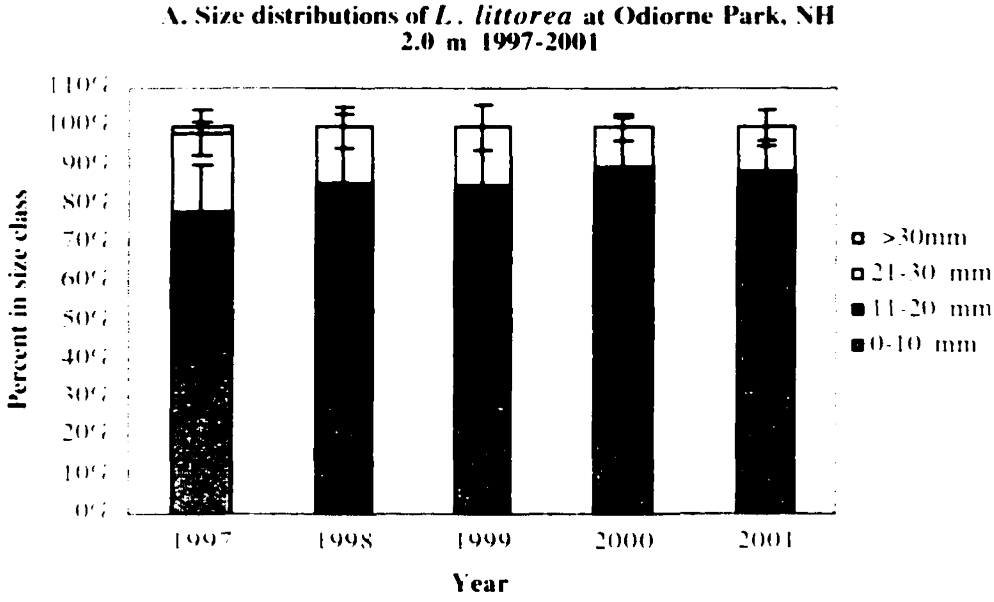


Figure 2.29a Average size distributions and standard error of *L. littorea* at 2.0 m above MLLW (mean lower low water) at Odiorne Park, NH from 1997 - 2001.

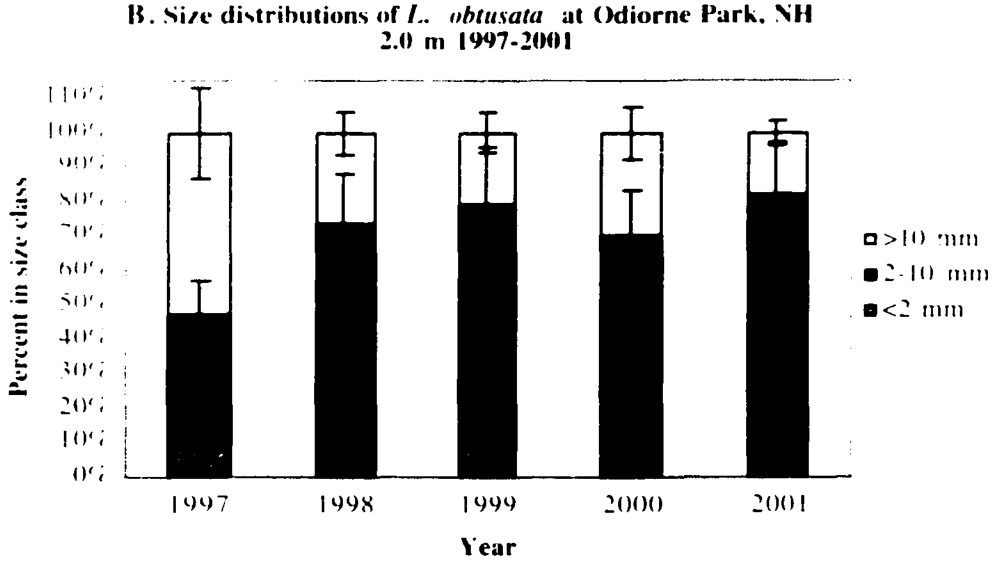


Figure 2.29b Average size distributions and standard error of *L. obtusata* at 2.0 m above MLLW at Odiorne Park, NH from 1997 - 2001.

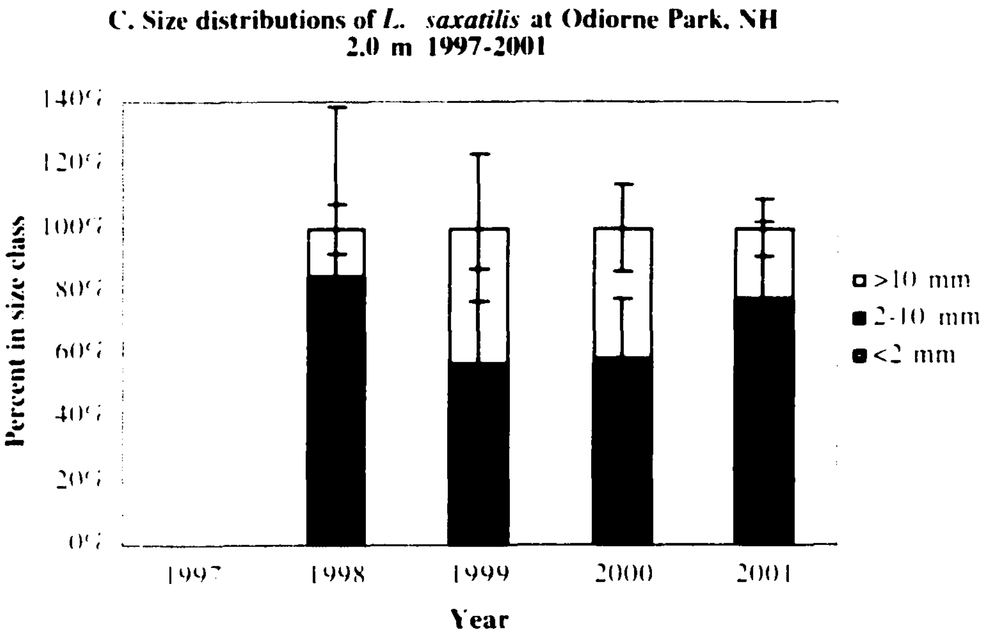


Figure 2.29c Average size distributions and standard error of *L. saxatilis* at 2.0 m above MLLW at Odiorne Park, NH from 1997 - 2001. There were no *L. saxatilis* present at this tidal height in 1997.

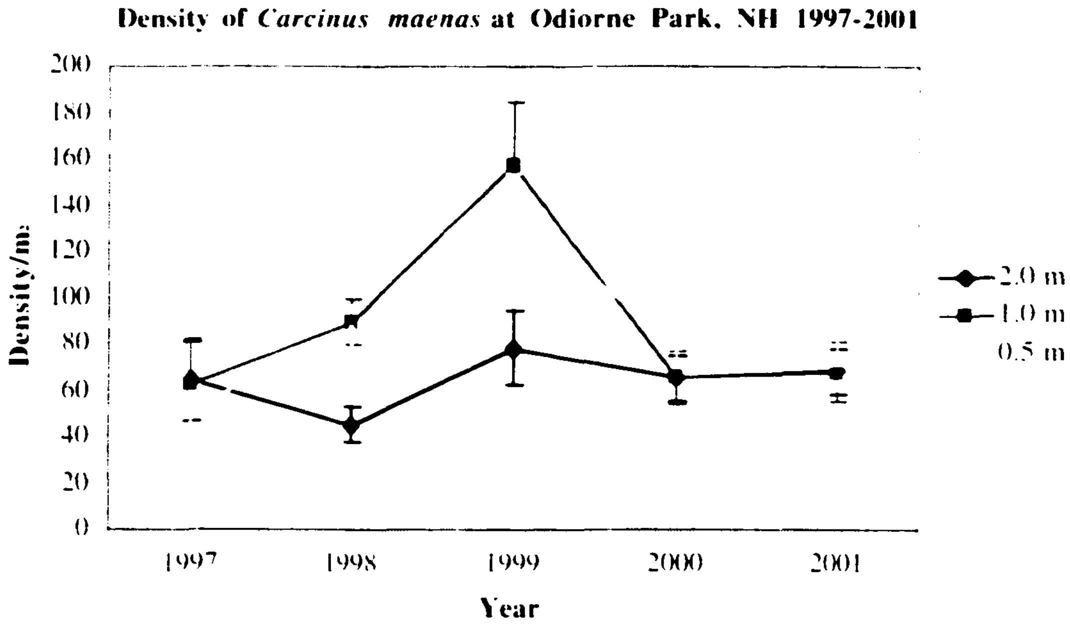


Figure 2.30 Average density/m^2 and standard error of *C. maenas* at Odiorne Park, NH from 1997 - 2001.

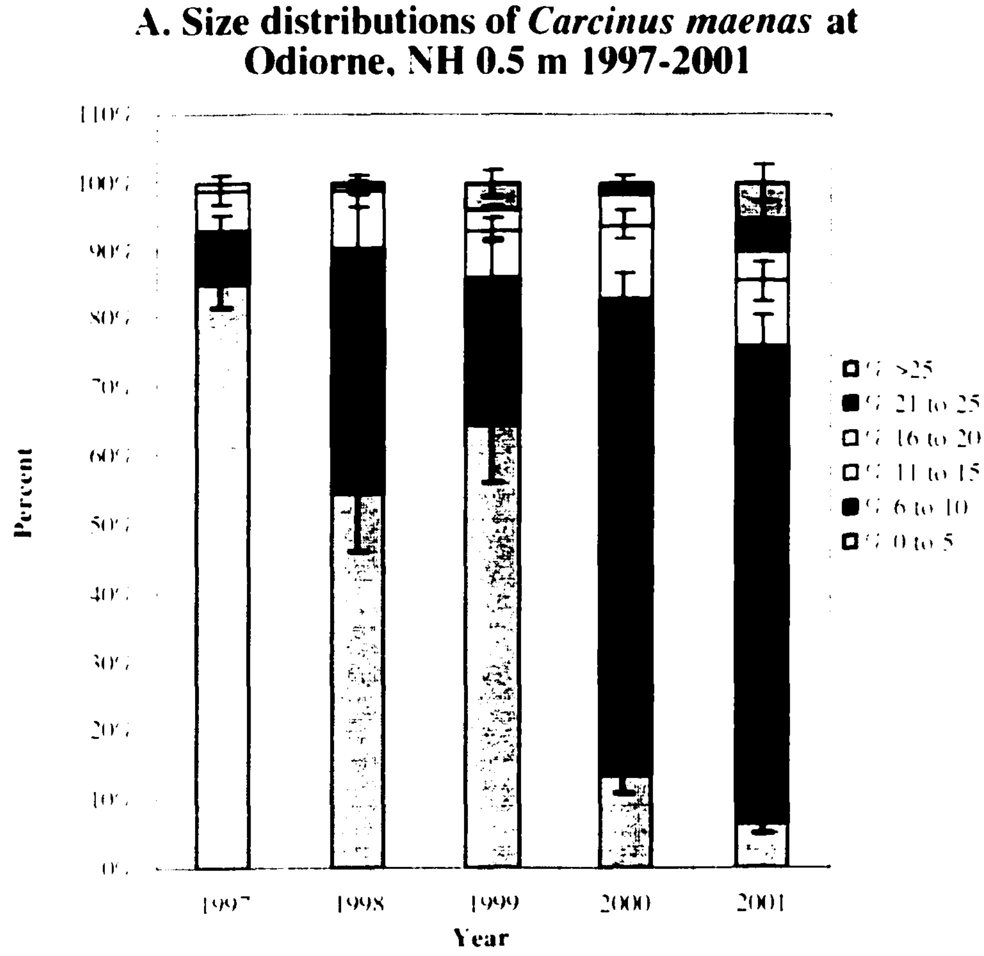


Figure 2.31a Average size distributions and standard error of *C. maenas* at 0.5 m above MLLW (mean lower low water) at Odiorne Park, NH from 1997 - 2001.

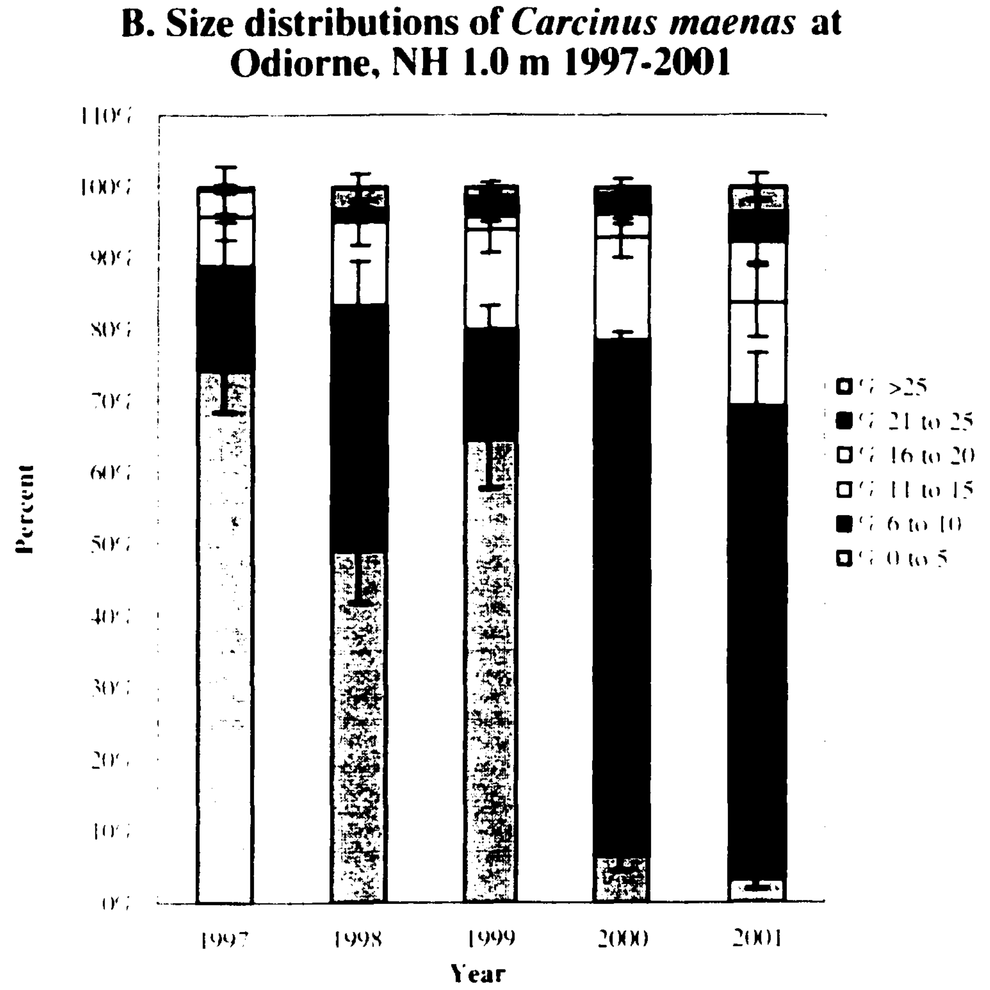


Figure 2.31b Average size distributions and standard error of *C. maenas* at 1.0 m above MLLW (mean lower low water) at Odiorne Park, NH from 1997 - 2001.

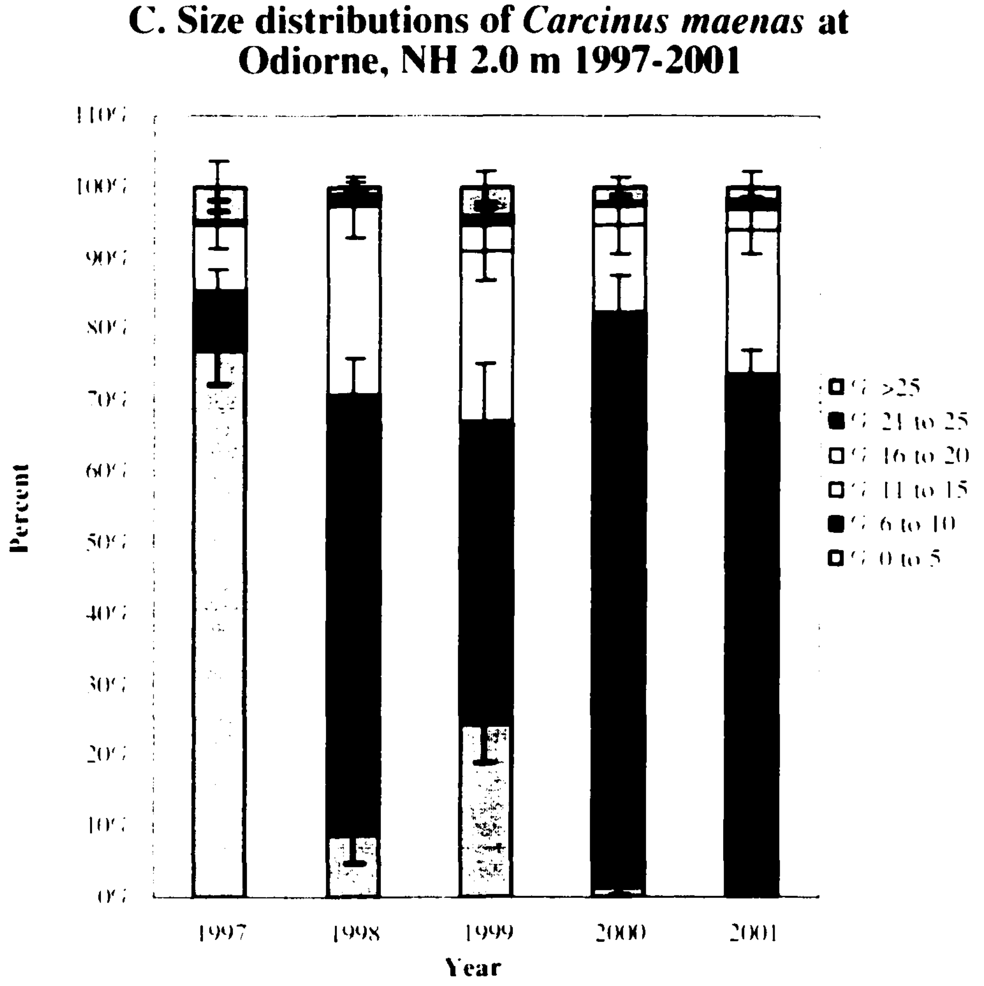


Figure 2.31c Average size distributions and standard error of *C. maenas* at 2.0 m above MLLW (mean lower low water) at Odiorne Park, NH from 1997 - 2001.

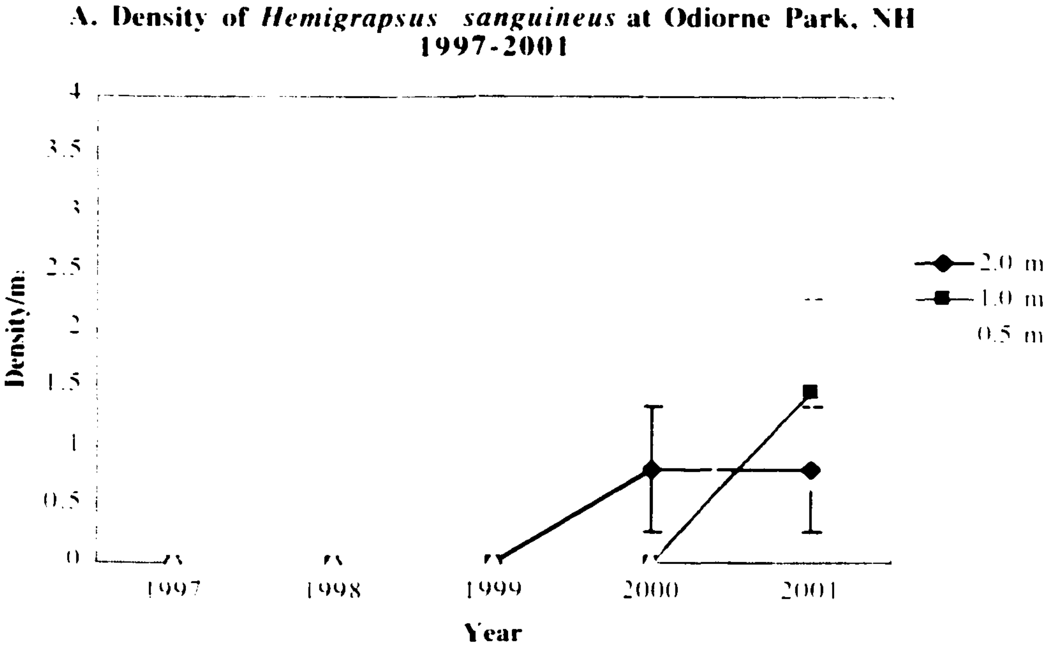


Figure 2.32a Average density/m² and standard error of *H. sanguineus* at Odiorne Park, NH from 1997 - 2001. There were no *H. sanguineus* found at this site from 1997-1999.

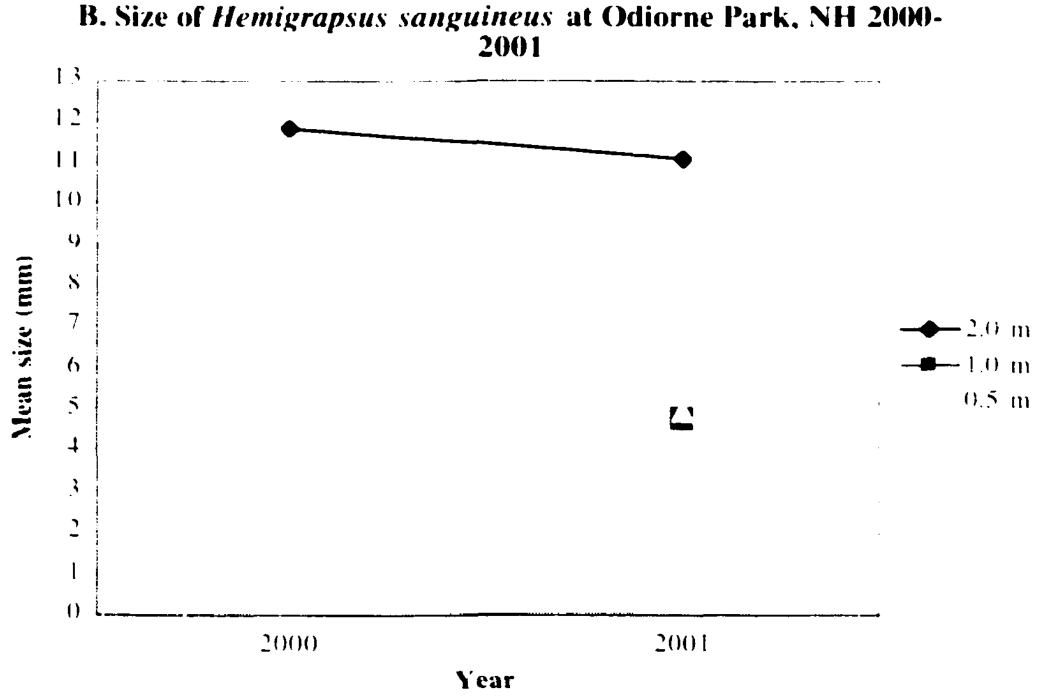


Figure 2.32b Average size and standard error of *H. sanguineus* at Odiorne Park, NH from 2000 - 2001.

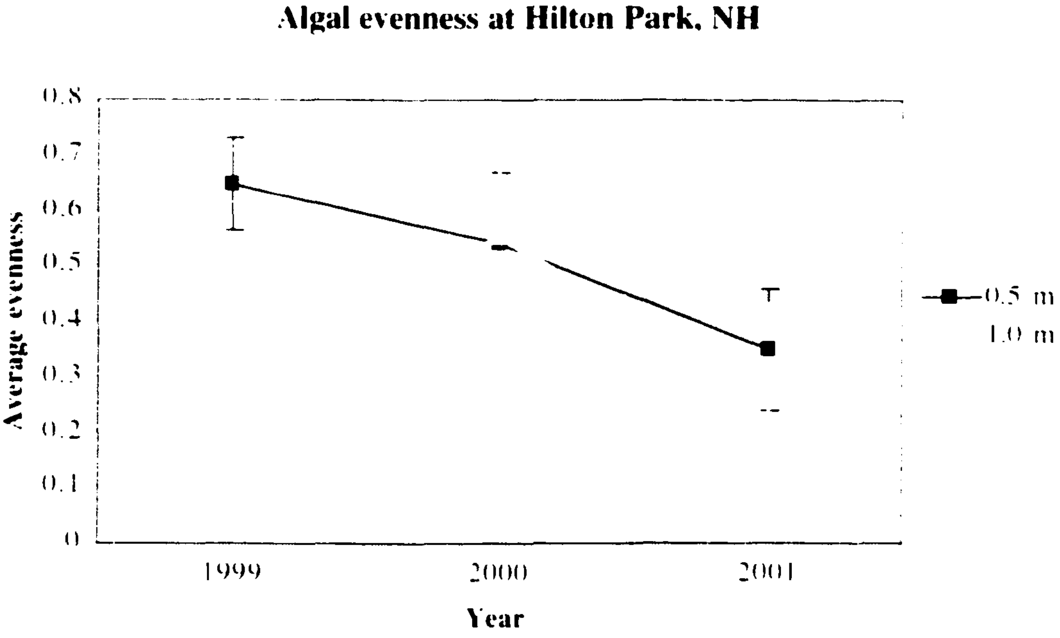
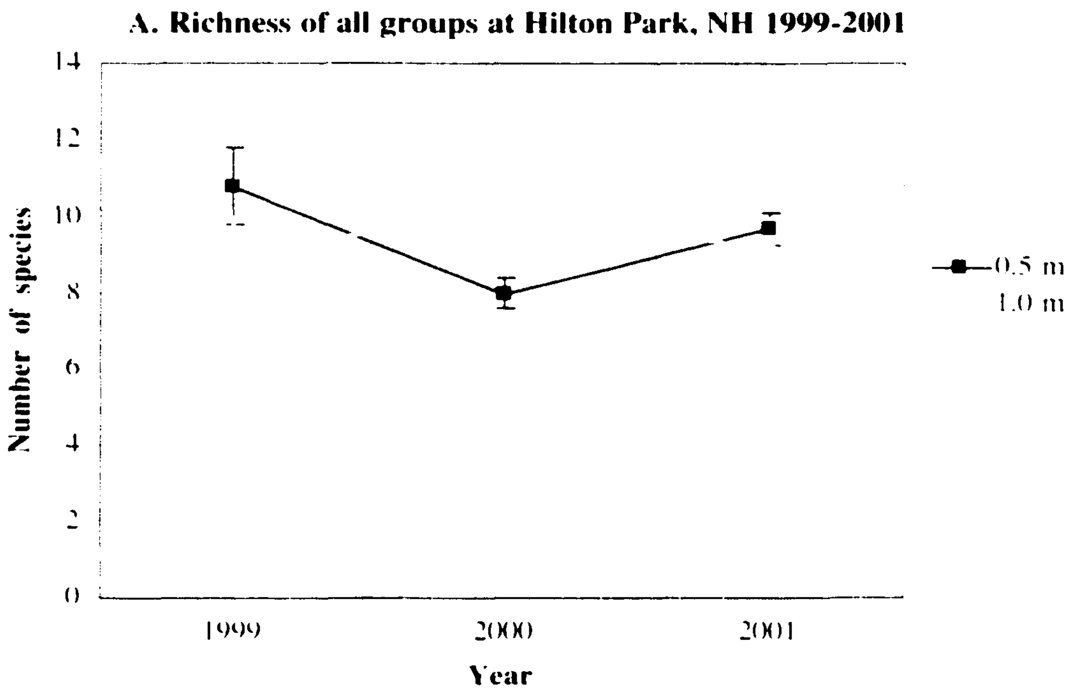
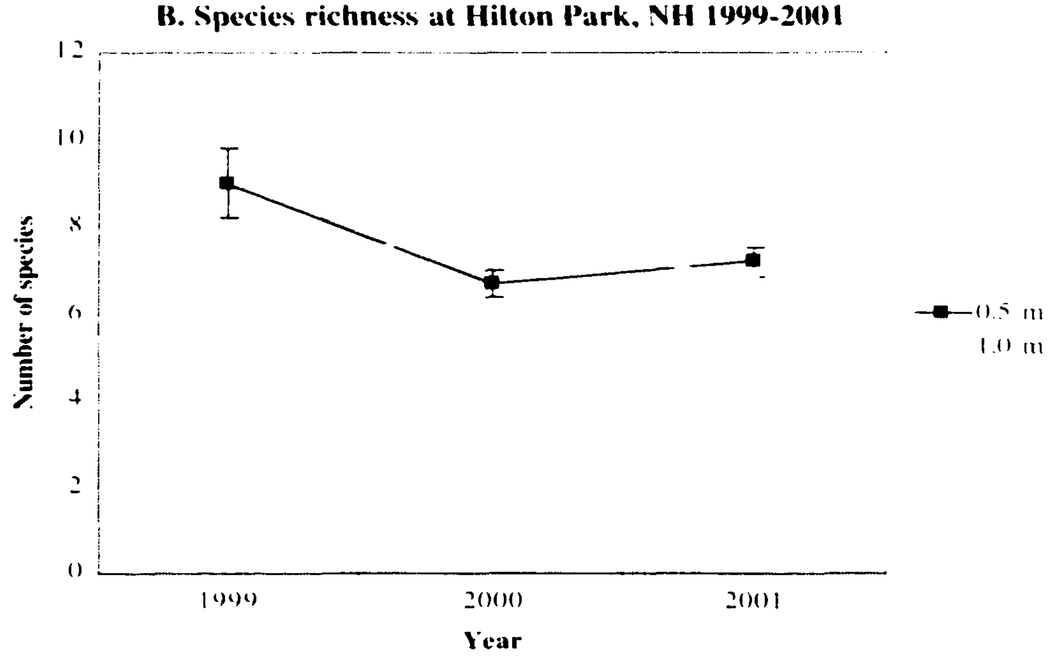


Figure 2.33 Average algal evenness and standard error at different tidal heights at Hilton Park, NH from 1999 to 2001 calculated using Pielou's J index for equitability.



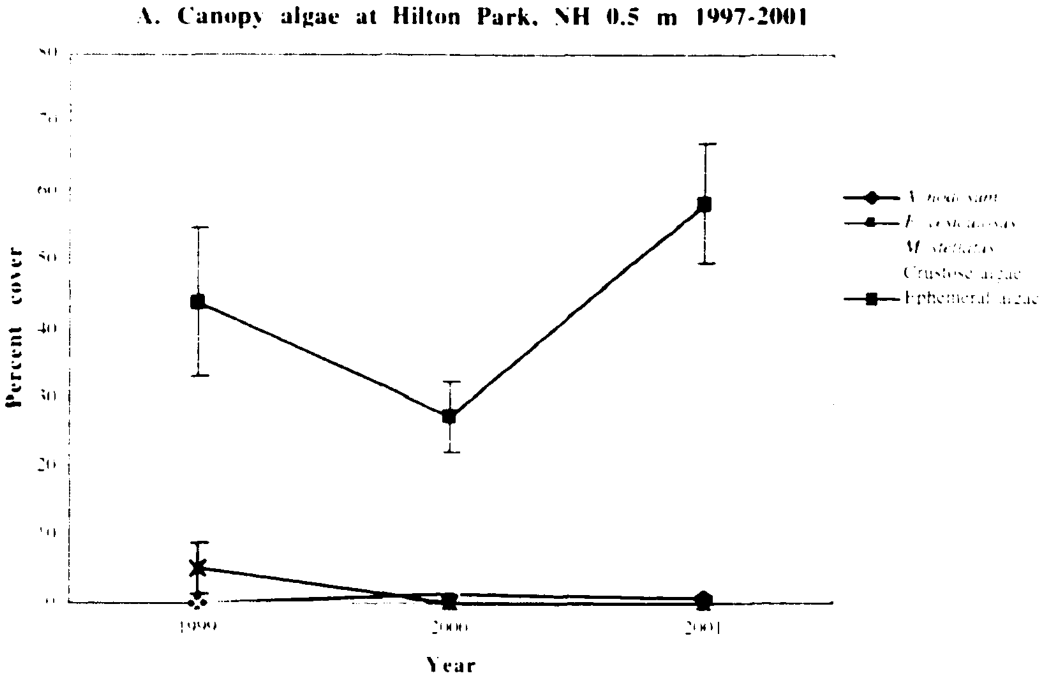
A. Richness of all groups at Hilton Park, NH 1999-2001

Figure 2.34a Average richness and standard error at different tidal heights at Hilton Park, NH from 1999 to 2001 calculated by including groups of species in the richness estimate.



B. Species richness at Hilton Park, NH 1999-2001

Figure 2.34b. Average species richness and standard error at different tidal heights at Hilton Park, NH from 1999 to 2001 calculated only including organisms identified to species in the estimate.



A. Canopy algae at Hilton Park, NH 0.5 m 1997-2001

Figure 2.35a Average percent cover and standard error of algae observed in the canopy analysis at 0.5 m above MLLW (mean lower low water) at Hilton Park, NH from 1999 - 2001. Cover types represent major algal canopy species; ephemeral algae were not identified to species because of their highly variable composition and abundance.

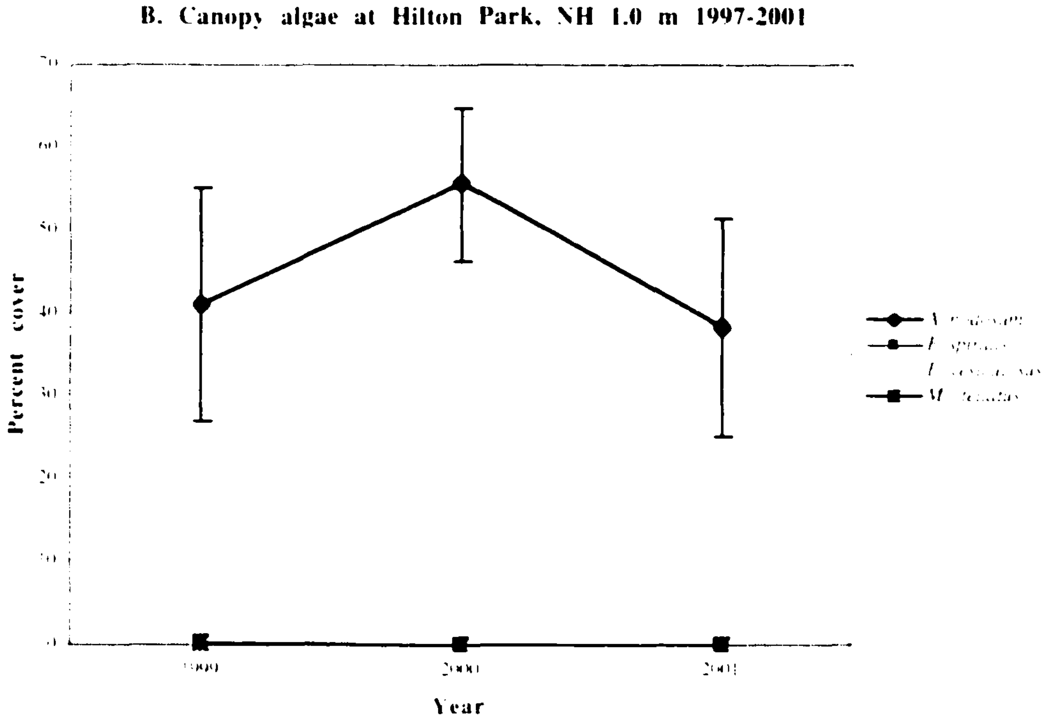


Figure 2.35b Average percent cover and standard error of algae observed in the canopy analysis at 1.0 m above MLLW at Hilton Park, NH from 1999 - 2001. Cover types represent major algal canopy species.

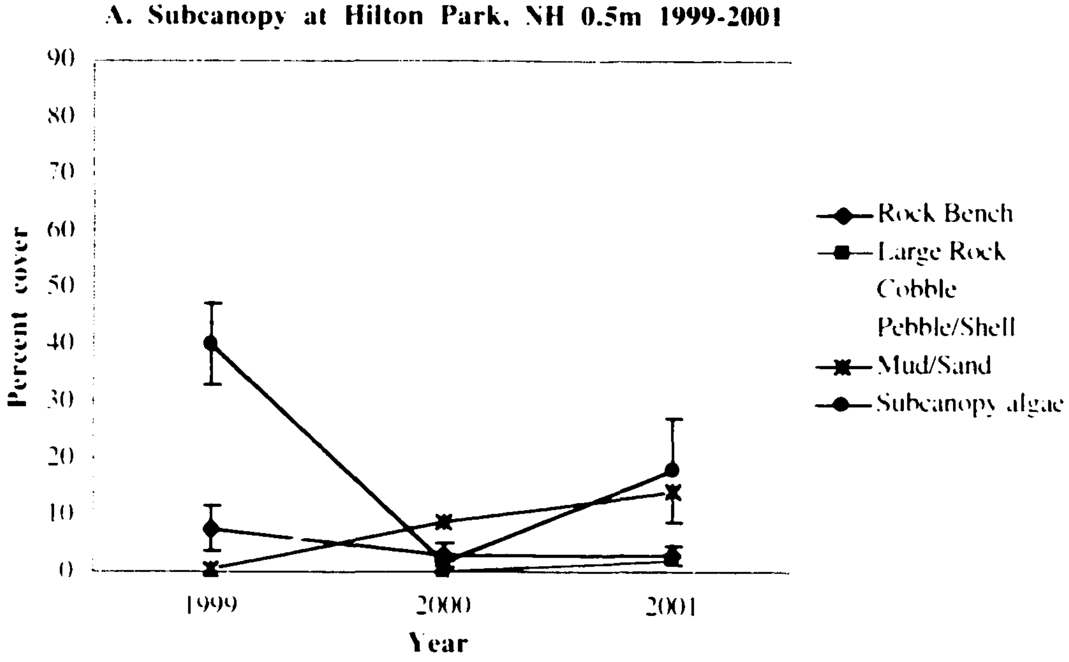


Figure 2.36a Average percent cover and standard error of substrates and subcanopy algae observed in subcanopy analysis at 0.5 m above MLLW (mean lower low water) at Hilton Park, NH from 1999 - 2001. The majority of the subcanopy algae category was *M. stellatus* and *Chondrus crispus* with some crustose coralline algae.

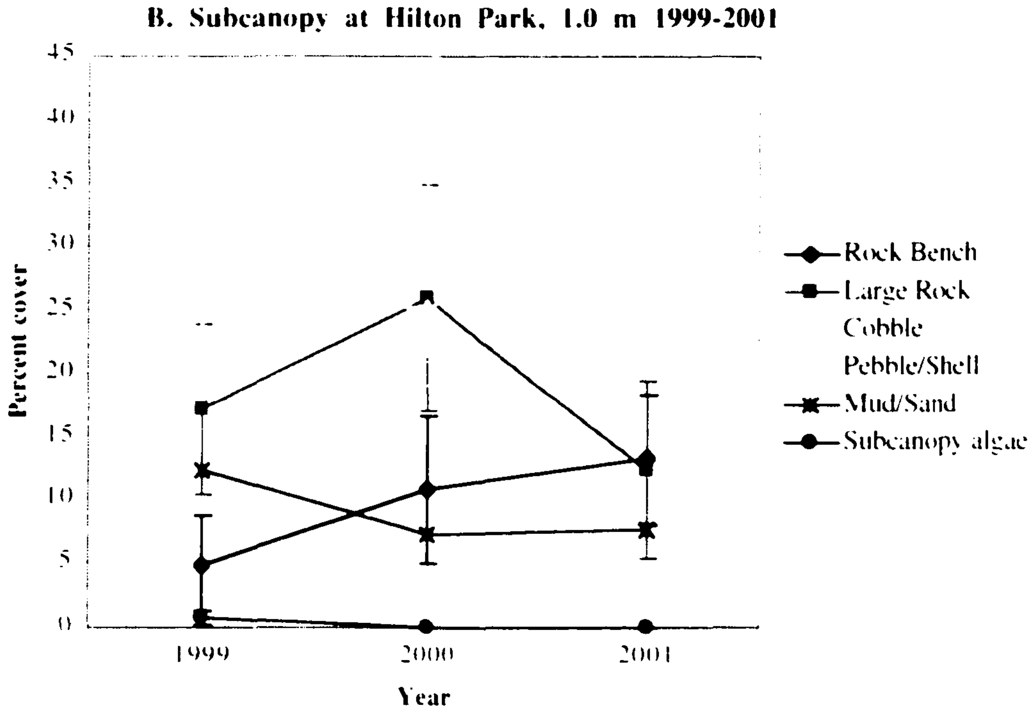


Figure 2.36b Average percent cover and standard error of substrates and subcanopy algae observed in subcanopy analysis at 1.0 m above MLLW at Hilton Park, NH from 1999 – 2001. The majority of the subcanopy algae category was *M. stellatus*.

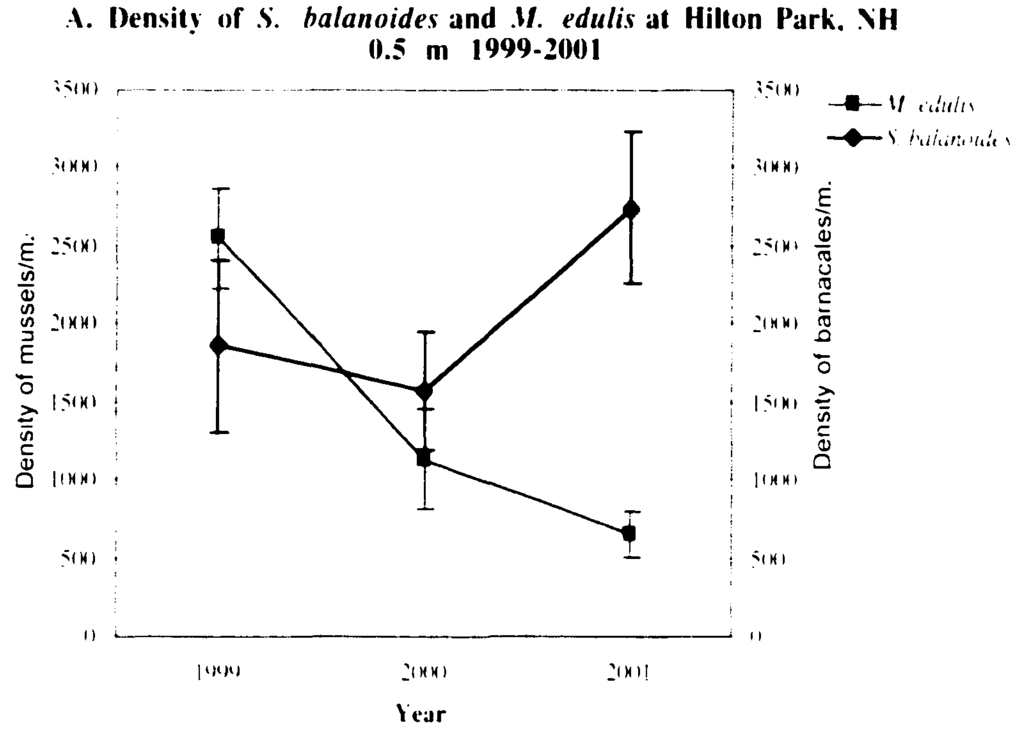


Figure 2.37a Average density/m² and standard error of *S. balanoides* and *M. edulis* at 0.5 m above MLLW (mean lower low water) at Hilton Park, NH from 1999 - 2001.

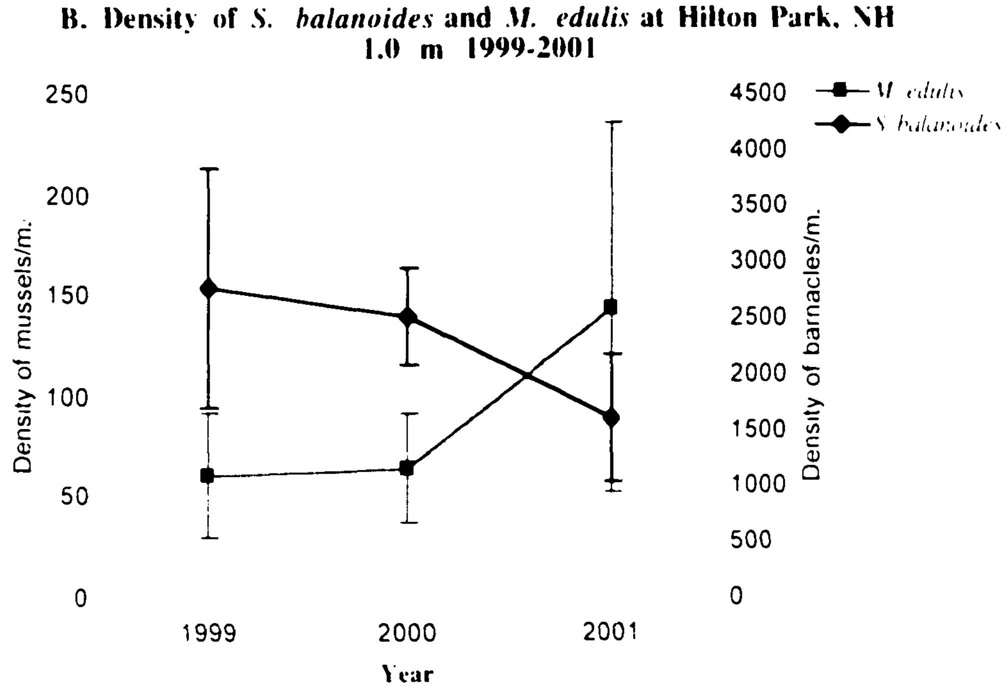


Figure 2.37b Average density/m² and standard error of *M. edulis* and *S. balanoides* at 1.0 m above MLLW at Hilton Park, NH from 1999 - 2001.

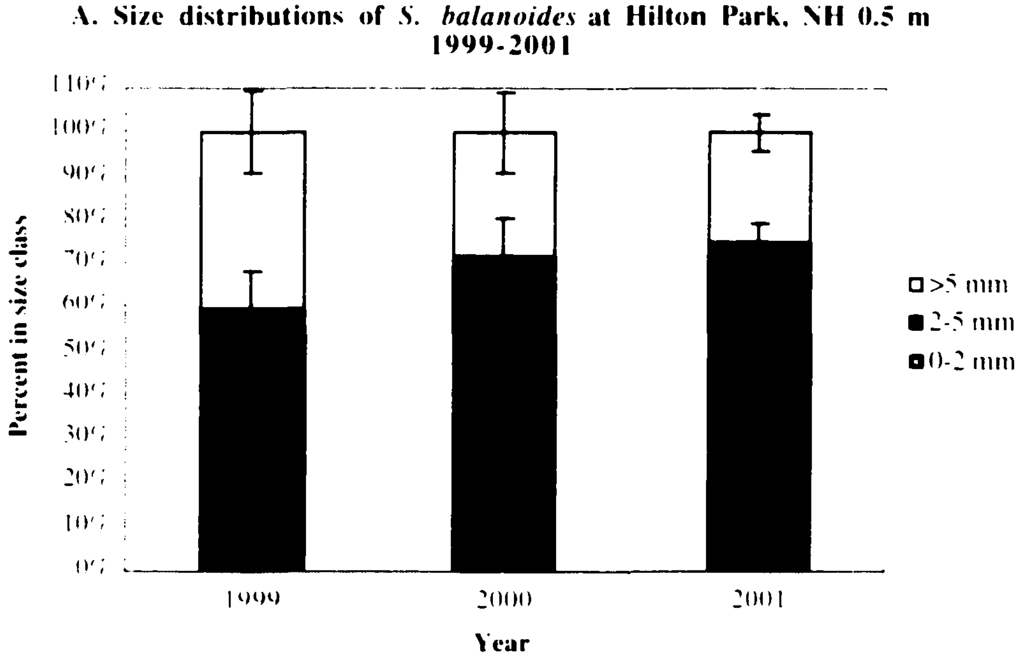


Figure 2.38a Estimated size class distribution of *S. balanoides* at 0.5 m above MLLW (mean lower low water) at Hilton Park, NH from 1999 - 2001.

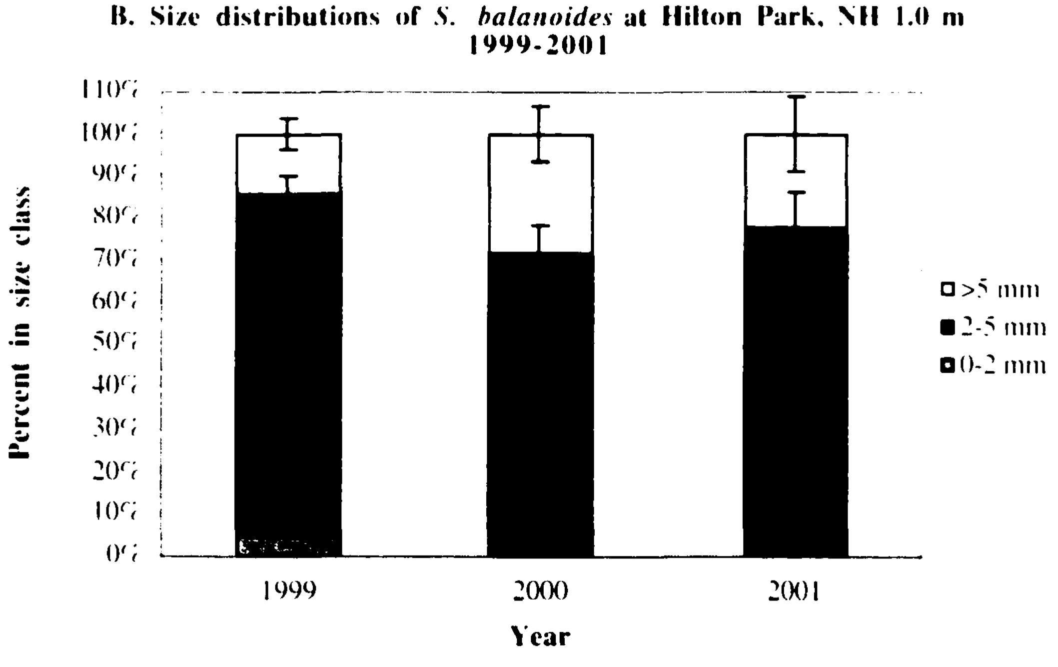


Figure 2.38b Estimated size class distribution of *S. balanoides* at 1.0 m above MLLW at Hilton Park, NH from 1999 - 2001.

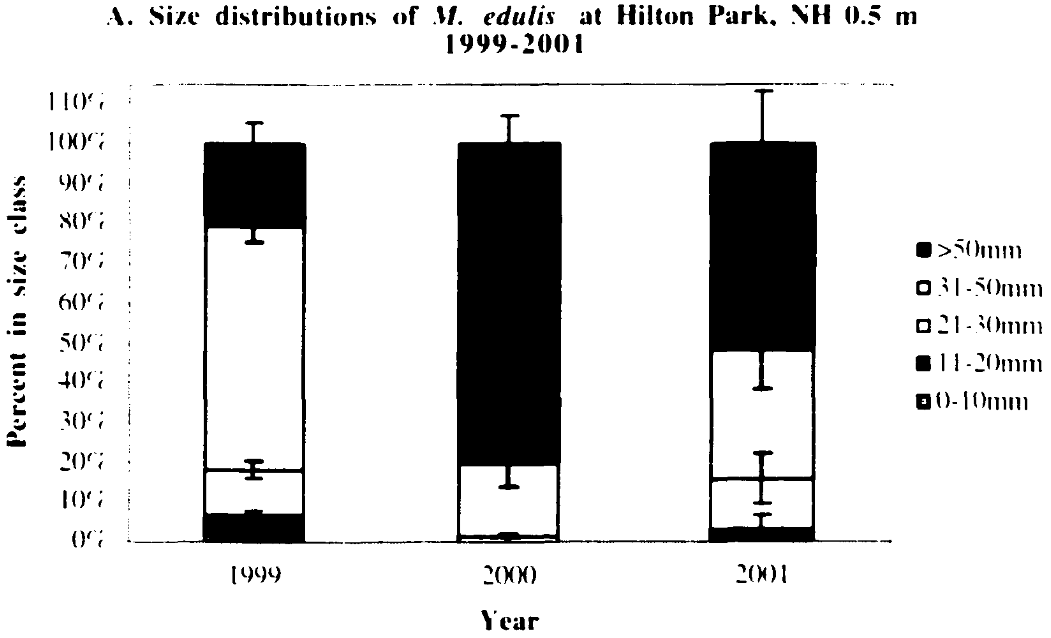


Figure 2.39a Estimated size class distribution of *M. edulis* at 0.5 m above MLLW (mean lower low water) at Hilton Park, NH from 1999 - 2001.

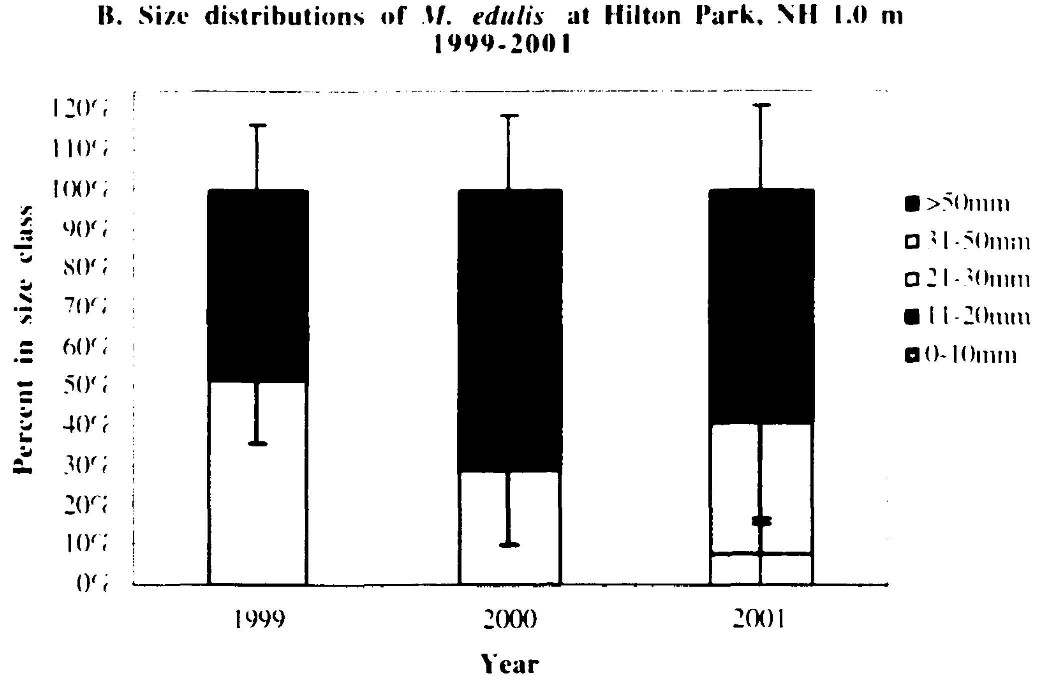


Figure 2.39b Estimated size class distribution of *M. edulis* at 1.0 m above MLLW at Hilton Park, NH from 1999 - 2001.

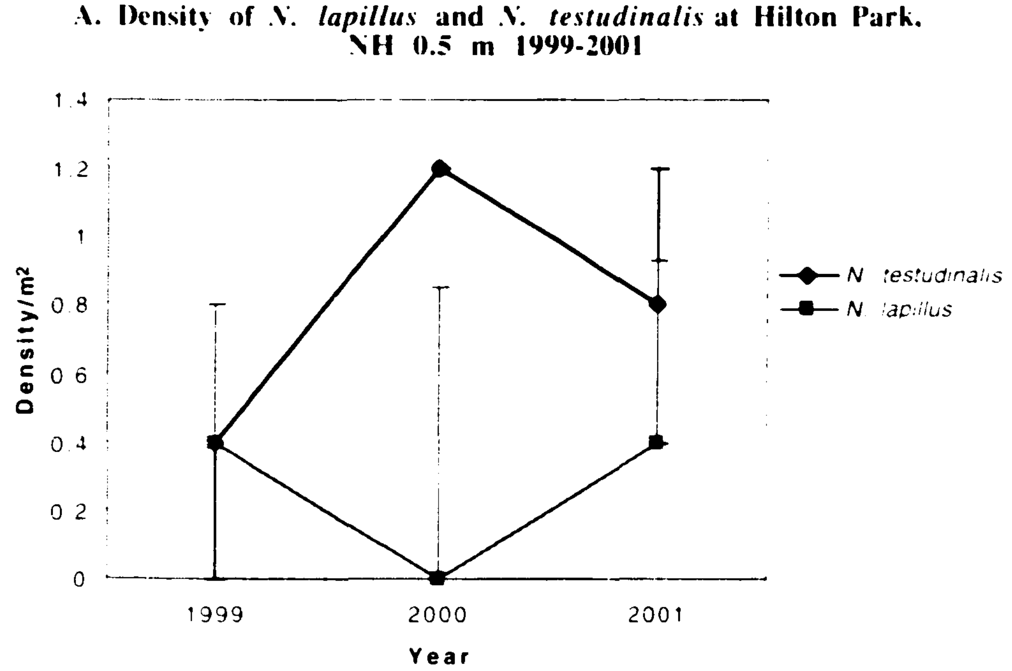


Figure 2.40a Average density/m² and standard error of *N. lapillus* and *N. testudinalis* at 0.5 m above MLLW (mean lower low water) at Hilton Park, NH from 1999 - 2001.

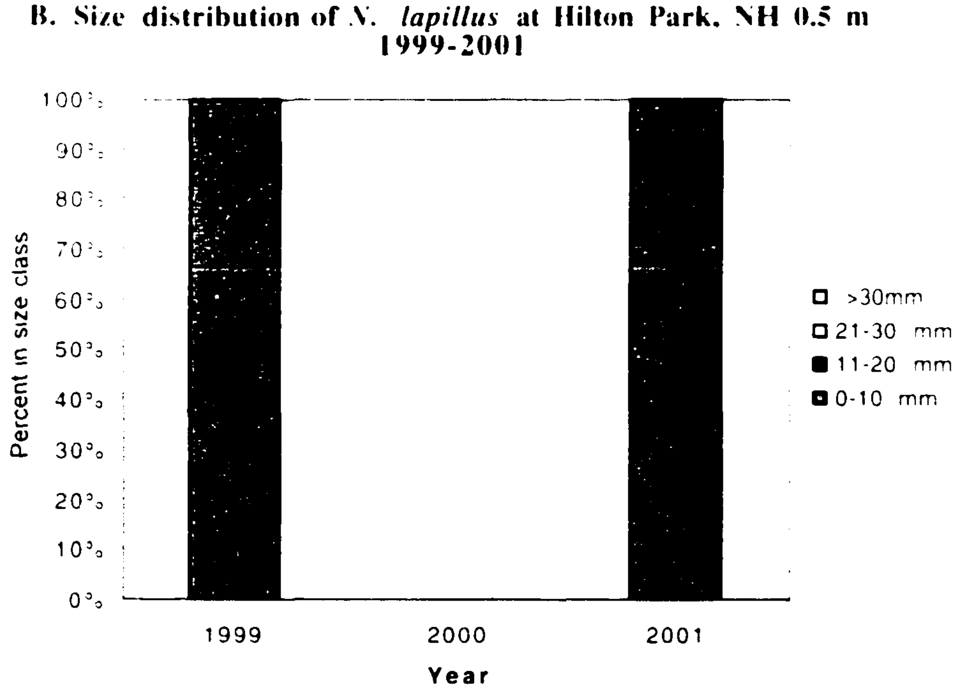


Figure 2.40b Average size distributions of *N. lapillus* at 0.5 m above MLLW at Hilton Park, NH from 1999 - 2001.

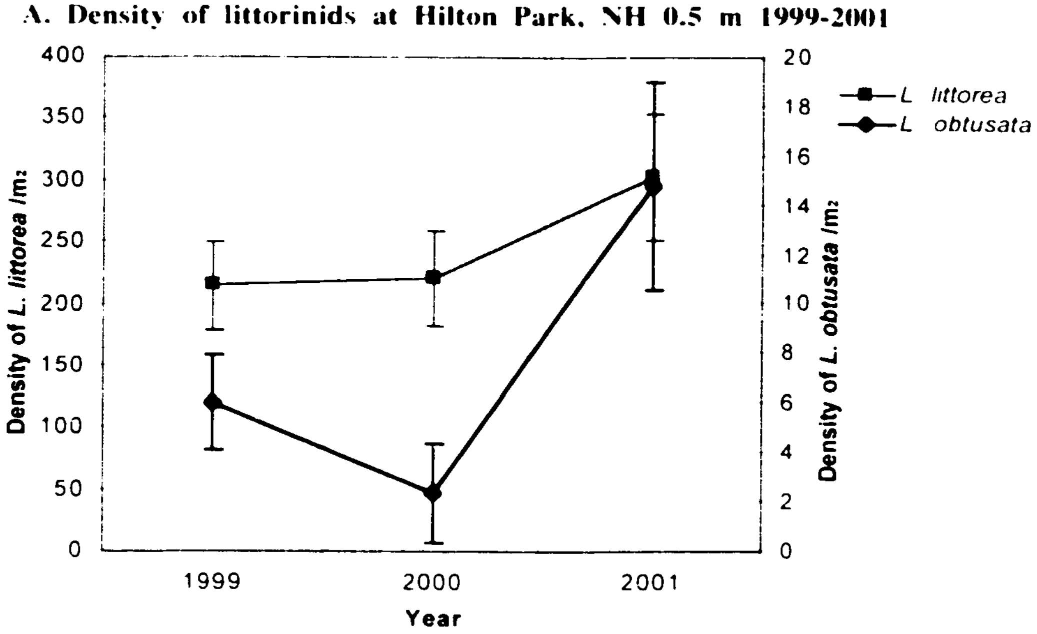


Figure 2.41a Average density/m² and standard error of Littorinid snails at 0.5 m above MLLW (mean lower low water) at Hilton Park, NH from 1999 - 2001. No *L. saxatilis* were ever found at this tidal height throughout the sampling period.

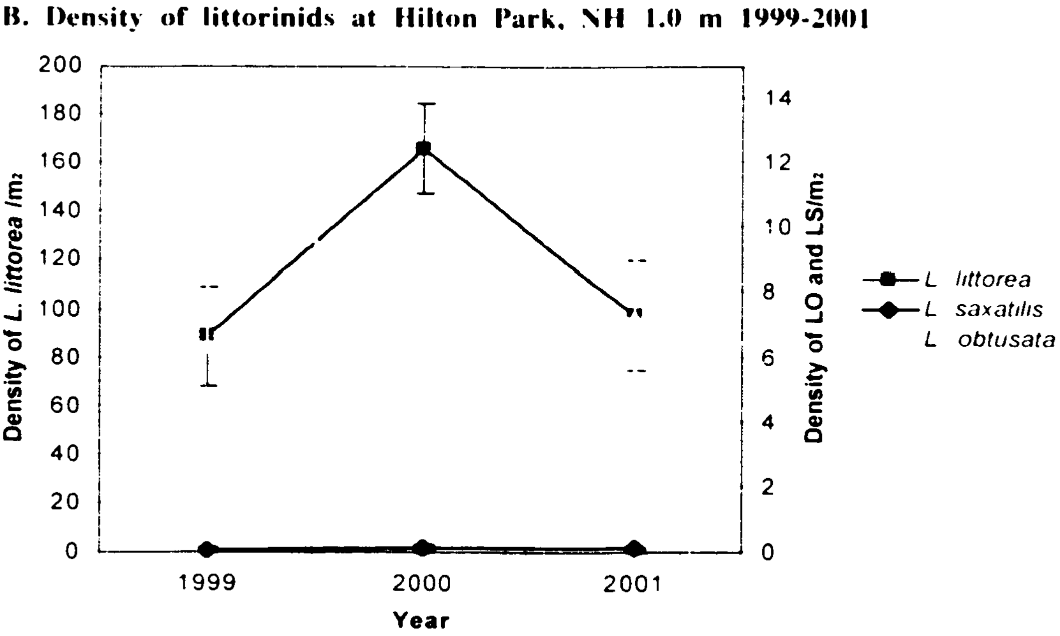


Figure 2.41b Average density/m² and standard error of Littorinid snails at 1.0 m above MLLW at Hilton Park, NH from 1999 - 2001. LO is *Littorina obtusata* and LS is *L. saxatilis*.

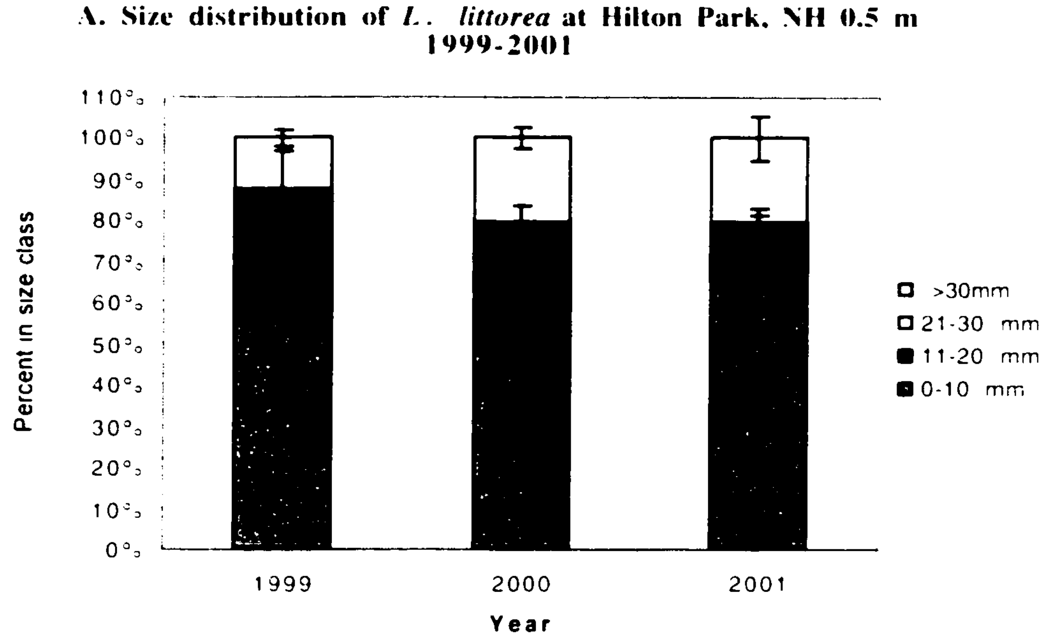

A. Size distribution of *L. littorea* at Hilton Park, NH 0.5 m 1999-2001

Figure 2.42a Average size distributions and standard error of *L. littorea* at 0.5 m above MLLW (mean lower low water) at Hilton Park, NH from 1999 - 2001.

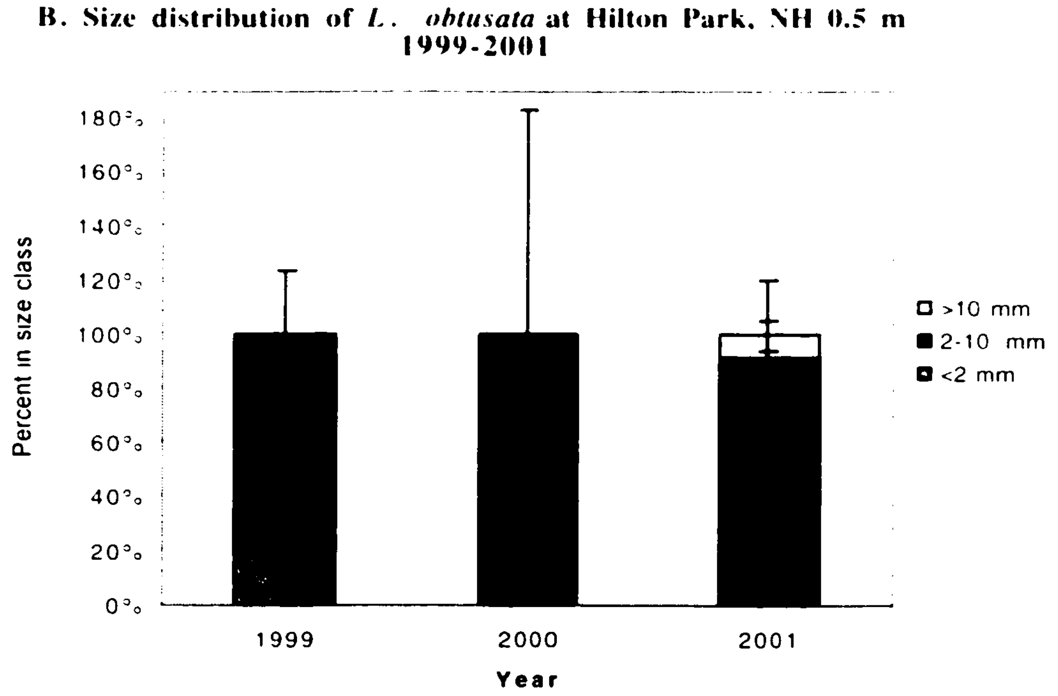

B. Size distribution of *L. obtusata* at Hilton Park, NH 0.5 m 1999-2001

Figure 2.42b Average size distributions and standard error of *L. obtusata* at 0.5 m above MLLW at Hilton Park, NH from 1999 - 2001.

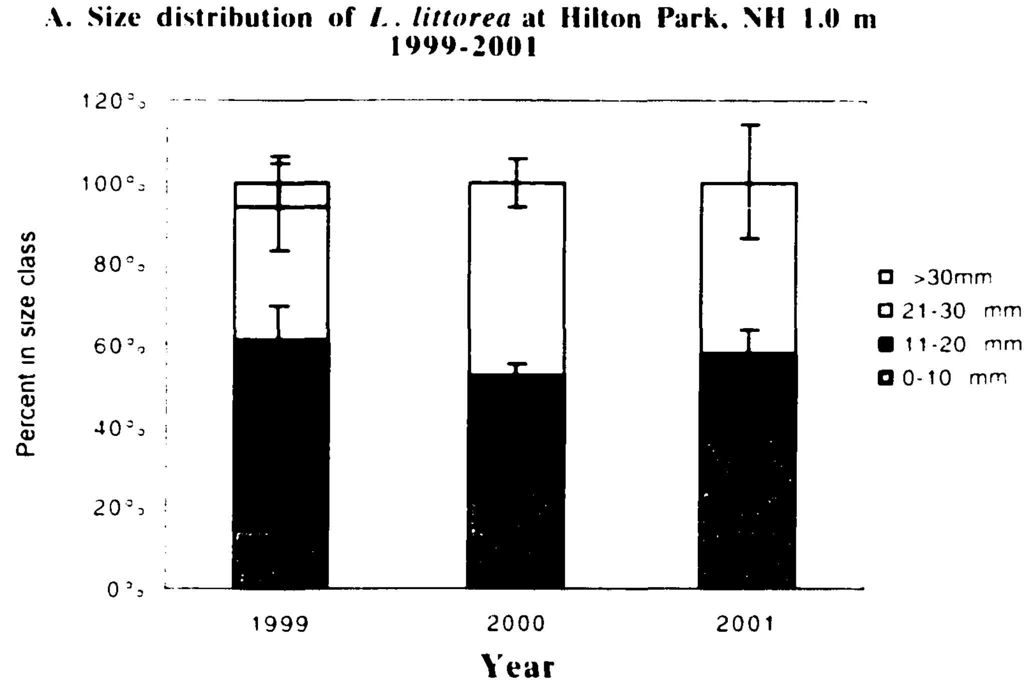


Figure 2.43a Average size distributions and standard error of *L. littorea* at 1.0 m above MLLW (mean lower low water) at Hilton Park, NH from 1999 - 2001.

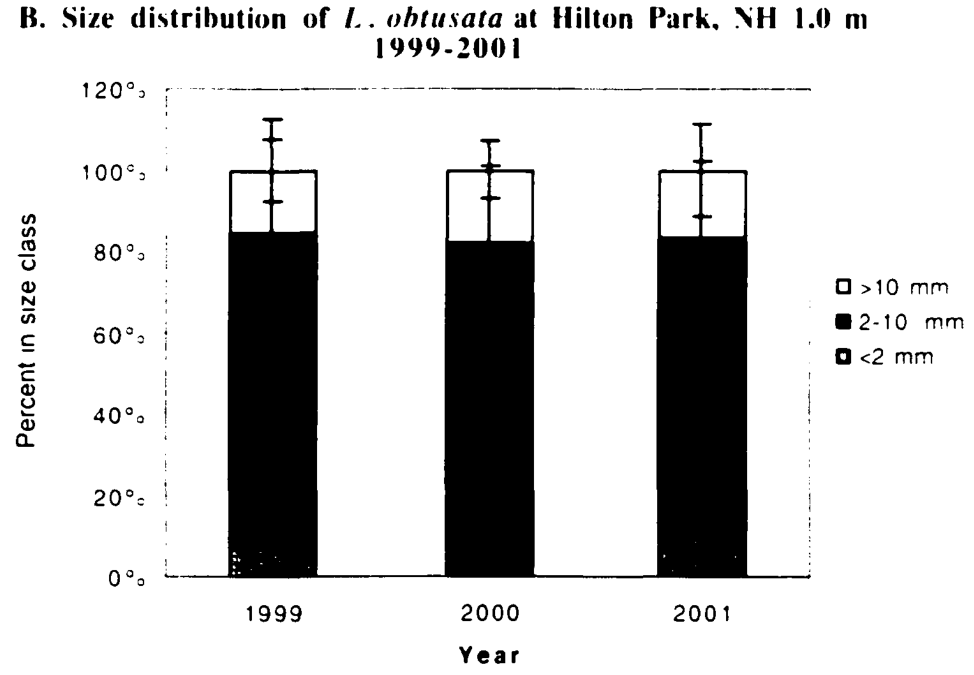


Figure 2.43b Average size distributions and standard error of *L. obtusata* at 1.0 m above MLLW at Hilton Park, NH from 1999 - 2001.

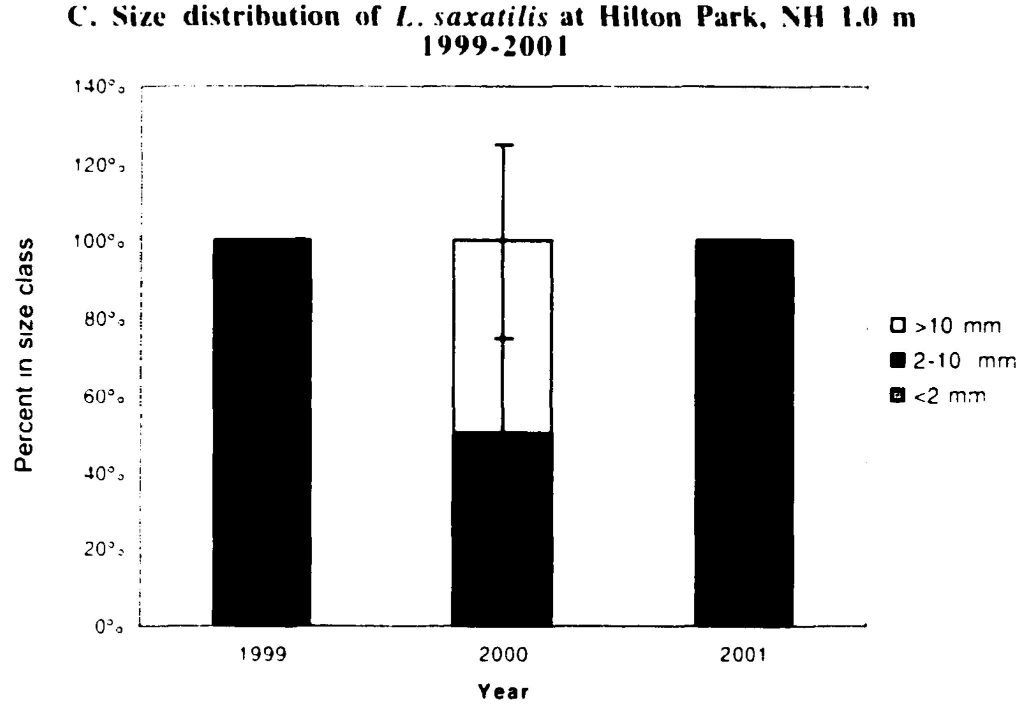


Figure 2.43c Average size distributions and standard error of *L. saxatilis* at 1.0 m above MLLW at Hilton Park, NH from 1999 - 2001.

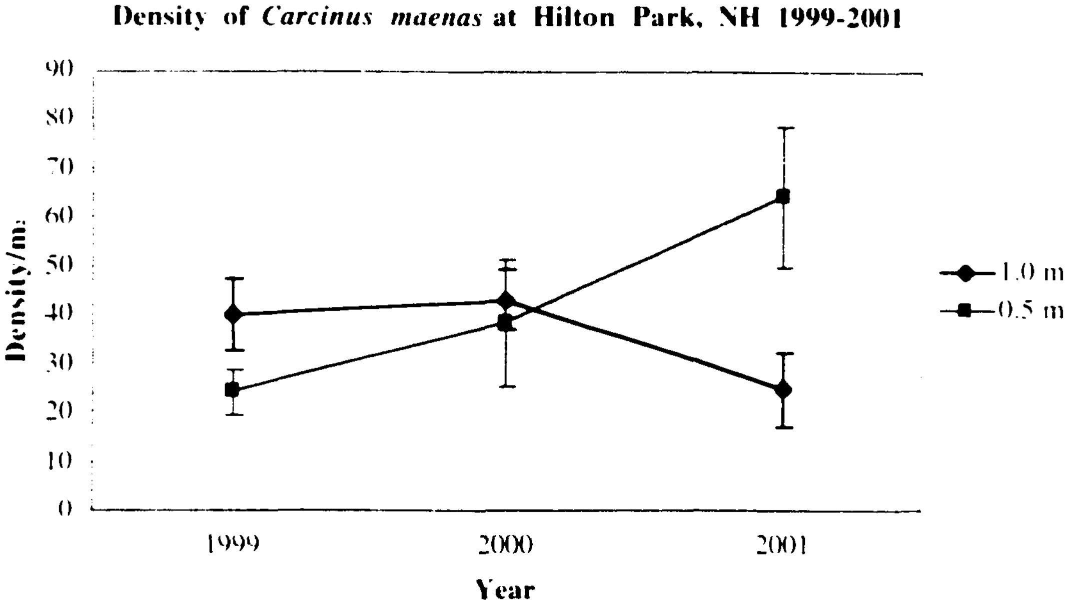
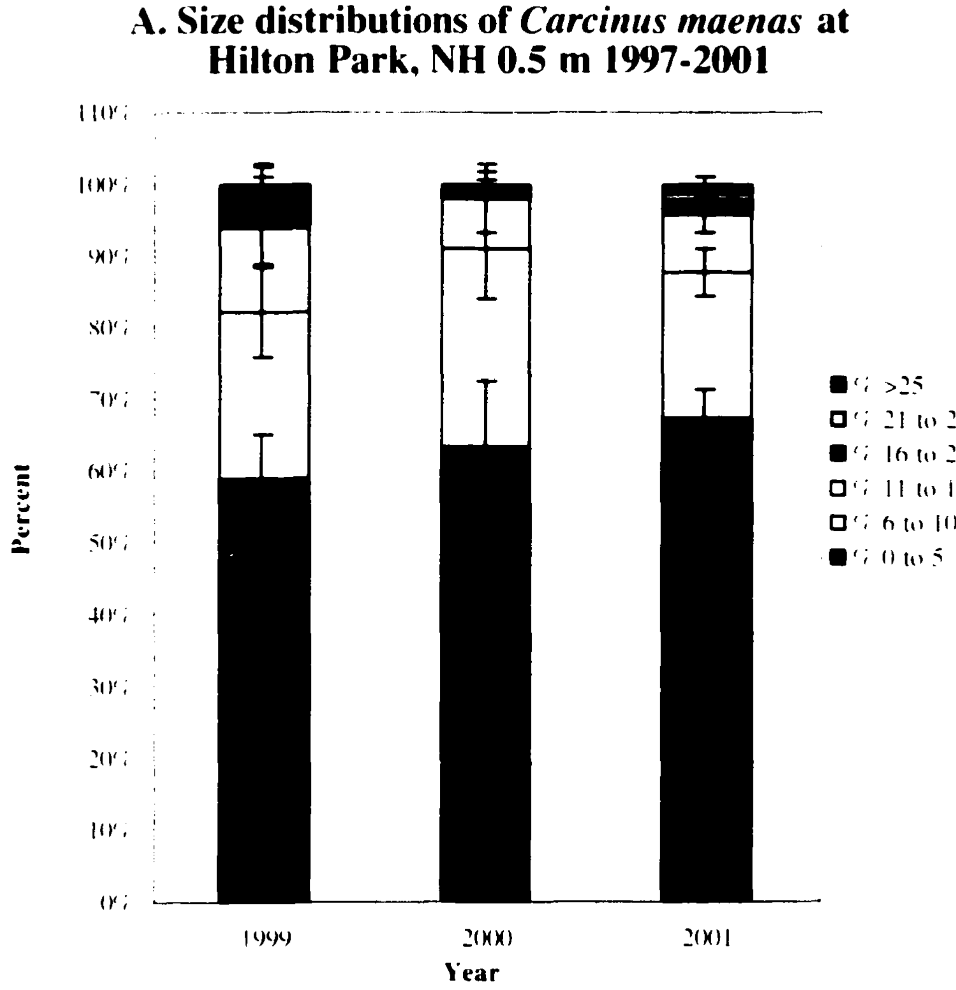


Figure 2.44 Average density/m^2 and standard error of *C. maenas* at Hilton Park, NH from 1999 - 2001.



A. Size distributions of *Carcinus maenas* at Hilton Park, NH 0.5 m 1997-2001

Figure 2.45a Average size distributions and standard error of *C. maenas* at 0.5 m above MLLW (mean lower low water) at Hilton Park, NH from 1997 - 2001.

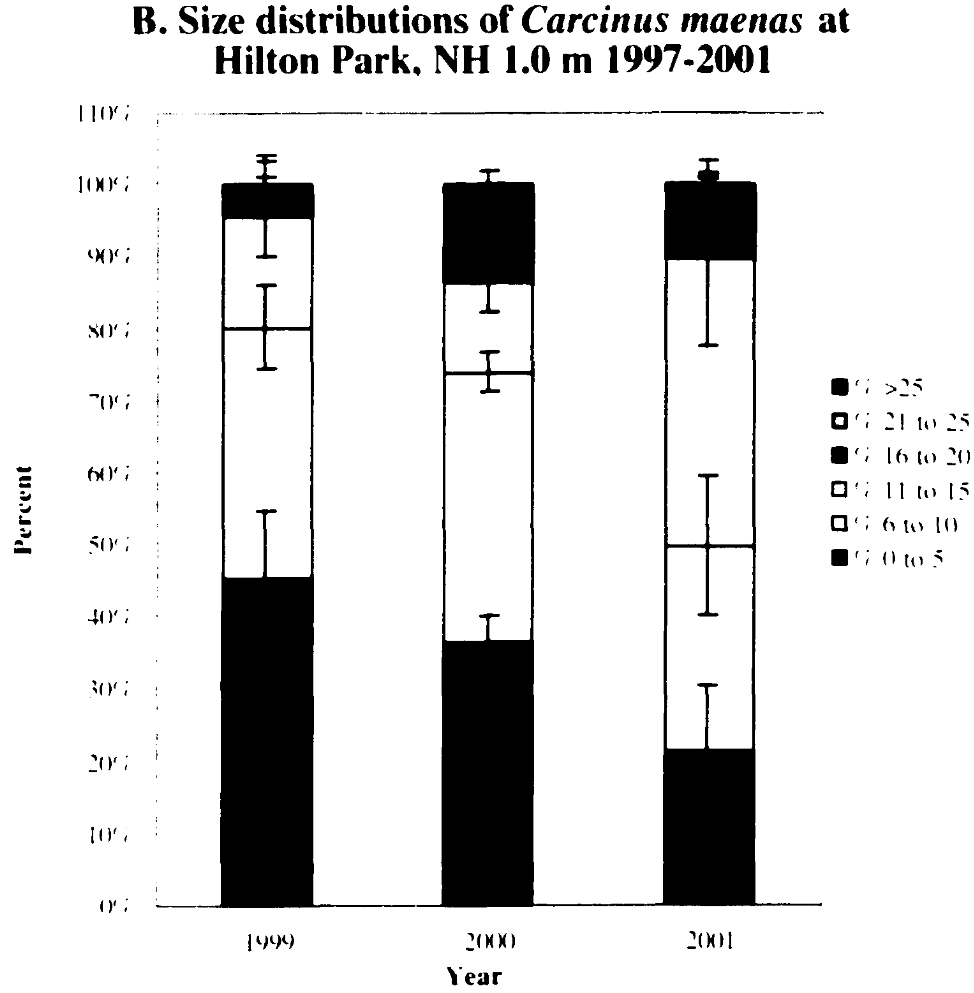

B. Size distributions of *Carcinus maenas* at Hilton Park, NH 1.0 m 1997-2001

Figure 2.45b Average size distributions and standard error of *C. maenas* at 1.0 m above MLLW (mean lower low water) at Hilton Park, NH from 1997 - 2001.

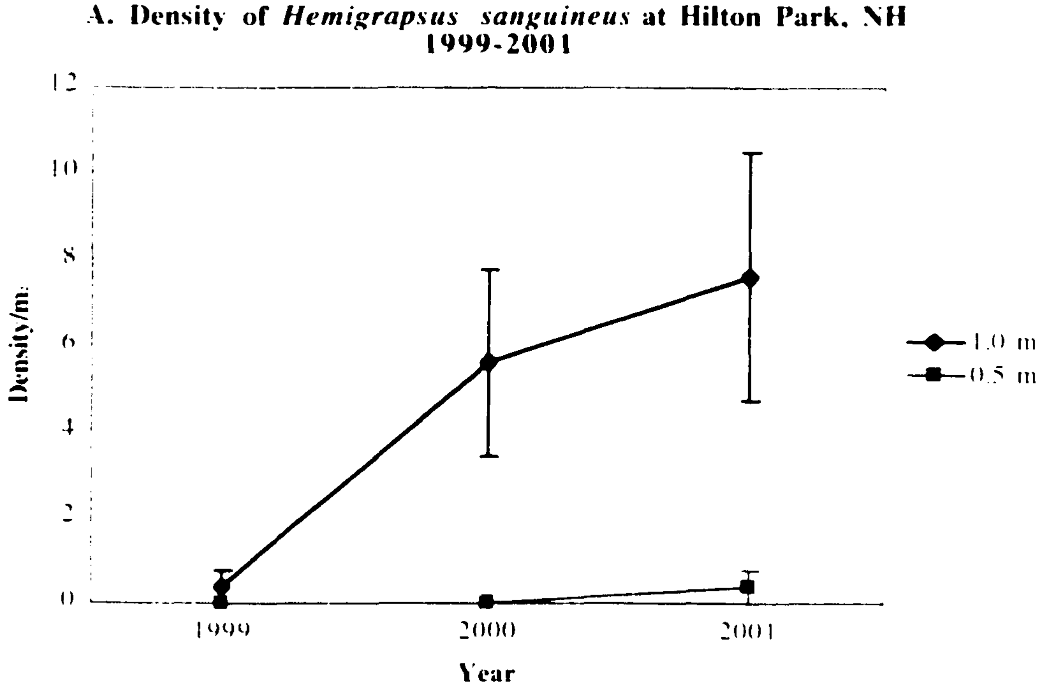


Figure 2.46a Average density/m^2 and standard error of *H. sanguineus* at Hilton Park, NH from 1999 - 2001.

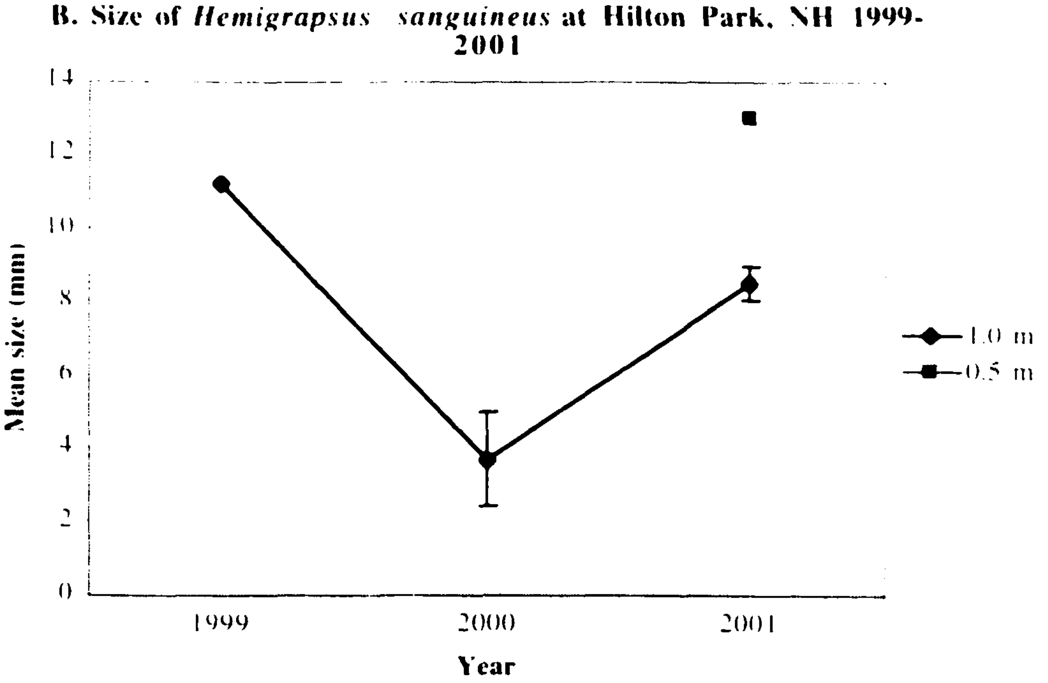
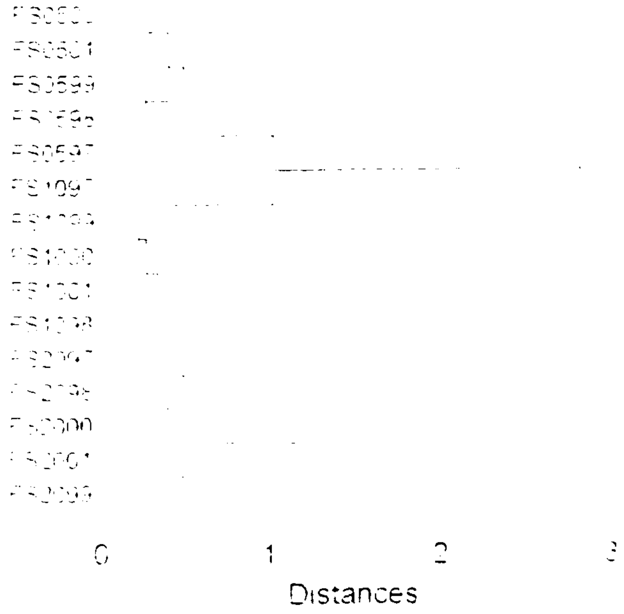


Figure 2.46b Average size and standard error of *H. sanguineus* at Hilton Park, NH from 1999 - 2001.

Figure 2.47a Cluster analysis depicting the relationships between tidal heights and sampling years at Ft. Stark. Each group is composed of the average value of 28 categories of abundance at each tidal height for each year. Codes for each group are as follows: the first two letters are for the site, the first two digits represent the tidal height and the last two digits represent the year the data were obtained.

Figure 2.47b Cluster analysis depicting the relationships between tidal heights and sampling years at Odiorne Park. Each group is composed of the average value of 28 categories of abundance at each tidal height for each year, except for the Odiorne 1997 groups. Subcanopy data was not taken in this year, therefore there are only 19 categories for 1997 data. Codes for each group are as follows: the first two letters are for the site, the first two digits represent the tidal height and the last two digits represent the year the data were obtained.

A. Ft. Stark



B. Odiorne Park

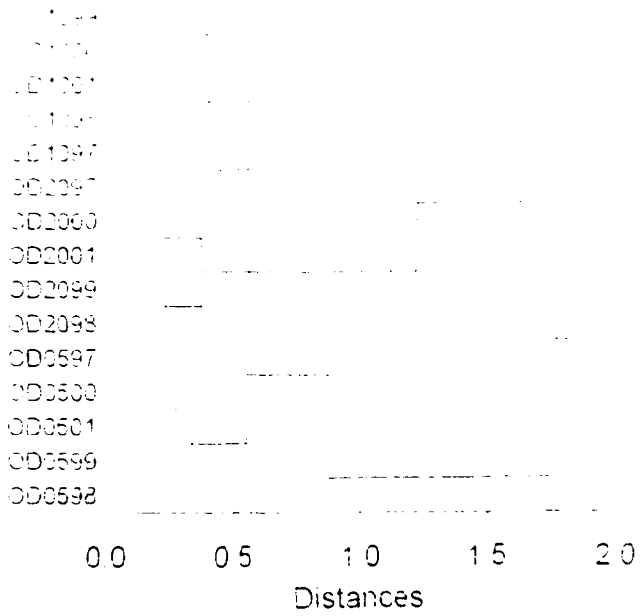


Figure 2.47c Cluster analysis depicting the relationships between tidal heights and sampling years at Hilton Park. Each group is composed of the average value of 28 categories of abundance at each tidal height for each year. Codes for each group are as follows: the first two letters are for the site, the first two digits represent the tidal height and the last two digits represent the year the data were obtained.

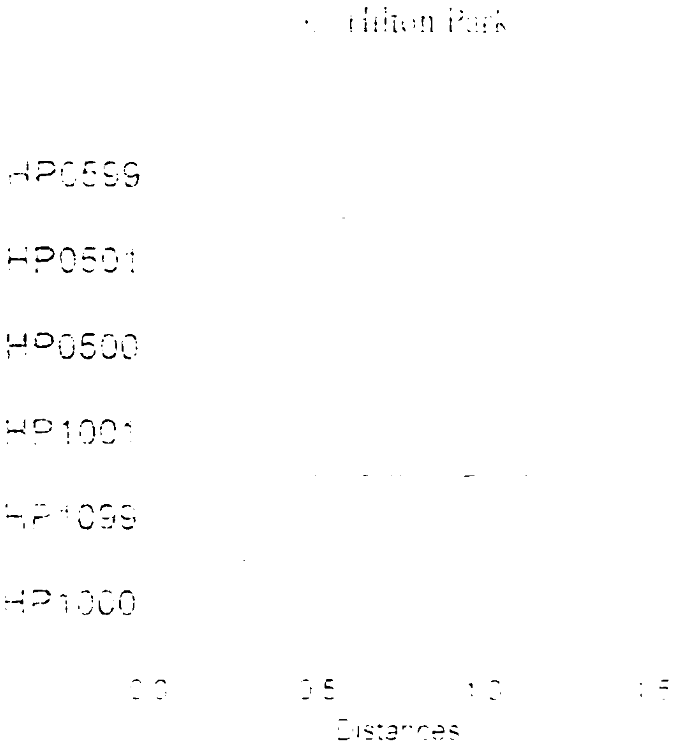

Hilton Park
HP0599
HP0501
HP0500
HP1001
HP1099
HP1000
0.0
0.5
1.0
1.5
Distances

Figure 2.48 Cluster analysis depicting the relationships between tidal heights and sampling years at all locations. Each group is composed of the average value of 28 categories of abundance at each tidal height for each year, except for the Odiorne 1997 groups. Subcanopy data was not taken in this year, therefore there are only 19 categories for Odiorne 1997 data. Codes for each group are as follows: the first two letters are for the site, the first two digits represent the tidal height and the last two digits represent the year the data were obtained.

All Locations

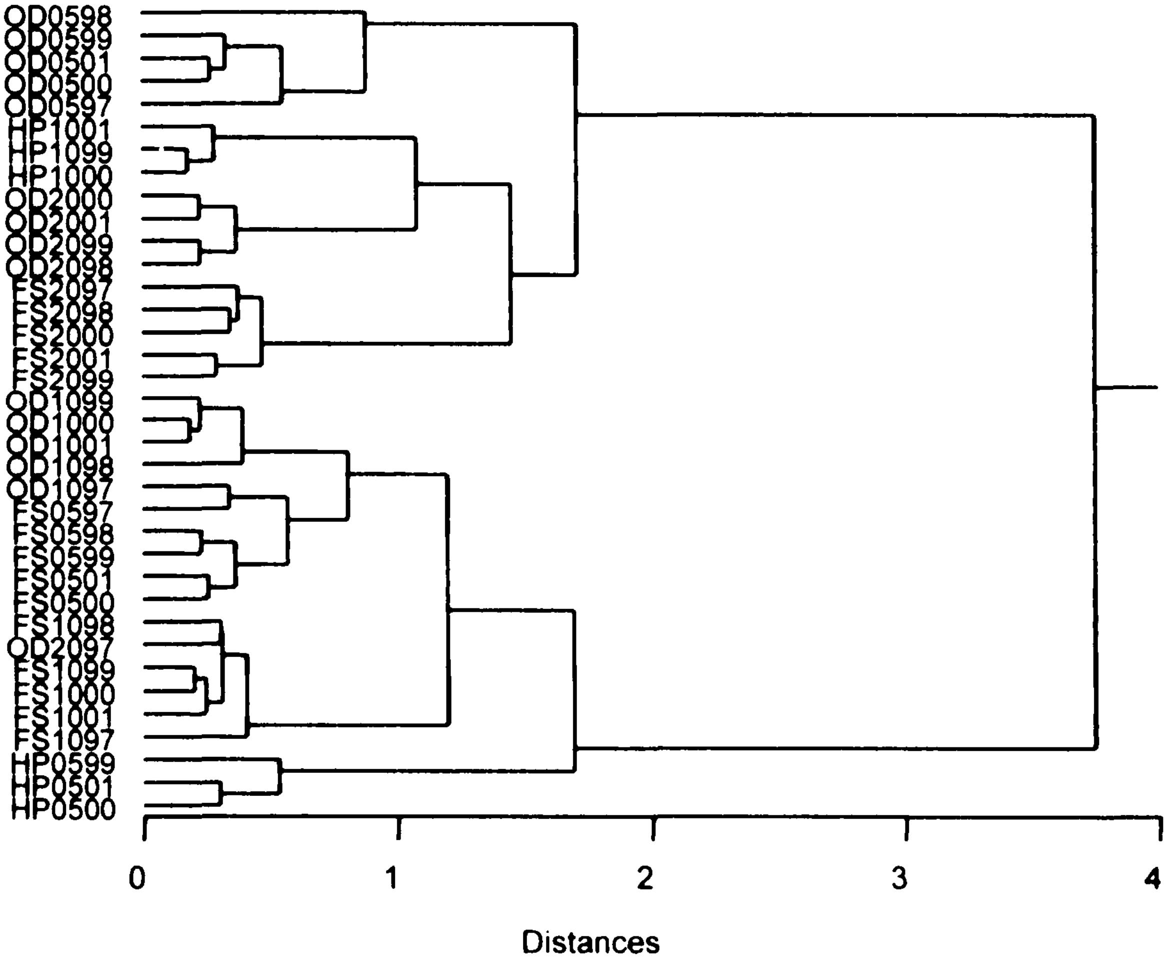


Figure 2.49a Nonmetric multidimensional scaling based on Bray-Curtis dissimilarity matrix of the relationships between tidal heights and sampling years at all locations. Each group is composed of the average value of 28 categories of abundance at each tidal height for each year, except for the Odiorne 1997 groups. Subcanopy data was not taken in this year, therefore there are only 19 categories for Odiorne 1997 data. Codes for each group are as follows: the first two letters are for the site, the first two digits represent the tidal height and the last two digits represent the year the data were obtained.

A. Multidimensional scaling

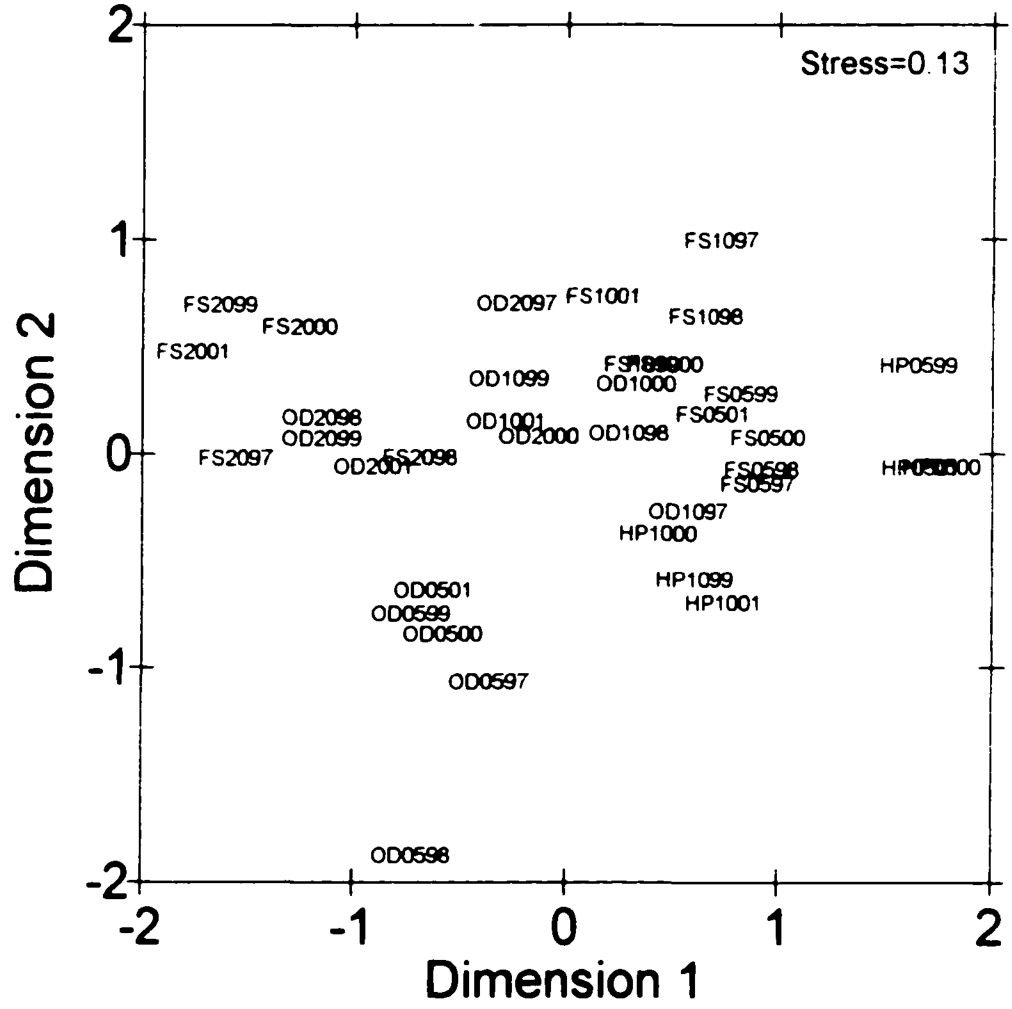
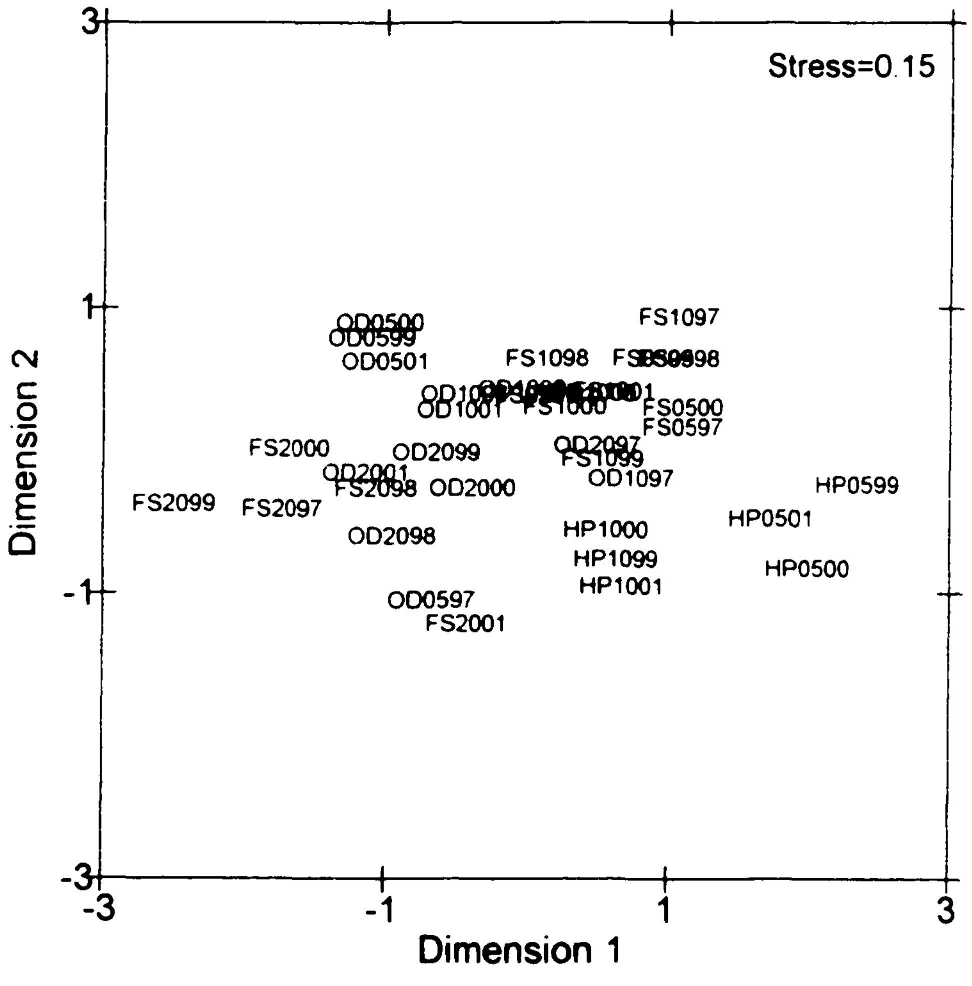


Figure 2.49b Nonmetric multidimensional scaling based on Bray-Curtis dissimilarity matrix of the relationships between tidal heights and sampling years at all locations except Odiorne 0.5 m tidal height in 1998. Each group is composed of the average value of 28 categories of abundance at each tidal height for each year, except for the Odiorne 1997 groups. Subcanopy data was not taken in this year, therefore there are only 19 categories for Odiorne 1997 data. Codes for each group are as follows: the first two letters are for the site, the first two digits represent the tidal height and the last two digits represent the year the data were obtained.



B. Multidimensional scaling

CHAPTER III

ABUNDANCE OF EPHEMERAL ALGAE IN UPPER INTERTIDAL POOLS PRIOR TO THE ESTABLISHMENT OF *Hemigrapsus sanguineus*

ABSTRACT

When herbivore densities are low, upper intertidal pools in rocky shores of northern New England are often dominated by short lived, palatable algae, such as *Enteromorpha* sp. In its native range in Asia, *Hemigrapsus sanguineus* is an omnivorous crab that occupies the mid to upper zone of rocky shores. Populations of this species are just beginning to become apparent in northern New England. This crab species readily consumes algae and prefers *Enteromorpha* sp. to four perennial algal species in lab feeding trials. The range expansion and population growth of this introduced crab in northern New England could lead to a decline in the abundance of ephemeral algae in upper intertidal pools. In this study, surveys of ephemeral algal cover in the upper intertidal zone of four New Hampshire locations were conducted twice a year for five years at the three coastal sites and for three years at the estuarine site. Relative homogeneity among substrates and overall percent cover of annual algae was observed among the four sampling locations. There was high availability of large rocks, cobble and pebbles in the pools; these substrates provide good shelter for crabs. The overall

average abundance of all ephemeral algal species varied from 89.4% to 14.6% in spring and 81.4% to 13.9% in fall at the coastal locations. At Hilton Park, an estuarine tidal rapids, the overall abundance of all annual algae varied from 32% to 19.5% in spring and from 15.5% to 4% in fall. Although there were some significant differences in the abundance of ephemeral algae within a pool between years, for the most part the overall temporal variation within the pools was low. These baseline data will provide pre-invasion variability in cover of *Enteromorpha* sp. and other annual algae species that can be used to compare post-invasion percent cover of these palatable algal species.

INTRODUCTION

Biological invasions are gaining attention in the scientific community and among the general public because of the dramatic ecological and economic impact that sometimes follows an invasion. Recent introductions, such as those of zebra mussels (*Dressina polymorpha*) and purple loosestrife (*Lythrum salicaria*) have caused drastic changes in communities where these organisms have successfully invaded (Vitousek et al. 1996). Clearing pipes clogged by zebra mussels is estimated to cost millions of dollars each year (Enserink, 1999) and an introduced "superbug" (*Bemisia tabaci*) was projected to cause $200 million worth of damage to crops in California's Imperial Valley (Culotta, 1991). The New England rocky intertidal zone has been influenced by many introduced species, including the common periwinkle, *Littorina littorea*, and the European green crab, *Carcinus maenas*. *Littorina littorea* is now the most common intertidal snail in New England, but was introduced less than 160 years ago (Bertness, 1999). In 1998, another introduced crab species, *Hemigrapsus sanguineus*, joined *C. maenas* and *L. littorea* in the northern New England rocky intertidal zone.

The effects of an invasion by *H. sanguineus* are beginning to be addressed by marine ecologists in the mid-Atlantic and southeastern New England (e.g. Lohrer and Whitlach, 1997; Gerard et al., 1999; Lesdesma and O'Connor, 2001) but in northern New England (north of Cape Cod, MA), this species is just beginning to become established. The first *H. sanguineus* for New Hampshire was found in North Hampton, NH in 1998 (McDermott, 2001). Since that time, I have found it at Ft. Stark in Newcastle, NH, Odiorne Park in Rye, NH and Hilton Park in Dover Point, NH (my major study sites: Chapter II) and at various other locations in New Hampshire and Maine. Based on its invasion history, it is likely that the abundance of this crab will continue to expand, and it may soon become a conspicuous member of the northern New England intertidal community.

Quantification of the impacts of marine introductions is extremely valuable (Grosholz and Ruiz, 1996) but unfortunately the opportunity to do so is limited because the location and timing of species invasions are often unpredictable. This study was unusual because the invasion of *H. sanguineus* in northern New England was anticipated and a concentrated effort was made to gather data on the community prior to its establishment. Accidental introductions of non-native species in marine systems are regrettable and inevitable, but they offer the opportunity to assess changes in interspecific interactions that may occur following the addition of the invasive species. One of the quantifiable changes that may occur following an invasion by *H. sanguineus* may include reduced algal abundance due to increased herbivory.

Algal/herbivore interactions in the rocky intertidal zone are of great interest to ecologists. The abundance of grazers, specifically limpets and littorinids, may influence algal species composition, recolonization, and abundance in the upper intertidal zone (Lubchenco, 1978; Cubit, 1984; Dye, 1993). In New England tide pools the ephemeral alga, *Enteromorpha* sp. is a competitively superior species but is kept from dominating by the grazing of *L. littorea* (Lubchenco, 1978). However, on emergent surfaces in the mid intertidal zone, perennial algae are competitively dominant and snail grazing on ephemeral species actually reduces algal diversity (Lubchenco, 1978). Additionally, the presence of herbivores may limit the lower distributions of preferred ephemeral algae (*Enteromorpha compressa* and *Ulva lactuca*), even though these species are capable of withstanding more benign subtidal conditions (Einav et al., 1995). *Hemigrapsus sanguineus* was initially reported to be a primarily herbivorous crab (Depledge, 1984; McDermott, 1992), but evidence of an omnivorous diet was found through gut content examinations (Lohrer and Whitlatch, 1997; Tyrrell and Harris, 2001). Wolcott and O'Connor (1992) report that predation and cannibalism are common among crabs that are reported to be primarily herbivorous, this carnivory may serve to supplement a plant diet.

The objective of this study was to quantify the cover of ephemeral algae in the upper intertidal zone and to monitor its seasonal fluctuations prior to the predicted establishment of *H. sanguineus*. Lohrer and Whitlatch (1997) found lowest abundance of *H. sanguineus* in the upper intertidal zone during August and December in Long Island Sound and consequently, I conducted surveys in the spring and fall. The effects of herbivory in upper intertidal pools should be limited to the times of year when environmental conditions are relatively benign and herbivores are most active (during winter on the Pacific coast, Cubit, 1984). I did not conduct surveys during winter or summer because environmental conditions in the pools during these seasons are probably too harsh for crabs or other grazing herbivores.

Due to its already observed rapid range expansion, it is expected that *H. sanguineus* will continue to increase in abundance on northern New England rocky coasts within a few years. This pre-invasion data on cover of *Enteromorpha* sp. and other ephemeral algae will be valuable for comparisons of post-invasion cover of these highly palatable algal species.

MATERIALS and METHODS

Four sites in New Hampshire were monitored for this project: Ft. Stark and Newcastle Commons in Newcastle, NH and Odiorne State Park in Rye, NH and Hilton Park, in Dover Point, NH (Fig. 3.1). All sampling locations were relatively sheltered from wave action, and the presence of *Carcinus maenas* indicated that there was suitable habitat for crabs. Transects were selectively placed in areas with high cover of ephemeral algae in the upper intertidal zone. Some of the areas surveyed were a section of shore that had occasional depressions filled with water and others were tidal pools in rock bench substrates. At the Hilton Park site, the pools were in the mid to lower intertidal zone because there were no pools in the upper intertidal zone. In contrast to the coastal sites, Hilton Park has less rock bench substrate, a higher proportion of sand and a lower abundance of canopy fucoid algae. Three transects (6.7 to 18.4 m long) were located in different areas at each site. Surveys to monitor cover of ephemeral algae were conducted in the spring, April and May (one survey conducted on June 1), and fall, October and November (one survey conducted on September 22). Surveys were initiated in the fall of 1996 at the three coastal sites and the estuarine Hilton Park site was added in the spring of 1999. Fall 2001 was the final sampling period.

Five quadrats (0.25 m^2) were randomly distributed along each transect using a random numbers table to dictate quadrat placement. In addition, three quadrats were selectively placed in areas with high ephemeral algal cover. For both random and selective placement, identical methods were used to estimate percent cover. Cover type (algal species, substrate, diatom film, etc.) was determined at 25 evenly spaced intersections of monofilament line. Substrate underlying each quadrat (cobble, rock bench with cobble, etc.) was also recorded. Descriptive data, including the presence of grazing herbivores (*Littorina* spp.), drift algae, and *C. maenas* were noted in each quadrat.

Algae were identified to species when possible, with the exception of juvenile fucoids (*Fucus spiralis* and *Fucus vesiculosus*), which were recorded as fucoid. Questionable identifications were taken back to the laboratory for examination under dissecting and compound microscopes. Species identifications were made using Villalard-Bohnsack, (1995) and with the assistance of Drs. A. Mathieson and S. Chavanich. Drift algae were not identified to species because both its species composition and presence in the sampling locations was highly variable.

There were numerous algal species that occurred infrequently or in low abundance in the surveys; therefore, they were grouped into an ephemeral algae category. The majority of species that were placed in this category had annual life histories but some were perennials. The ephemeral algae category at Hilton Park consisted of: *Scytosiphon simplicissimus, Monostroma grevellei, Dumontia contorta* and *Ulva lactuca. Cladophora sericea, Scytosiphon simplicissimus, Polysiphonia lanosa, Ulva lactuca, Chaetomorpha* sp., and *Pseudendoclonium submaririum* comprised the ephemeral algae category at Newcastle Commons. At Odiorne, this category was made up of: *Ulva lactuca* and *Scytosiphon simplicissimus* and at Ft. Stark, *Cladophora sericea, Scytosiphon simplicissimus, Sphacelaria* sp. and *Polysiphonia lanosa* were included in the ephemeral algae category. Finally, a crustose algae category was created that was mostly composed of crustose coralline algae (e.g. *Phymatolithon* sp.) as well as *Ralfsia* sp.

Statistical analyses were performed using Systat version 10 (SAS Institute). Percent cover data were square root arcsine transformed prior to being subjected to analysis of variance (ANOVA). Post hoc comparisons were performed using Tukey's test. The overall differences in the abundance of *Enteromorpha* sp. and all annual species (the sum of *Enteromorpha* sp., diatoms and ephemeral algae) were compared between locations using ANOVA. ANOVA was used to compare the overall (regardless of season and year) abundance of *Enteromorpha* sp. between locations. An additional ANOVA was used to compare the overall abundance of all annual species (the sum of *Enteromorpha* sp., diatoms and ephemeral algae) between locations. The difference in the total abundance of annual species in each pool between seasons was also compared using ANOVA. Finally, the presence of littorinids in each pool during each season was compared with the (untransformed) percent cover of the ephemeral algae category using point-biserial correlations.

RESULTS

A total of 903 quadrats were analyzed for the surveys, of these 585 were randomly placed and used in cover analysis of *Enteromorpha* sp. and other ephemeral algae. Selectively placed quadrats were not included in statistical analyses and the results that are depicted graphically only include random quadrats.

Selectively placed quadrats

Selective placement of the quadrat in areas with high cover of *Enteromorpha* sp. resulted in an overall average percent cover of 30-36% at the three coastal sites. However, there was very little *Enteromorpha* sp. at Hilton Park, the estuarine site, and selective placement of the quadrat resulted in an overall average of 1.5 % cover of *Enteromorpha* sp. When all of the ephemeral algae, *Enteromorpha* sp. and diatoms were grouped, the overall average percent cover of all quadrats at Ft. Stark was 64%. At Odiorne and Newcastle Commons, this category encompassed 42 and 44% cover in all of the quadrats respectively. Finally, at Hilton Park, the majority of the ephemeral algae category was composed of *Ulva lactuca* and when this was combined with *Enteromorpha* sp. and diatoms, the average cover in all quadrats was 39%.

Random quadrats

When the abundance of all algae (both perennials and annuals) was compared, the overall abundance in spring was higher than in fall, although this result varied between locations (Fig 3.2a). Cover of *Enteromorpha* sp. varied inconsistently among sampling locations in spring and fall, but the overall percent cover of this species was slightly higher during the spring surveys (Figs. 3.4a- 3.6b; 3.8a- 3.10b; 3.12a- 3.13b; 3.17b and 3.18b). Cover of *Enteromorpha* sp. was not significantly different between the three coastal locations (Table 3.1a) indicating that the overall abundance of this species was similar between these sites. However, the abundance of *Enteromorpha* sp. was significantly different between the Hilton Park site and each of the three coastal locations (Table 3.1a).

Diatom film on rock substrate constituted a substantial part of the community at Fort Stark and Newcastle Commons (Figs. 3.4a and b, 3.5a and b and 3.8a and b). Diatom film may replace recently grazed *Enteromorpha* sp.; both types of flora were often found in close association. For example, small strands of the filamentous alga frequently were found among the diatom film and quadrats that had high cover of *Enteromorpha* sp. often had diatom film under the canopy. Because of this close association, diatom film was regarded as a potential food source and was placed in the annual algae category, along with *Enteromorpha* sp. in Figs. 3.3a and b, 3.7a and b, 3.11a and b and 3.15 a and b. In all of the other figures, diatoms and *Enteromorpha* sp. were listed separately from ephemeral algae to illustrate their importance within the pools.

The vast majority of the algae that made up the ephemeral algae category in this study were reported to be highly palatable to *Littorina littorea* by Lubchenco (1978). Lubchenco reported that *Enteromorpha* sp. was highly preferred by *L. littorea* in laboratory preference trails and Tyrrell and Harris (2001) also found that *H. sanguineus* preferred *Enteromorpha intestinalis* to four perennial algal species. Because the majority of species in the ephemeral algae category were highly palatable and because I judged that it was unlikely that *H. sanguineus* would discriminate between many of these species. I grouped the ephemeral algae category with *Enteromorpha* sp. and diatoms (the annual algae category) to determine the total abundance of palatable species in each pool (Figs. 3.3a and b; 3.7a and b; 3.11a and b; 3.15a and b). The one apparent disparity between Lubchenco's results for *L. littorea* feeding preferences and my observations of *H. sanguineus* was with *Chaetomorpha* sp.. Lubchenco (1978) reported that *Chaetomorpha* spp. were a low preference food item for *L. littorea* while my personal observations indicated *Chaetomorpha* sp. are readily consumed by *H. sanguineus*. Methodological problems with Lubchenco's preference experiment may contribute to the discrepancy; she only had one or two replicates. *Chorda filum* and *Desmarestia viridis* were both encountered at Odiorne Park and both of these species were listed as low preference by Lubchenco (1978). I have not observed *H. sanguineus* feeding on either of these species and therefore I did not include them in the ephemeral algae category. Only one point with *D. viridis* underneath it was recorded at Odiorne, while *C. filum* composed 11% cover of pool 3 at Odiorne Park in spring of 1997.

When the abundance of all annual algae (*Enteromorpha* sp., diatoms and the ephemeral algae category) was compared between the sampling locations, Ft. Stark was significantly different from all other sites, and Newcastle Commons and Hilton Park were also significantly different from each other (Table 3.1b). The total abundance in the annual algae category was higher in the spring (Fig. 3.2b) at all locations except Odiorne, and annual algae was more abundant in the spring overall. At Odiorne, ephemeral algae other than *Enteromorpha* sp. were only present in the spring (Fig. 3.12b and 3.14b). The overall average abundance of all annual algal species varied from 89.4% to 14.6% in spring and 81.4% to 13.9% in fall at the coastal locations. At Hilton Park, the estuarine tidal rapids, the overall abundance of all annual species varied from 15.5% to 4% in fall and from 32% to 19.5% in spring. ANOVA was used to compare the percent cover of the annual species in each pool between years. Separate analyses were performed for each pool and for fall and spring surveys. Results are listed in Table 3.2. Although there were some significant differences in the abundance of all annual species within a pool between years (particularly in pool two at Odiorne), the overall temporal variation within each pool was relatively low.

Substrate type affects both the percent cover of algae and the amount of refuge for crabs, therefore the presence of large rocks, cobble, pebble/shell hash was noted in each quadrat. All of the quadrats at Hilton Park had large rock, cobble or pebble/shell hash substrates. Newcastle Commons had the next highest proportion of quadrats that had good substrates for crabs: over 85% of the quadrats had at least one of these three types of substrates in them. Odiorne Park ranked third in its proportion of quadrats with good crab refuge: 77% of the quadrats had large rocks, cobble or pebble/shell substrates. Ft. Stark had the least amount of substrates that provide refuge for crabs, only 63% of the quadrats had either large rocks, cobble or pebble/shell hash substrates. *Carcinus maenas* were only rarely spotted within the quadrats: a total of eight crabs were observed among the 585 random quadrats. It is unlikely that this data accurately reflects the abundance of crabs, because both the algal canopy and the non-rock bench substrates could have easily obscured crabs from view. However, the fact that *C. maenas* were found within these high intertidal pools indicates that other crab species, such as *H. sanguineus*, are also likely to be able to tolerate the conditions within the pools.

Littorinids consume ephemeral algae and may compete with *Hemigrapsus sanguineus* for food. The majority of Littorinids in the pools were *L. littorea*, and some *L. saxatilis*, were also observed. Littorinids were present in 36% of the random quadrats at Ft. Stark, in 61% at Newcastle Commons, and in 56% of the random quadrats at Odiorne. In contrast, only 2% of the randomly placed quadrats at Hilton Park did not have littorinids present in them. No other herbivores (i.e. *Notoacmea testudinalis*) were observed. None of the point biserial correlations indicated that there was a significant correlation between cover of annual algae and the presence of Littorinids (data not shown).

DISCUSSION

All three coastal locations, and the pools nested within them, were deliberately chosen for these surveys because they initially had high cover of *Enteromorpha* sp.. The Hilton Park estuarine site was added three years after the coastal surveys began, when it became apparent that *H. sanguineus* could also readily colonize estuaries. Aside from their location in an estuarine tidal rapids, the pools at Hilton Park differed substantially from the coastal pools because they were lower in the intertidal zone and had little cover by *Enteromorpha* sp. The location of the pools in the low, rather than high zone at Hilton Park, probably contributes greatly to the differences in algal composition between these pools and that of the pools at the coastal sites. Interestingly, the highest density of *H. sanguineus* was also found at Hilton Park (Chapter II), although their densities are still very low overall. Large differences in the algal composition between the estuarine site and the coastal sites prohibits using the Hilton Park pools as references for the coastal pools. However, it is likely that pools in the lower intertidal zone at the coastal sites also lack *Enteromorpha* sp. because of the very high densities of herbivores, especially *L. littorea* (Chapter II).

The focus of this project was to monitor variation in cover by *Enteromorpha* sp. and other ephemeral algal species prior to the predicted establishment of *H. sanguineus*. Laboratory feeding preference studies have shown that in multichoice feeding trials *H. sanguineus* significantly prefers *Enteromorpha* sp. to three fucoids (*Ascophyllum nodosum*, *F. vesiculosus* and *F. spiralis*) and *Mastocarpus stellatus* (Tyrrell and Harris, 2001). Drift algae were common in the stomachs of *H. sanguineus* collected from

Quissett, MA (41°32'N, 70°39'W) (Tyrrell, 1999; Tyrrell and Harris, 2001) indicating that drift algae could also be an important food item for *H. sanguineus* in northern New England. However, because the abundance of drift algae is highly variable (both temporally and by specific locations), a potential decline following the establishment of *H. sanguineus* may be difficult to detect.

As previously stated, the location of each transect was dictated by presence of ephemeral algae and suitability as habitat for crabs (i.e. exposed sites were avoided). The relative homogeneity among sites for substrate and cover types is probably due to the fact that each site had an entire transect or part of a transect that encompassed a cobble field. It was surprising that *Enteromorpha* sp. was attached both to cobble and to rock benches in pools; many species of algae are not so flexible in the kinds of substrate that they can colonize. However, *Enteromorpha* sp. are opportunistic and can quickly colonize open space and occupy a variety of substrate types (Lubchenco, 1978). Ephemeral green algae in general are very tolerant to a wide range of environmental conditions, including fluctuations in temperature and salinity as well as desiccation stress (Einav et al., 1995). Dominance by ephemeral algae can be indicative of a frequently disturbed habitat or of the absence of herbivores (Lubchenco, 1978; Sousa, 1980). There was a combination of these conditions at all sampling locations. Although none of the sites were in locations that were likely to have high exposure to wave action, when storm swells occur, the cobble could shift and create unsuitable conditions both for long lived algae and slow moving herbivores. In addition to providing substrate for ephemeral algae, cobble and pebbles provide refuge for crabs. In quantitative community analyses, Tyrrell (1999) found that 51% of the variation in *C. maenas* density at Ft. Stark was explained by the amount of substrate that was classified as large rock, cobble or pebble/shell. *Hemigrapsus sanguineus* may flourish in these upper intertidal pools that support both a rich growth of annual algal species and that provide refuges.

The indirect effect of crabs in maintaining a canopy of ephemeral algae (*Enteromorpha intestinalis*) has been documented for the New England rocky intertidal zone (Lubchenco, 1978). She reports that juvenile *Carcinus maenas* utilize dense stands of *Enteromorpha* sp. as protection from gull predation and they maintain the canopy by consuming juvenile *Littorina littorea* as they recuit in from the plankton (they will not eat medium or large *L. littorea*) (Lubchenco, 1978). The presence of *C. maenas* therefore facilitates the existence of the highly palatable *Enteromorpha* sp. in tidal pools. In contrast, *H. sanguineus* (which may have a slightly more herbivorous diet than *C. maenas*; Lohrer and Whitlatch, 1997; Tyrrell, 1999, but see Chapter IV and V) may consume *Enteromorpha* sp. and other ephemeral algae rather than *L littorea*. In addition, adult *H. sanguineus* may consume the juvenile *C. maenas* (Lohrer, 2000 and pers. obs.) that seek refuge in these tidepools, exacerbating the decline in cover of ephemeral algae. It is unclear whether *H. sanguineus* will consume juvenile *L. littorea*, laboratory preference tests indicate that this species is lowest on the preference hierarchy for both *C. maenas* and *H. sanguineus* (Tyrrell and Harris, 2001), although *C. maenas* have been reported to readily consume small *L. littorea* in the lab (Lubchenco, 1978). The establishment of *H. sanguineus* could have a large impact on algae in upper tide pools both because *H. sanguineus* readily consumes algae, but also because *H. sanguineus* may consume both juvenile *L. littorea* or *C. maenas*.

The lack of significant correlations between the cover of annual algae and Littorinids is likely due to the coarse nature of presence/absence data. The objective of these surveys was to obtain baseline data on the temporal fluctuations in annual algae and quantifying the density of Littorinids or other herbivores (amphipods, isopods, etc) would have vastly increased the amount of time that each survey required. It is possible that the presence of an algal canopy may indicate that snails have not had time (or are not in high enough density) to suppress rapidly growing algae.

As previously stated, temporal variability in cover of ephemeral algae was relatively low at the study sites, potentially facilitating detection of changes due to establishment of *H. sanguineus*. It is expected that *H. sanguineus* would be most active during spring and fall in the upper intertidal zone (when environmental conditions are more benign) and could noticeably suppress the abundance of ephemeral algae. Environmental conditions in the upper intertidal zone during summer and winter are likely to limit herbivore activity. Mortality of limpets in the upper intertidal zone due to desiccation stress was highest during the summer in Oregon (Cubit, 1984). Freezing temperatures and frequent storms are also likely to limit consumers in the upper intertidal zone during the winter in New England.

Hemigrapsus sanguineus' chelae are particularly well suited to scrape algae off of rocks (Depledge, 1984) and it is likely that they will readily consume diatom film. Fucoid algae are also readily consumed by *H. sanguineus* (although they are lower on the preference hierarchy than *Enteromorpha intestinalis*; Tyrrell, 1999) but they collectively constitute a relatively minor part of the community in upper intertidal pools (Figs. 3.4a – 3.6b; 3.9a –3.10b; 3.12a –3.14b; 3.16a – 3.18b). Lubchenco (1978) found that high densities of *L. littorea* in upper intertidal pools favored *Chondrus crispus* because this species is very low in their preference hierarchy. Although *H. sanguineus*' preferences are similar it is likely these crabs could cause a decline in even unpalatable algae such as *C. crispus* (pers. obs.) through their comparatively high per capita feeding rate. If *H. sanguineus* is able to utilize all of the algae in these pools as predicted, these pools may be able to support high densities of this gregarious crab because of the availability of both food and shelter.

The sites sampled in this study should continue to be monitored to determine if there are declines in the abundance of ephemeral algae following the establishment of *H. sanguineus*. It is necessary to have baseline data on the natural temporal variation of ephemeral algal cover in order to make any conclusions about the effect of an additional consumer on algal abundance. One method to assess the impact of an introduced species would be through the use of a Before-After-Control-Impact (BACI) design that was developed by Stewart-Oaten et al. (1986). The sampling protocol of these surveys were designed so that they fit the requirements of the BACI design as closely as possible (e.g. high number of pools, sampling effort focused on assessing the abundance of a particular group of species, long time series of sampling prior to the proposed impact). However, the BACI design was aimed at assessing temporally predictable impacts (e.g. effluents from power plants) and the establishment of an introduced species at a particular location is a highly unpredictable process in comparison. The best solution to the problem of assessing the impacts of an introduced species is to combine monitoring efforts (this study, Chapter II) with manipulative experiments conducted both under controlled (lab) and natural conditions.

In conclusion, it appears from these spring and fall surveys that these pools predictably harbor ephemeral algae that could be a reliable food source for *H. sanguineus*. The potential impact of *H. sanguineus* on rocky shores will not be limited to these upper intertidal pools. However, because of *H. sanguineus*' preference for *Enteromorpha intestinalis*, their ability to reach high densities (70/m^2, Lohrer, 2000), and their high feeding rate (Chapters IV and V), it is possible that the abundance of palatable algal species may decline in these upper intertidal pools following the establishment of this introduced crab.

Table 3.1a: ANOVA and Tukey's post hoc comparison of the abundance (square root, arc sine transformed) of *Enteromorpha* sp. between sampling locations. Values in bold indicate statistical significance (p<0.05).

***Enteromorpha* sp.**	Overall model	p=**0.000**	
	Ft. Stark	Newcastle Commons	Odiorne
Newcastle Commons	0.654		
Odiorne	0.998	0.752	
Hilton Park	**p=0.000**	**p=0.000**	**p=0.000**

Table 3.1b: ANOVA and Tukey's post hoc comparison of the abundance (square root, arc sine transformed) of all annual algae between sampling locations. Values in bold indicate statistical significance (p<0.05).

All annual algae	Overall model	p=**0.000**	
	Ft. Stark	Newcastle Commons	Odiorne
Newcastle Commons	**p=0.000**		
Odiorne	**p=0.000**	0.265	
Hilton Park	**p=0.000**	**p=0.000**	0.065

Table 3.2: ANOVA and Tukey's post hoc comparison of the abundance (square root, arc sine transformed) of all annual algal species between years at all four locations. Values in bold indicate statistical significance (p<0.05).

Location	Pool	**Fall**	post hoc	**Spring**	post hoc
Ft. Stark	1	p=0.292		**p=0.047**	all p> 0.05
	2	**p=0.033**	1996 vs. 1997, **p=0.053**	p=0.272	
	3	**p=0.029**	all p> 0.05	p=0.293	
Newcastle Commons	1	**p=0.009**	1997 vs. 1999, **p=0.042** 1997 vs. 2000, **p=0.012**	p=0.426	
	2	p=0.359		p=0.678	
	3	**p=0.001**	1996 vs. 1997, **p=0.015** 1996 vs. 2000, **p=0.000** 1996 vs. 2001, **p=0.025**	p=0.222	
Odiorne	1	p=0.656		**p=0.025**	1997 vs. 1998, **p=0.041**
	2	p=0.094		**p=0.000**	1997 vs. 1998, **p=0.018** 1997 vs. 1999, **p=0.001** 1997 vs. 2000, **p=0.037** 1998 vs. 2001, **p=0.015** 1999 vs. 2001, **p=0.001** 2000 vs. 2001, **p=0.031**
	3	**p=0.001**	1996 vs. 2001, **p=0.049** 1998 vs. 1999, **p=0.005** 1998 vs. 2000, **p=0.021** 1998 vs. 2001, **p=0.004**	p=0.660	
Hilton Park	1	p=0.065		p=0.116	
	2	p=0.111		**p=0.016**	1999 vs. 2001, **p=0.016**
	3	p=0.261		p=0.245	

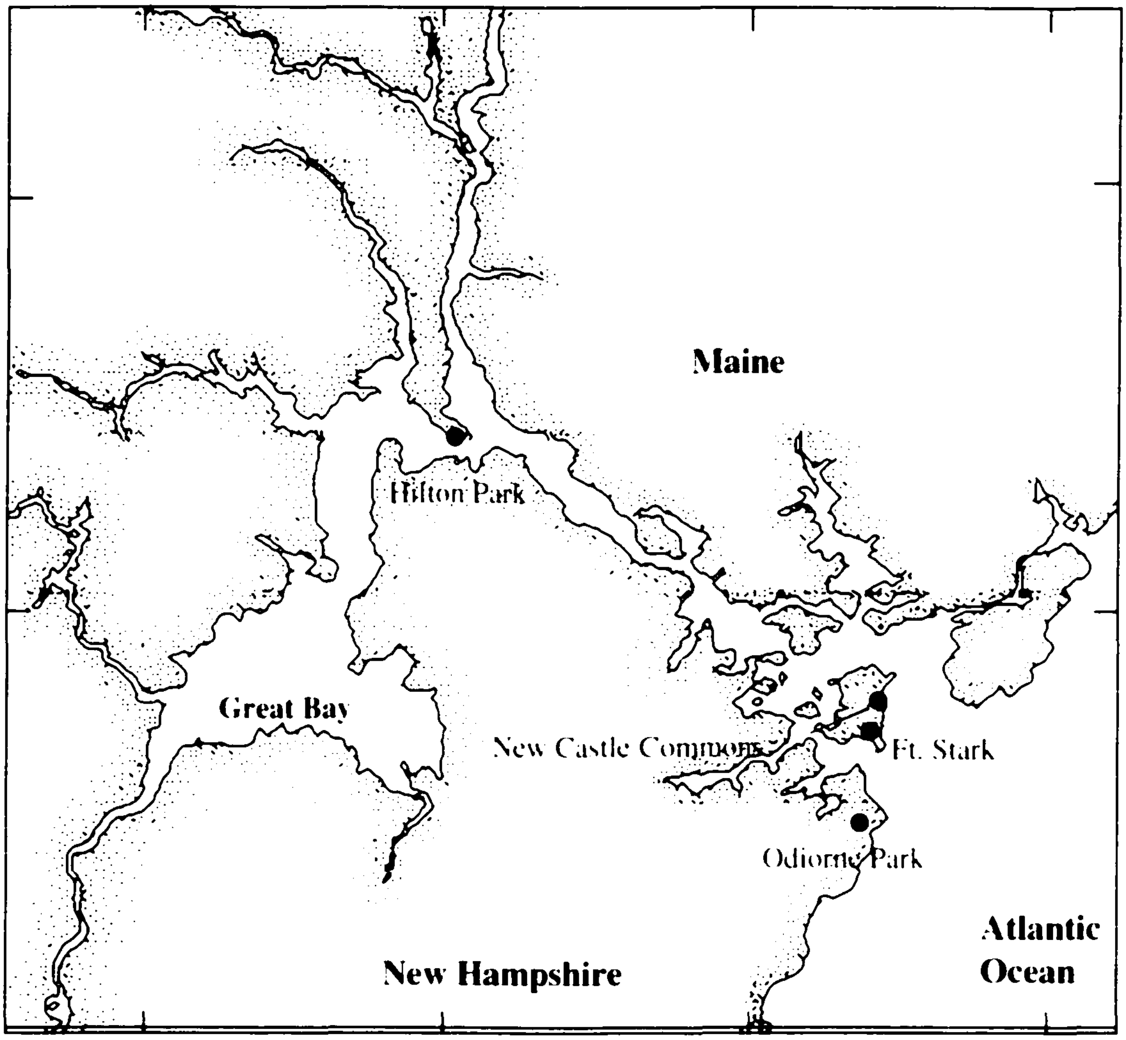


Figure 3.1: Map of sampling locations for algal surveys: Ft. Stark and Newcastle Commons are located in Newcastle, NH. Odiorne State Park is located in Rye, NH and Hilton Park is located in Dover Point, NH.

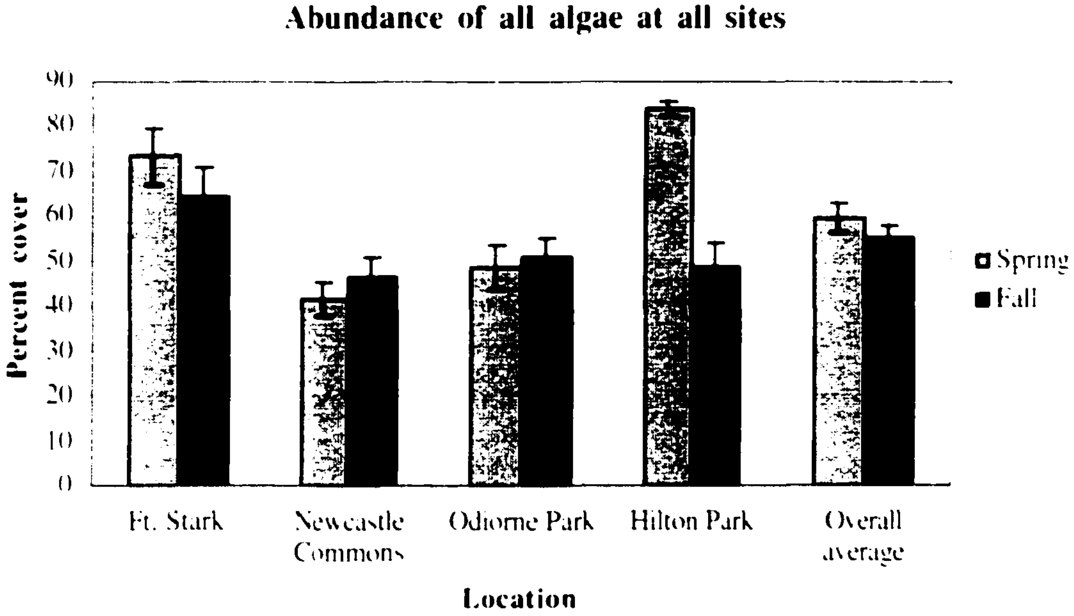


Figure 3.2a: Average percent cover and standard error of all algal species (perennial and annual) in upper intertidal pools at four New Hampshire locations between fall and spring, 1996 to 2001 (Hilton Park 1999 to 2001).

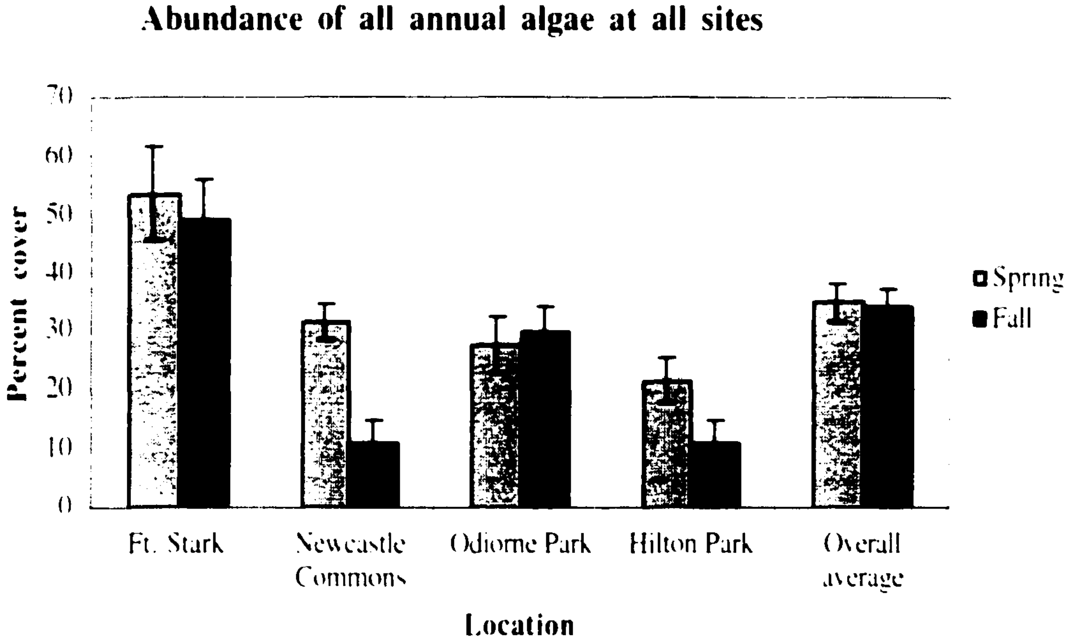


Figure 3.2b: Average percent cover and standard error of all algae in the annual algae category at all four New Hampshire locations between fall and spring 1996 to 2001 (Hilton Park 1999 to 2001).

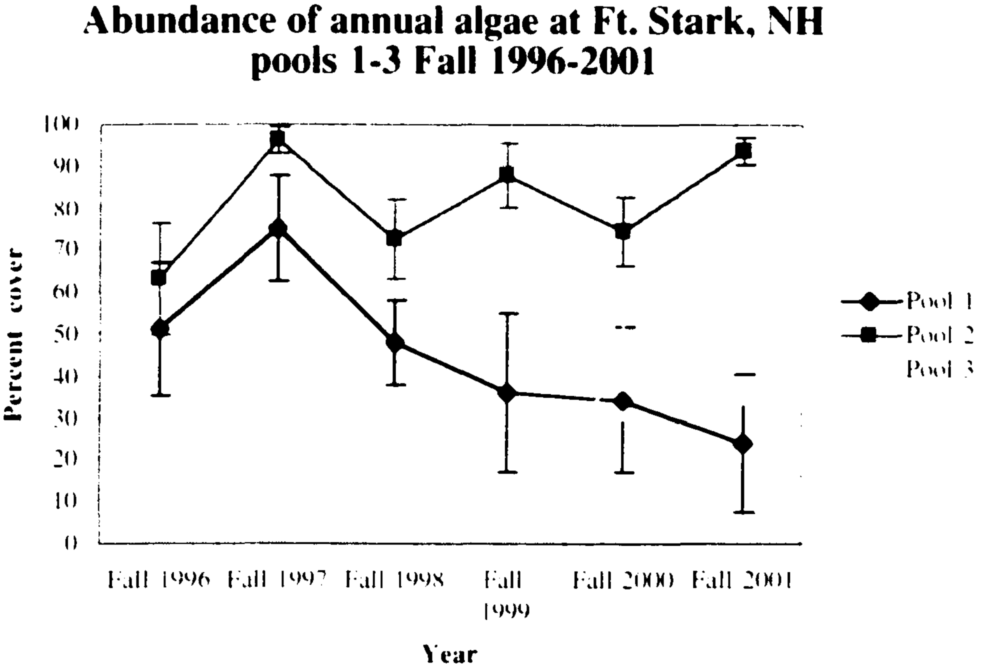


Figure 3.3a: Temporal variation in average percent cover (and standard error) of the annual algae category in all three pools at Ft. Stark, NH from Fall 1996 to Fall 2001.

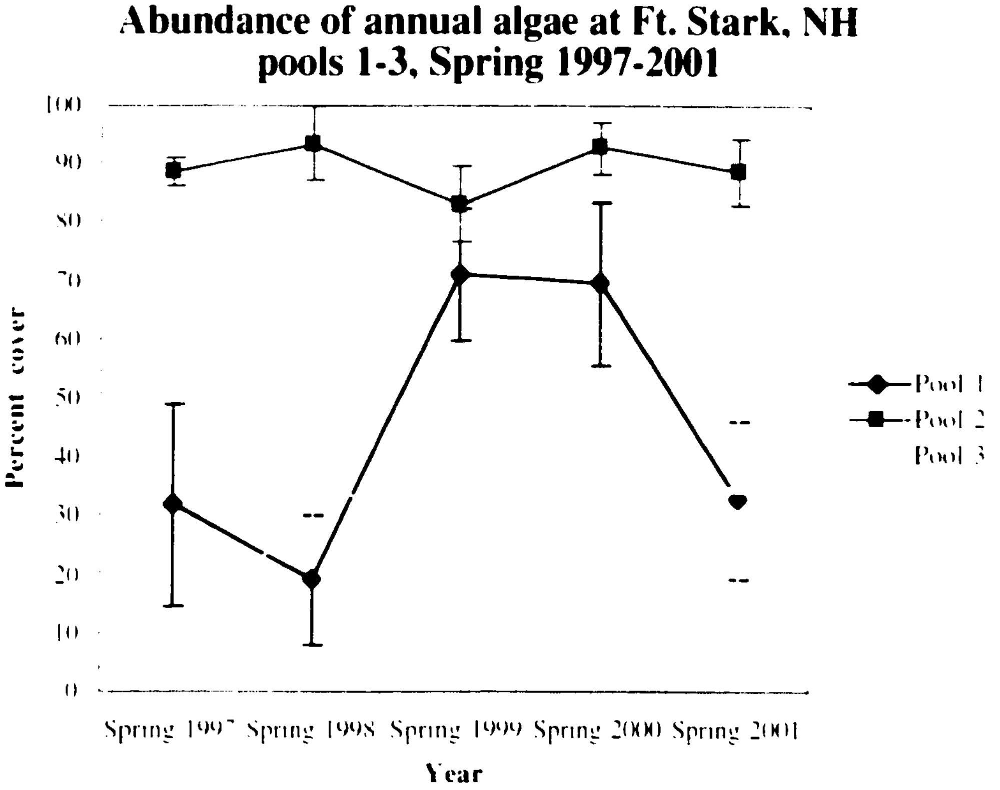


Figure 3.3b: Temporal variation in average percent cover (and standard error) of the annual algae category in all three pools at Ft. Stark, NH from Spring 1997 to Spring 2001.

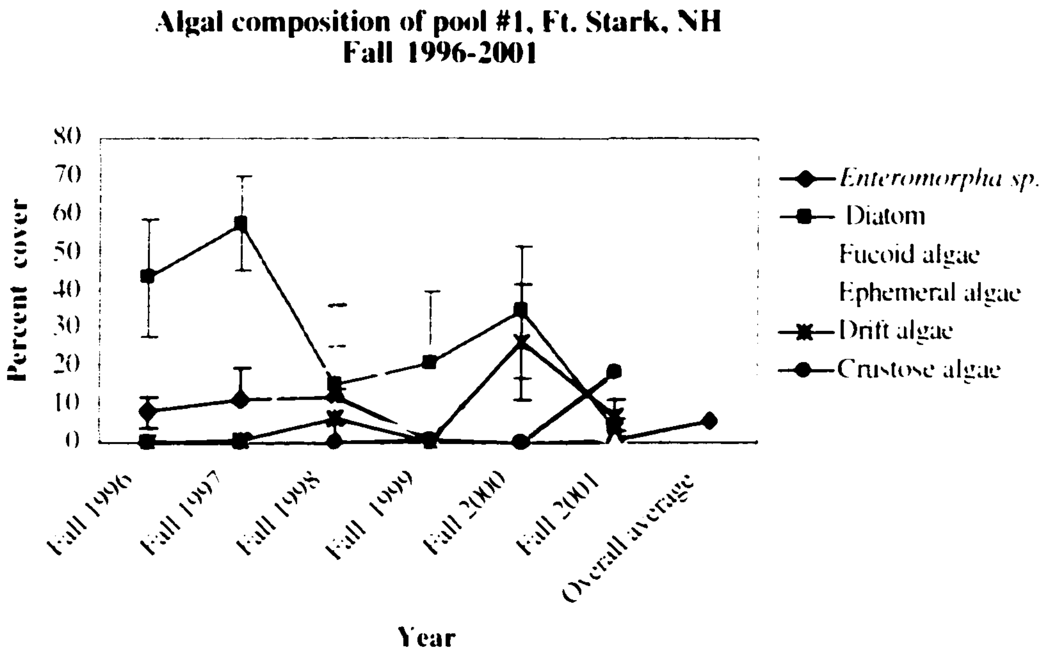


Figure 3.4a: Temporal variation in average percent cover (and standard error) of various groups of algae in an upper intertidal pool at Ft. Stark, NH from Fall 1996 to Fall 2001. The overall mean percent cover of *Enteromorpha* sp. in fall is also shown.

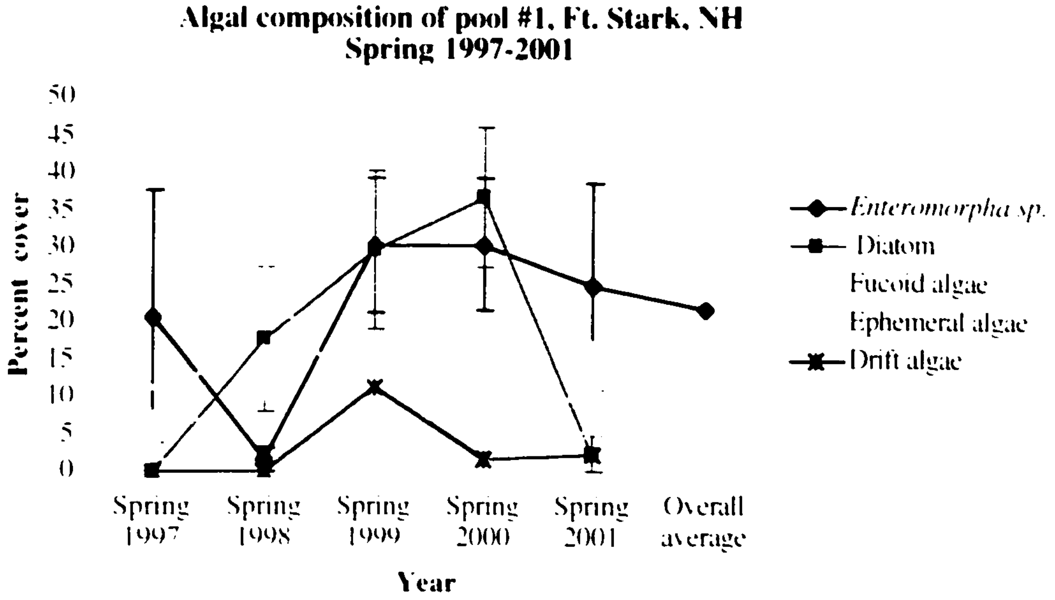


Figure 3.4b: Temporal variation in average percent cover (and standard error) of various groups of algae in an upper intertidal pool at Ft. Stark, NH from Spring 1997 to Spring 2001. The overall mean percent cover of *Enteromorpha* sp. in spring is also shown.

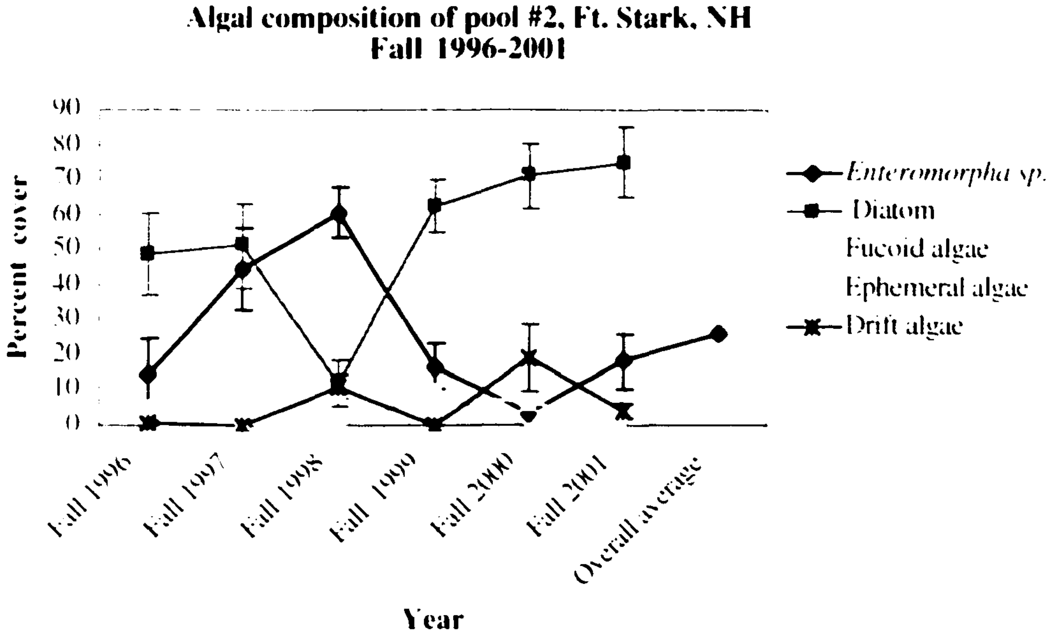


Figure 3.5a: Temporal variation in average percent cover (and standard error) of various groups of algae in an upper intertidal pool at Ft. Stark, NH from Fall 1996 to Fall 2001. The overall mean percent cover of *Enteromorpha* sp. in fall is also shown.

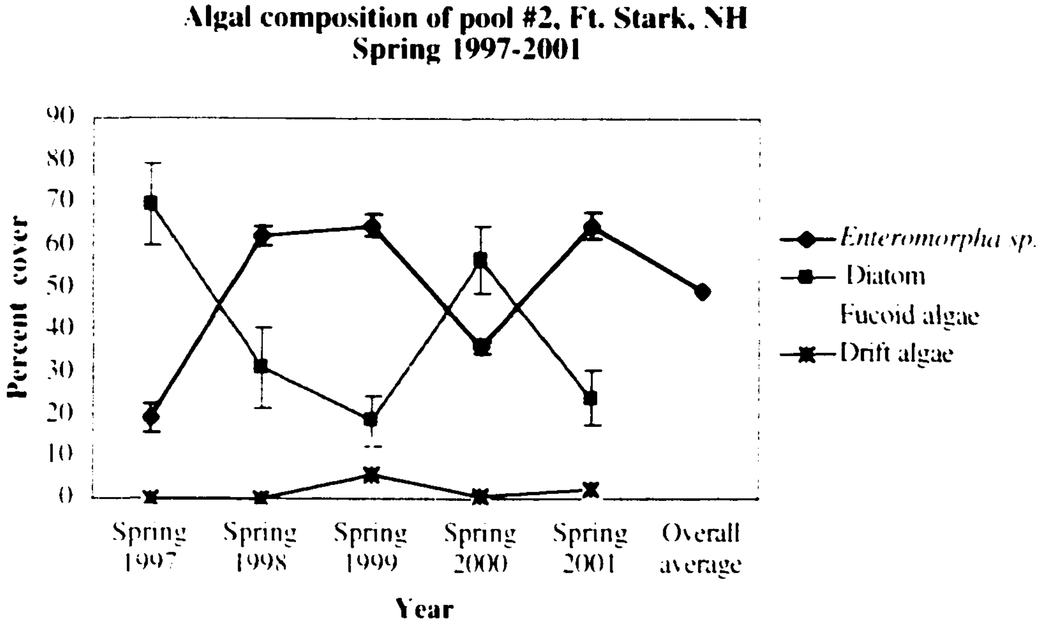


Figure 3.5b: Temporal variation in average percent cover (and standard error) of various groups of algae in an upper intertidal pool at Ft. Stark, NH from Spring 1997 to Spring 2001. The overall mean percent cover of *Enteromorpha* sp. in spring is also shown.

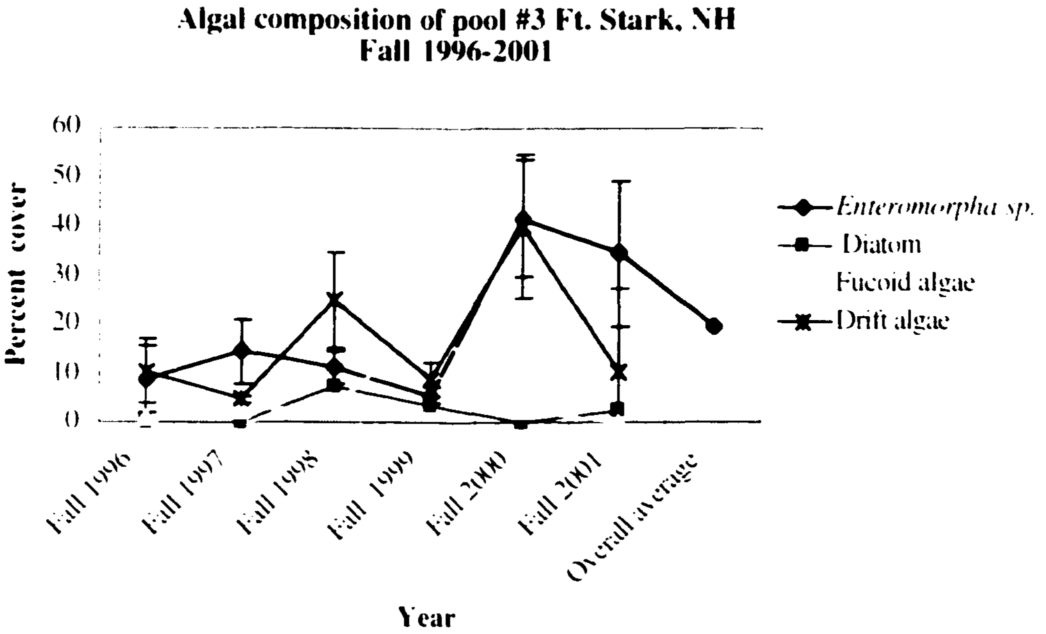


Figure 3.6a: Temporal variation in average percent cover (and standard error) of various groups of algae in an upper intertidal pool at Ft. Stark, NH from Fall 1996 to Fall 2001. The overall mean percent cover of *Enteromorpha* sp. in fall is also shown.

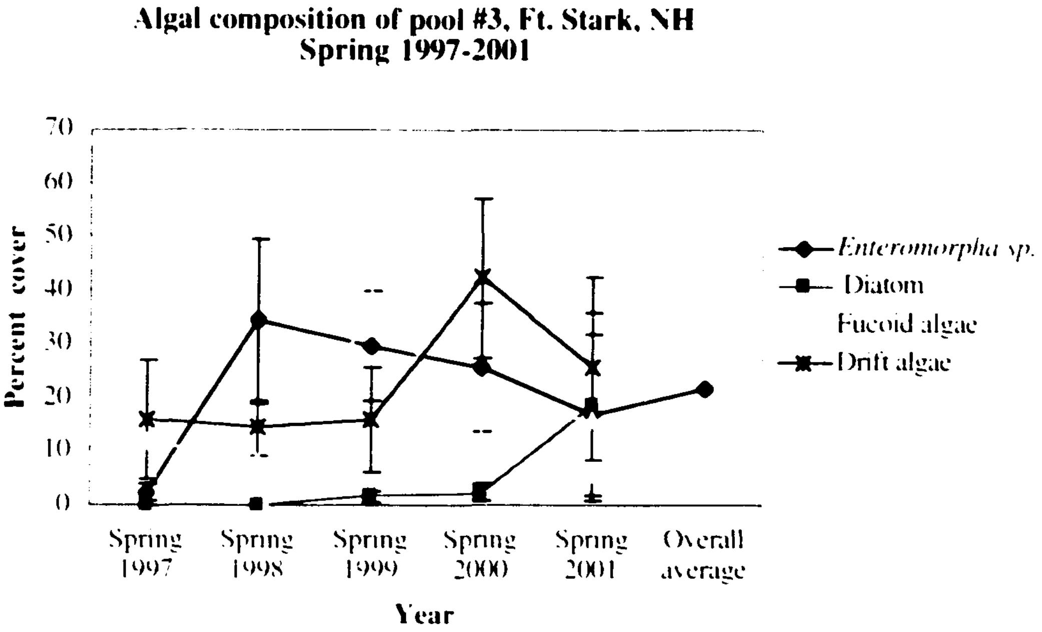


Figure 3.6b: Temporal variation in average percent cover (and standard error) of various groups of algae in an upper intertidal pool at Ft. Stark, NH from Spring 1997 to Spring 2001. The overall mean percent cover of *Enteromorpha* sp. in spring is also shown.

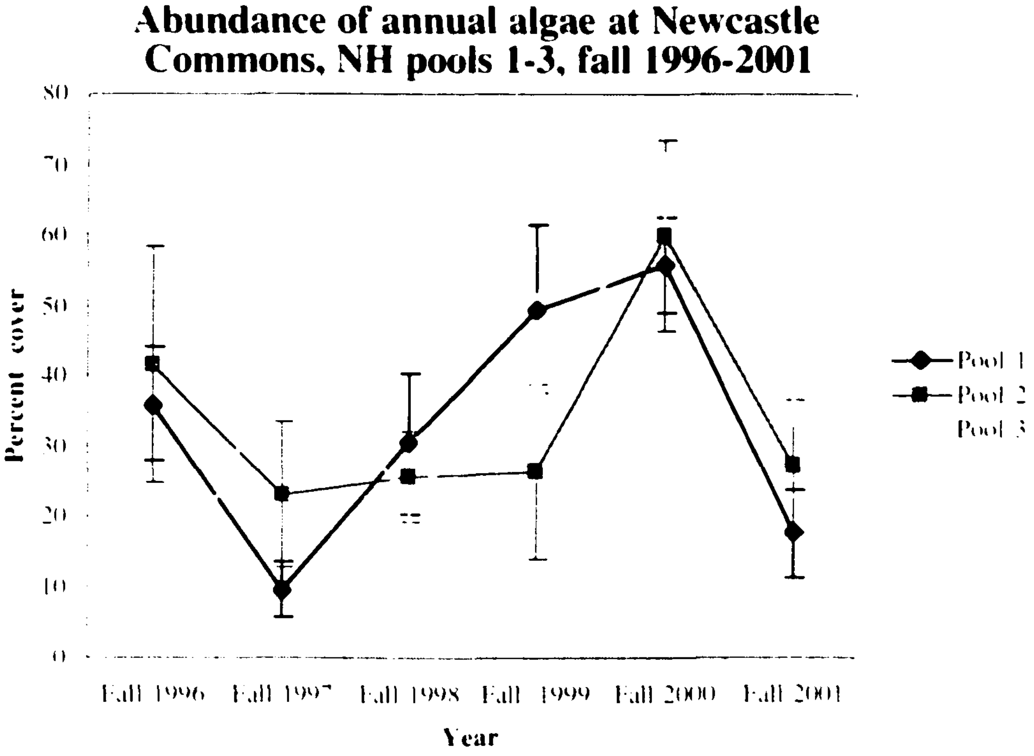


Figure 3.7a: Temporal variation in average percent cover (and standard error) of the annual algae category in all three pools at Newcastle Commons, NH from Fall 1996 to Fall 2001.

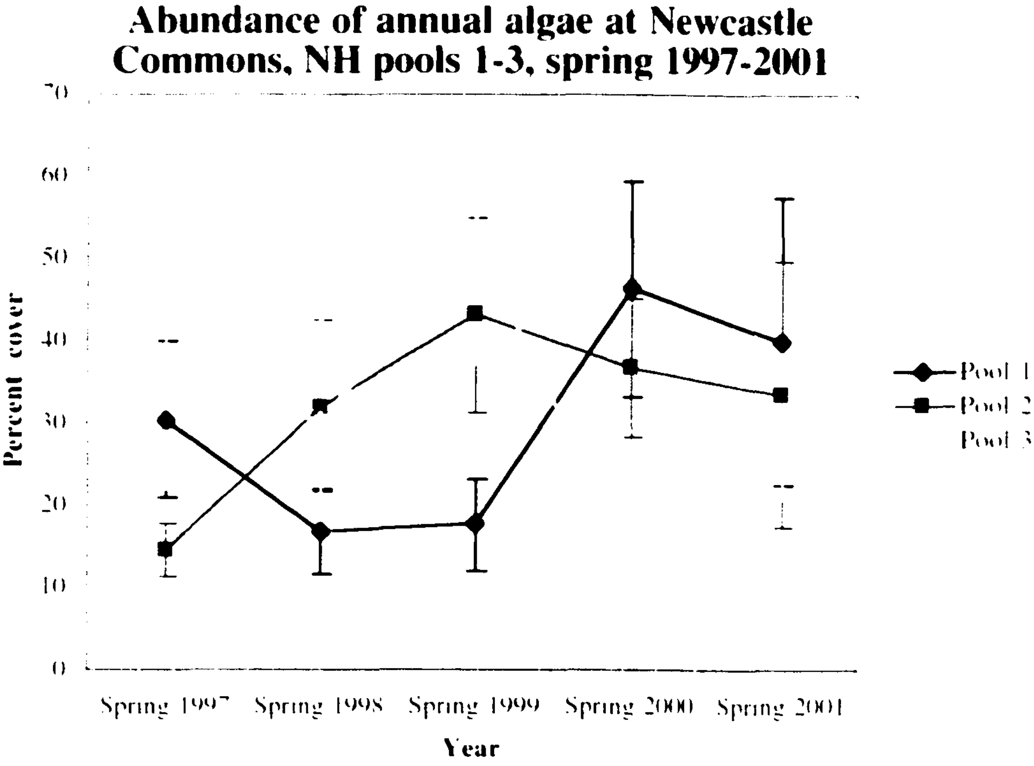


Figure 3.7b: Temporal variation in average percent cover (and standard error) of the annual algae category in all three pools at Newcastle Commons, NH from Spring 1997 to Spring 2001.

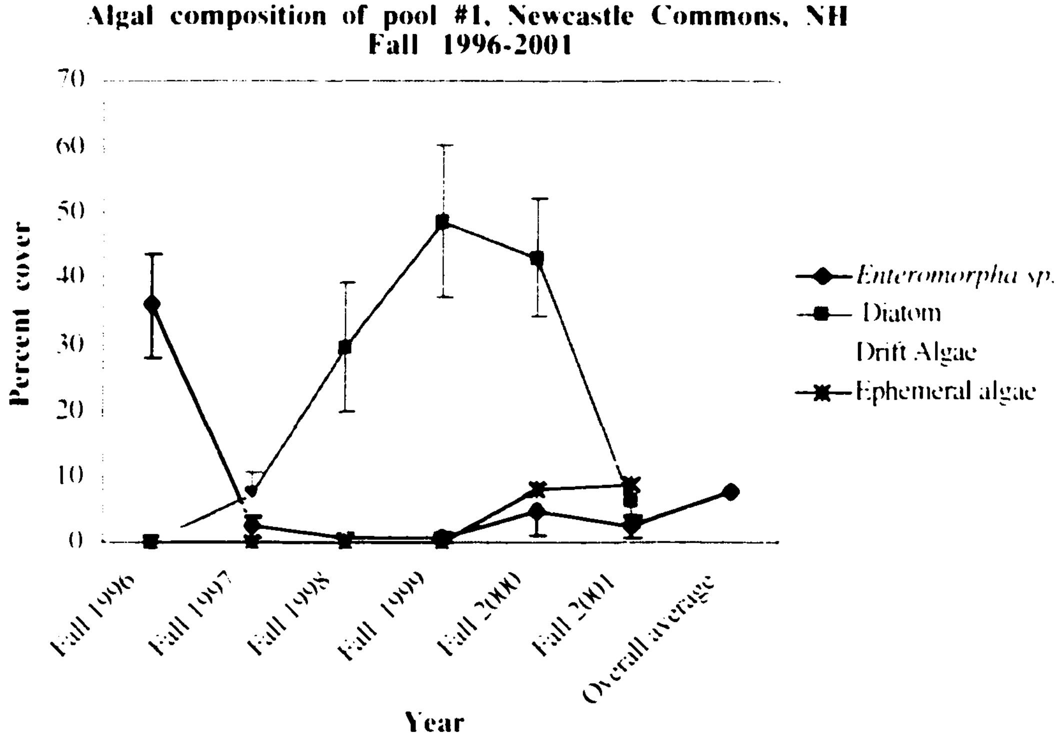


Figure 3.8a: Temporal variation in average percent cover (and standard error) of various groups of algae in an upper intertidal pool at Newcastle Commons, NH from Fall 1996 to Fall 2001. The overall mean percent cover of *Enteromorpha* sp. in fall is also shown.

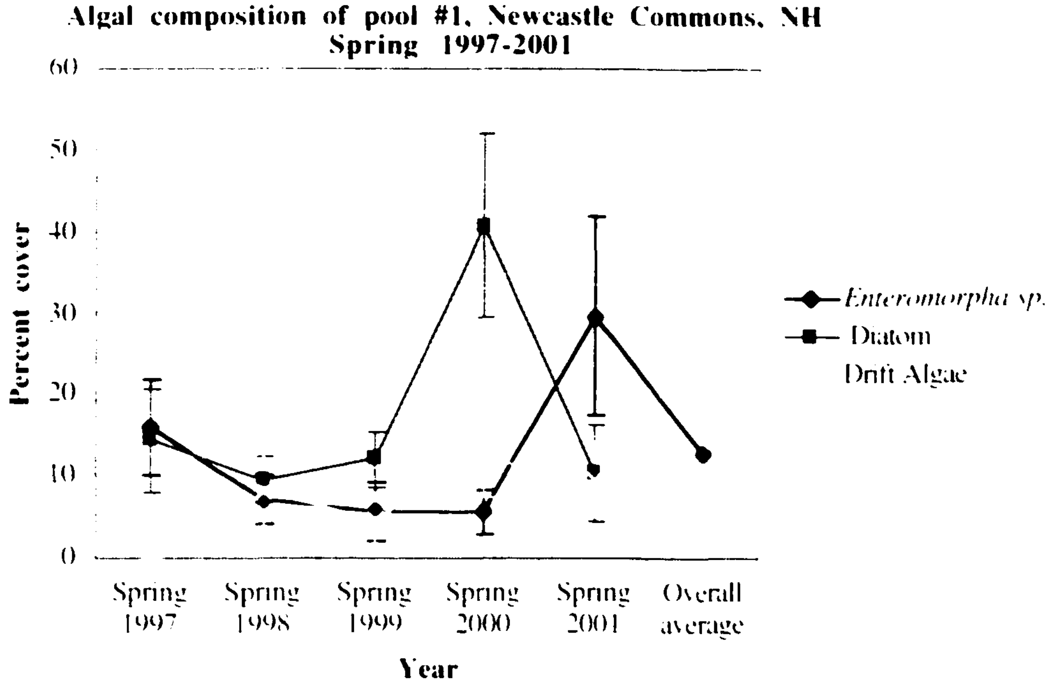


Figure 3.8b: Temporal variation in average percent cover (and standard error) of various groups of algae in an upper intertidal pool at Newcastle Commons, NH from Spring 1997 to Spring 2001. The overall mean percent cover of *Enteromorpha* sp. in spring is also shown.

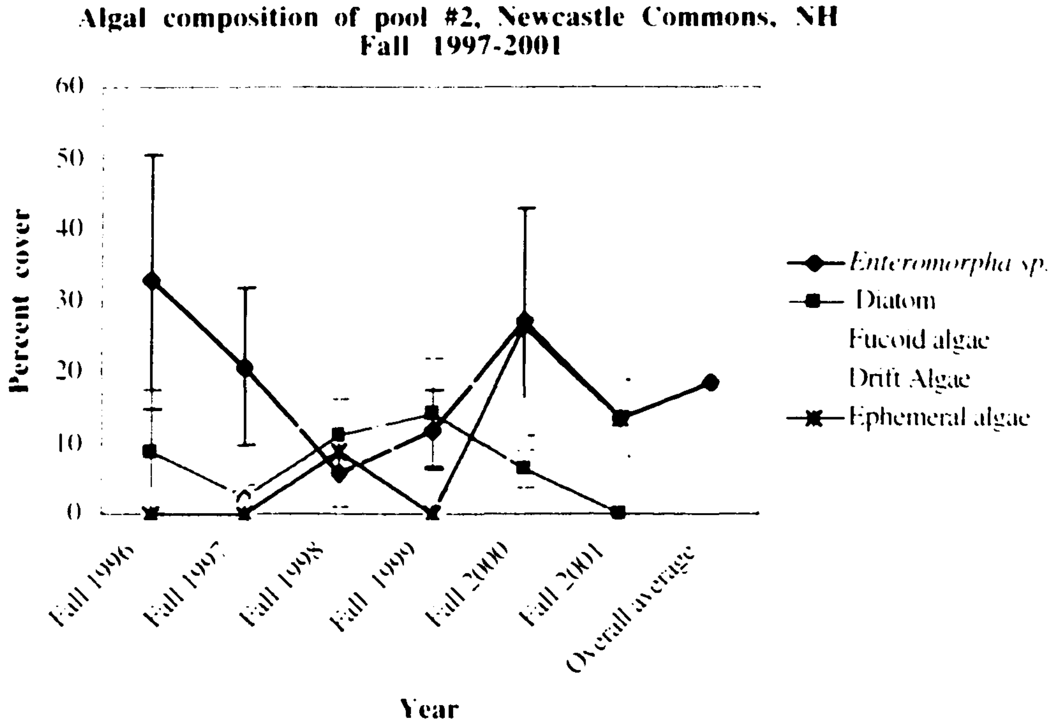


Figure 3.9a: Temporal variation in average percent cover (and standard error) of various groups of algae in an upper intertidal pool at Newcastle Commons, NH from Fall 1996 to Fall 2001. The overall mean percent cover of *Enteromorpha* sp. in fall is also shown.

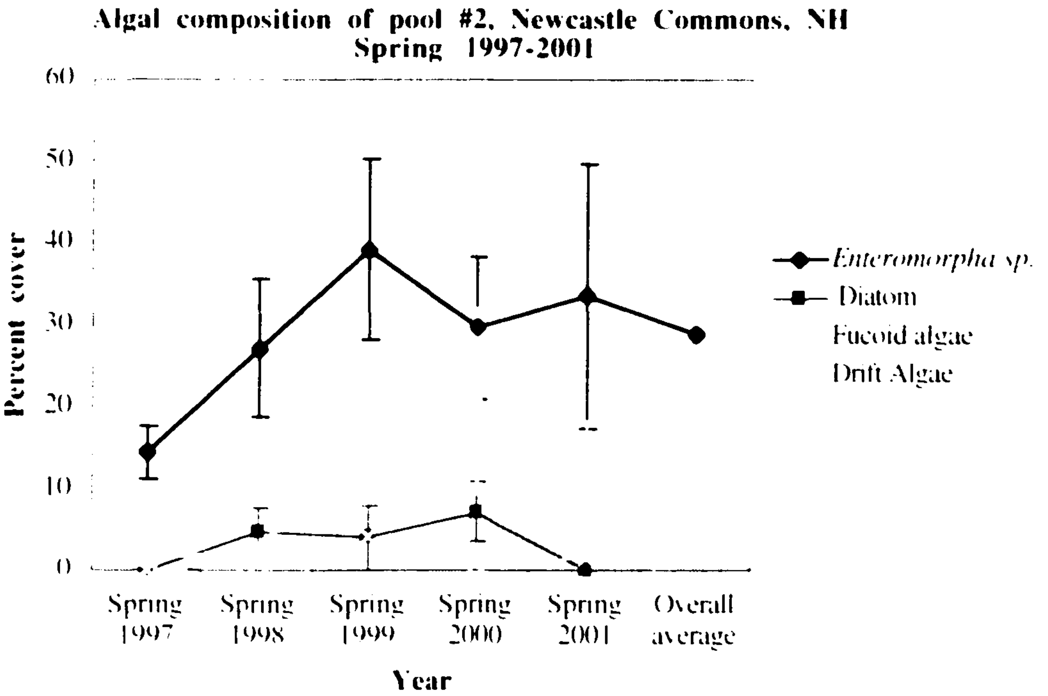


Figure 3.9b: Temporal variation in average percent cover (and standard error) of various groups of algae in an upper intertidal pool at Newcastle Commons, NH from Spring 1997 to Spring 2001. The overall mean percent cover of *Enteromorpha* sp. in spring is also shown.

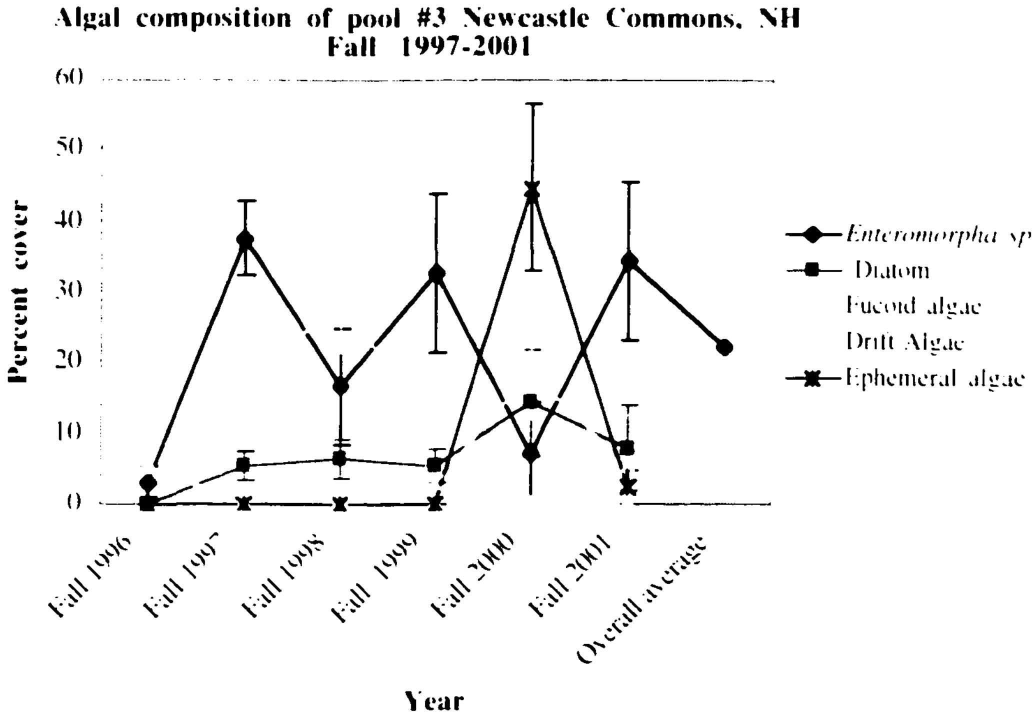


Figure 3.10a: Temporal variation in average percent cover (and standard error) of various groups of algae in an upper intertidal pool at Newcastle Commons, NH from Fall 1996 to Fall 2001. The overall mean percent cover of *Enteromorpha* sp. in fall is also shown.

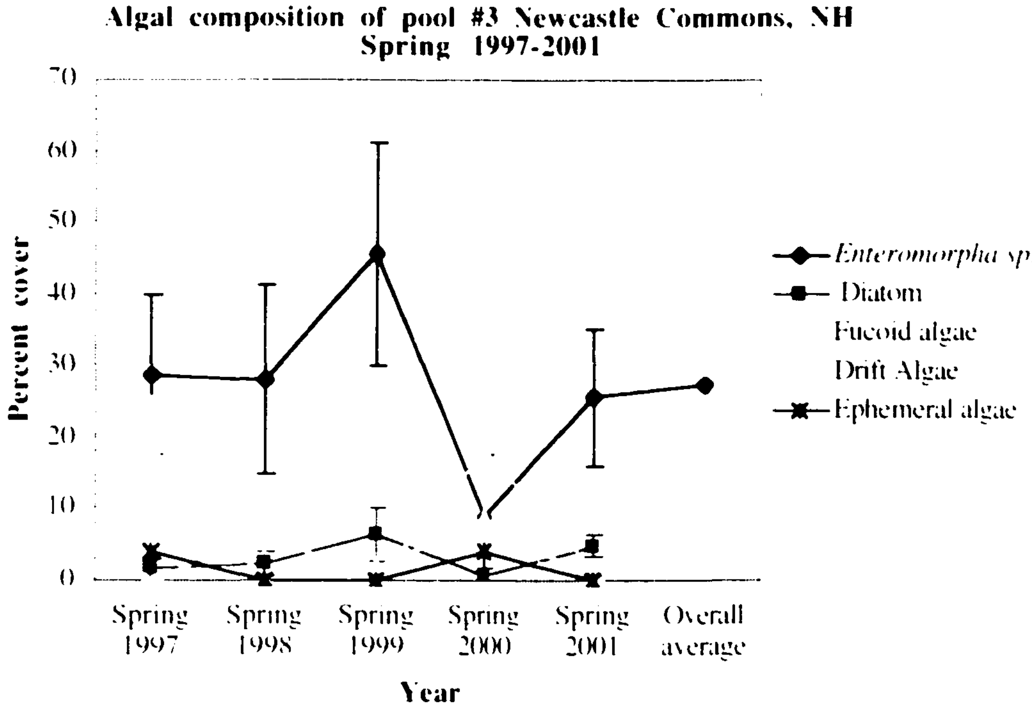


Figure 3.10b: Temporal variation in average percent cover (and standard error) of various groups of algae in an upper intertidal pool at Newcastle Commons, NH from Spring 1997 to Spring 2001. The overall mean percent cover of *Enteromorpha* sp. in spring is also shown.

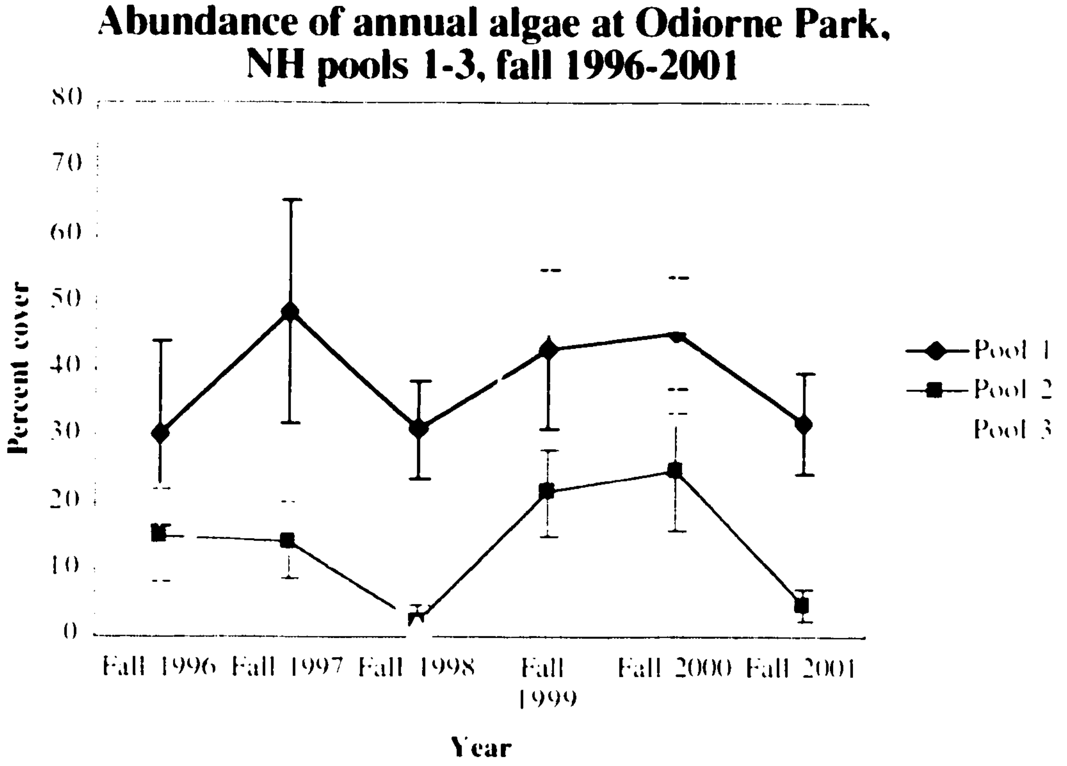


Figure 3.11a: Temporal variation in average percent cover (and standard error) of the annual algae category in all three pools at Odiorne Park, NH from Fall 1996 to Fall 2001.

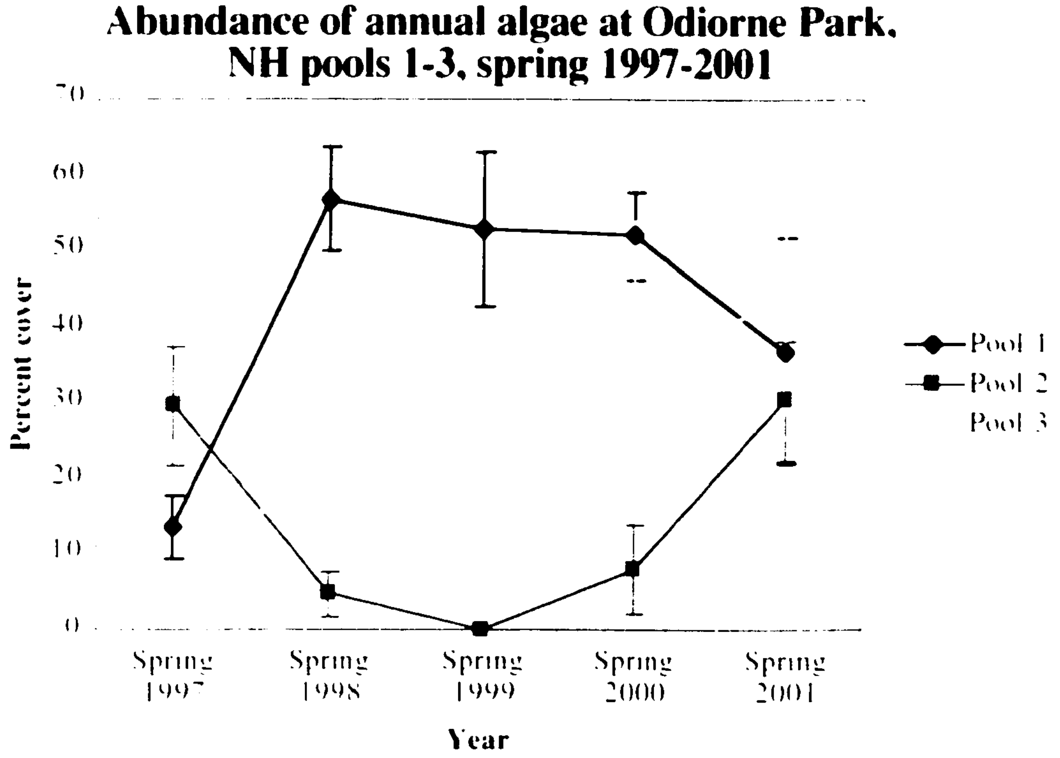


Figure 3.11b: Temporal variation in average percent cover (and standard error) of the annual algae category in all three pools at Odiorne Park, NH from Spring 1997 to Spring 2001.

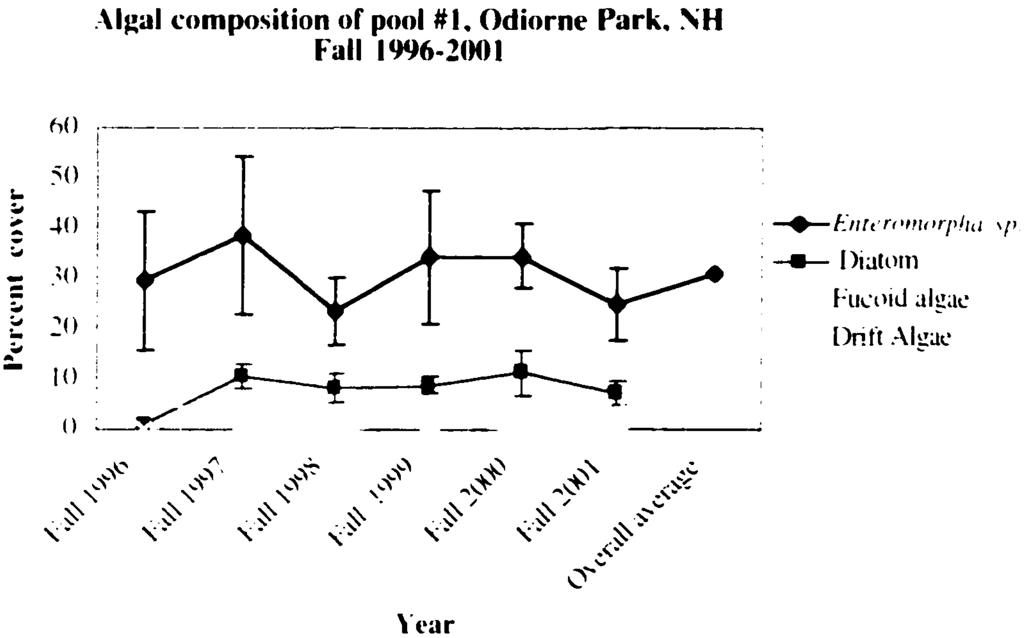


Figure 3.12a: Temporal variation in average percent cover (and standard error) of various groups of algae in an upper intertidal pool at Odiorne Park, NH from Fall 1996 to Fall 2001. The overall mean percent cover of *Enteromorpha* sp. in fall is also shown.

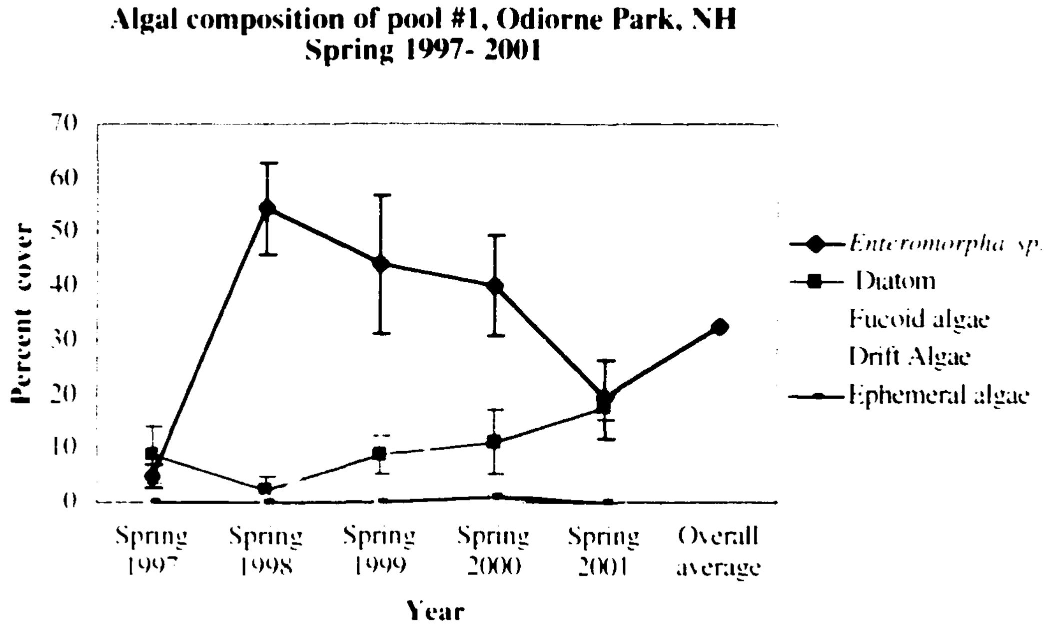


Figure 3.12b: Temporal variation in average percent cover (and standard error) of various groups of algae in an upper intertidal pool at Odiorne Park, NH from Spring 1997 to Spring 2001.

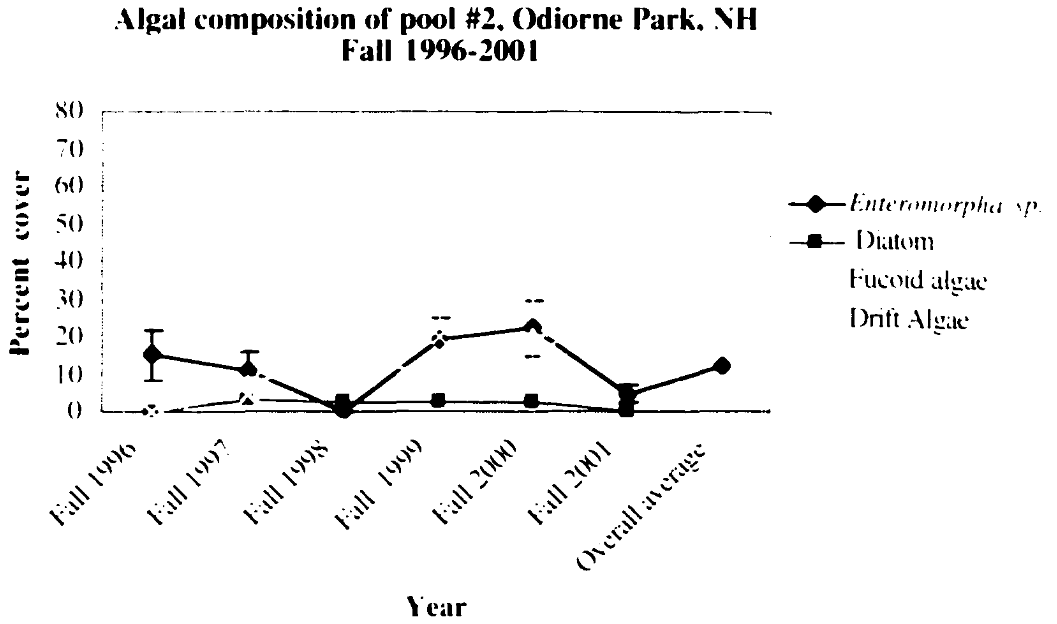


Figure 3.13a: Temporal variation in average percent cover (and standard error) of various groups of algae in an upper intertidal pool at Odiorne Park, NH from Fall 1996 to Fall 2001. The overall mean percent cover of *Enteromorpha* sp. in fall is also shown.

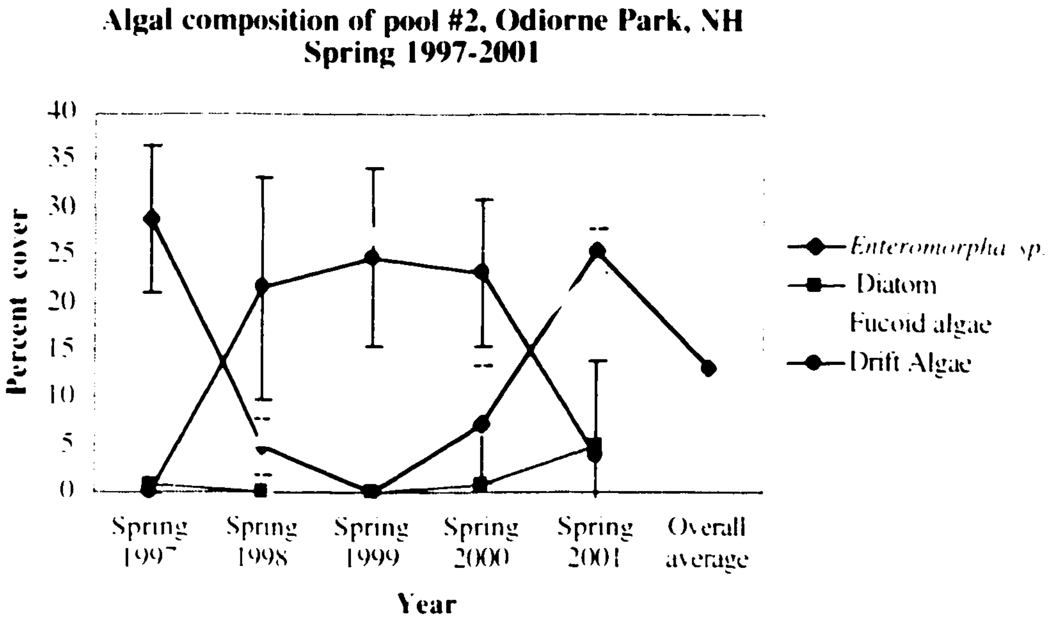


Figure 3.13b: Temporal variation in average percent cover (and standard error) of various groups of algae in an upper intertidal pool at Odiorne Park, NH from Spring 1997 to Spring 2001. The overall mean percent cover of *Enteromorpha* sp. in spring is also shown.

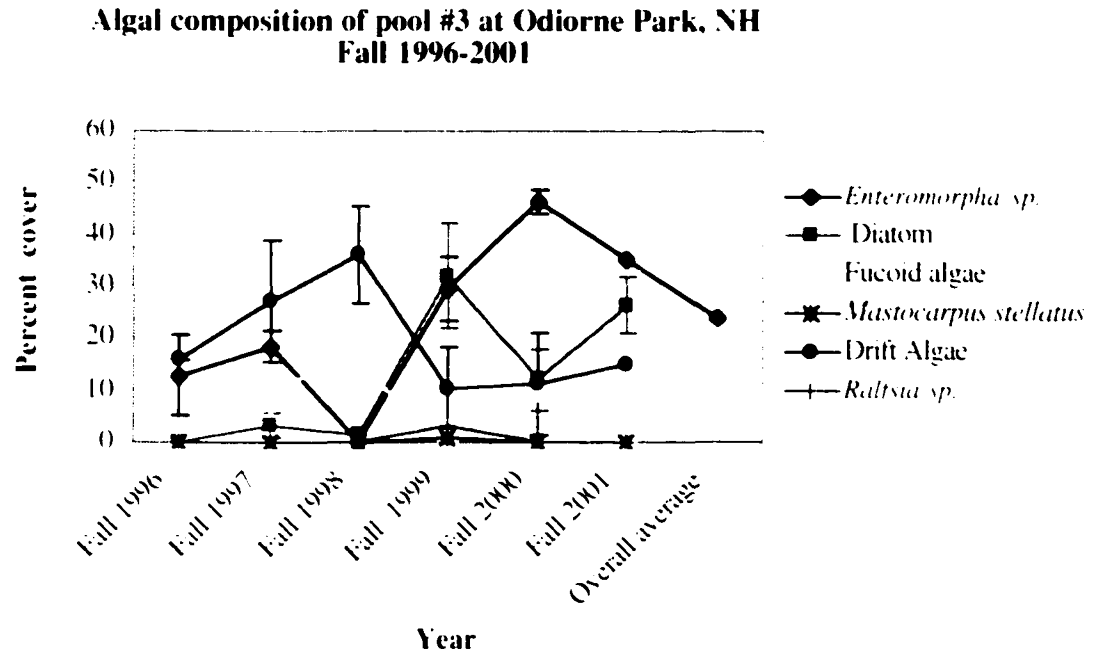


Figure 3.14a: Temporal variation in average percent cover (and standard error) of various groups of algae in an upper intertidal pool at Odiorne Park, NH from Fall 1996 to Fall 2001. The overall mean percent cover of *Enteromorpha* sp. in fall is also shown.

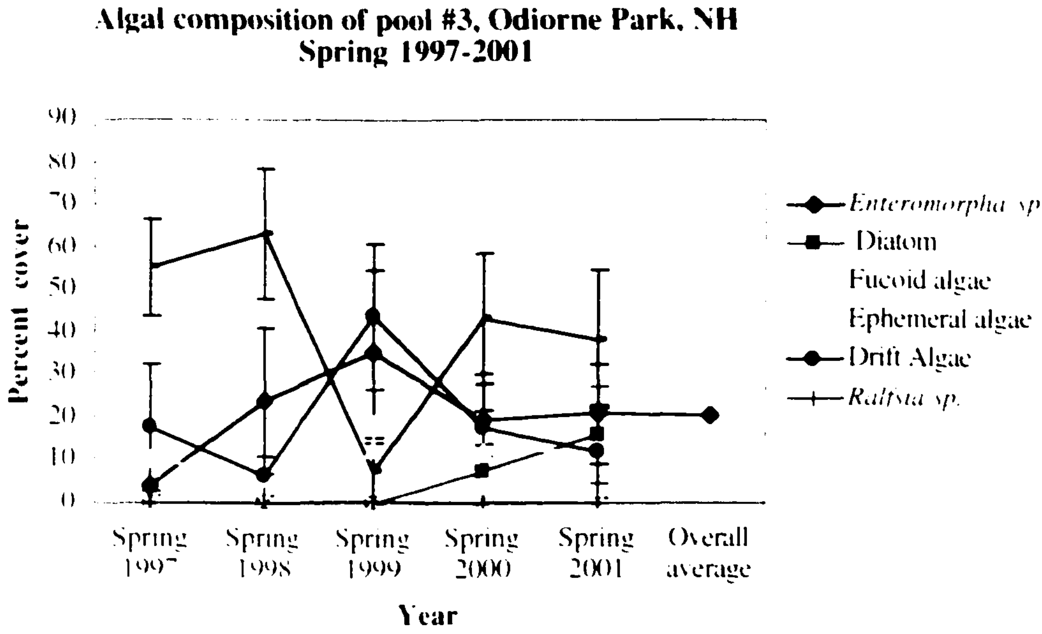


Figure 3.14b: Temporal variation in average percent cover (and standard error) of various groups of algae in an upper intertidal pool at Odiorne Park, NH from Spring 1997 to Spring 2001. The overall mean percent cover of *Enteromorpha* sp. in spring is also shown.

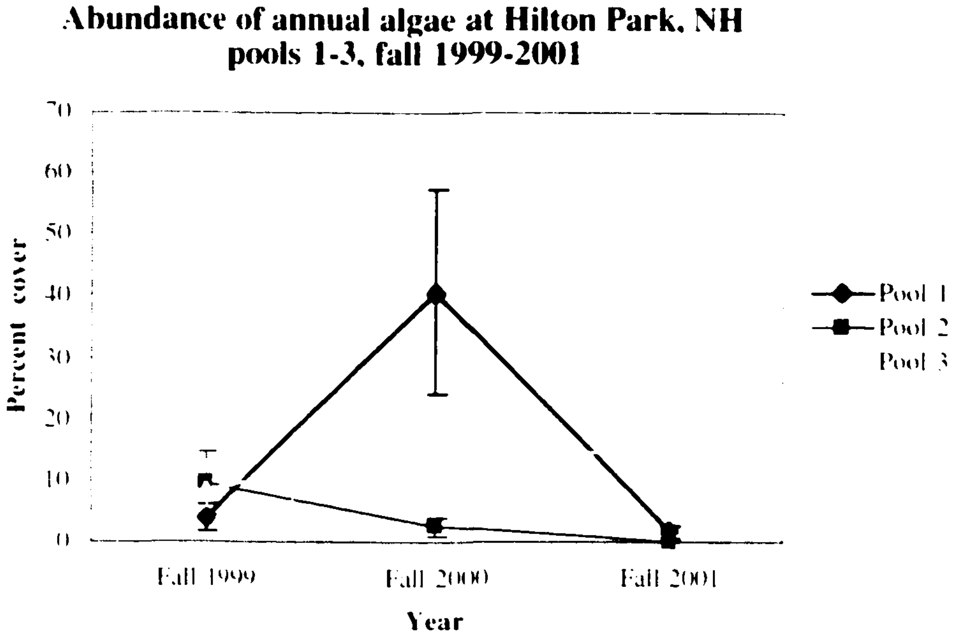


Figure 3.15a: Temporal variation in average percent cover (and standard error) of the annual algae category in all three pools at Hilton Park, NH from Fall 1996 to Fall 2001.

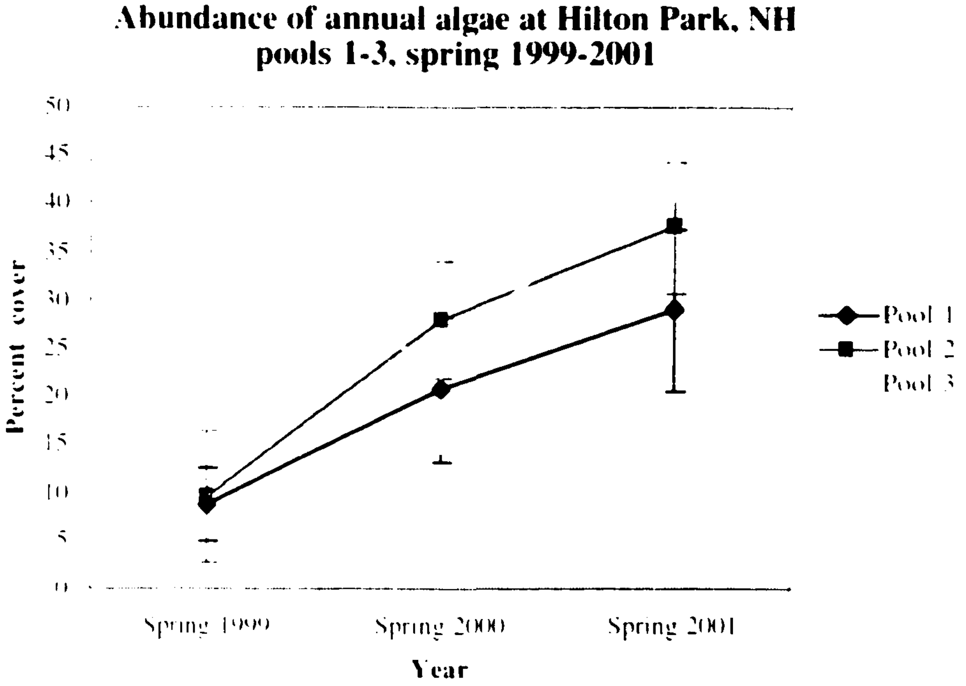

Abundance of annual algae at Hilton Park, NH pools 1-3, spring 1999-2001

Figure 3.15b: Temporal variation in average percent cover (and standard error) of the annual algae category in all three pools at Hilton Park, NH from Spring 1997 to Spring 2001.

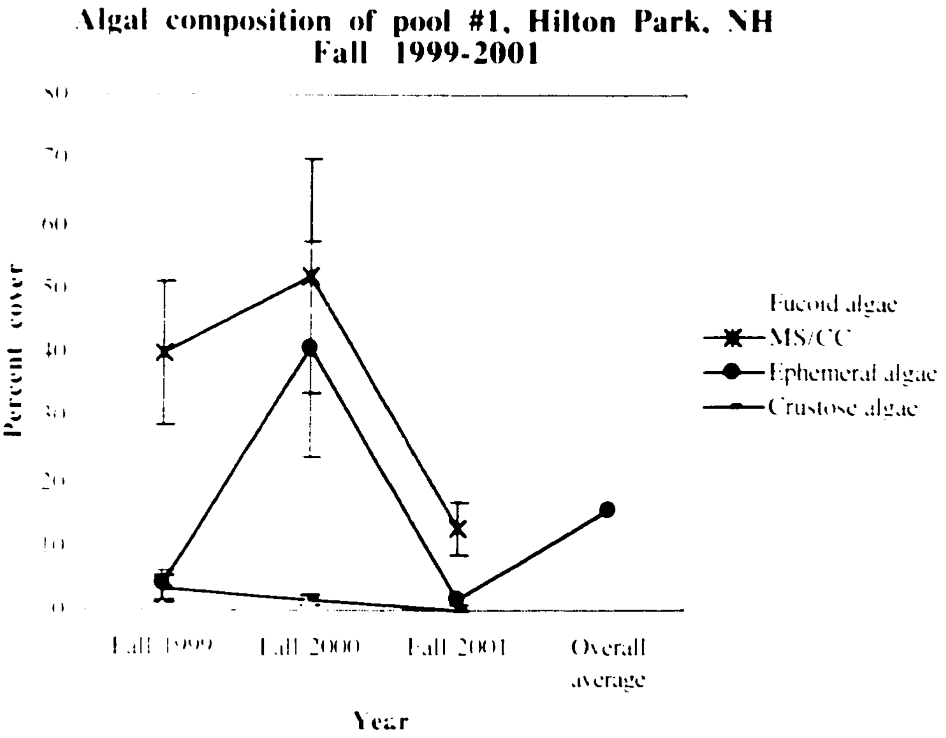


Figure 3.16a: Temporal variation in average percent cover (and standard error) of various groups of algae in an intertidal pool at Hilton Park, NH from Fall 1999 to Fall 2001. The overall mean percent cover of *Enteromorpha* sp. in fall is also shown. MS/CC is *M. stellatus* and *Chondrus crispus*.

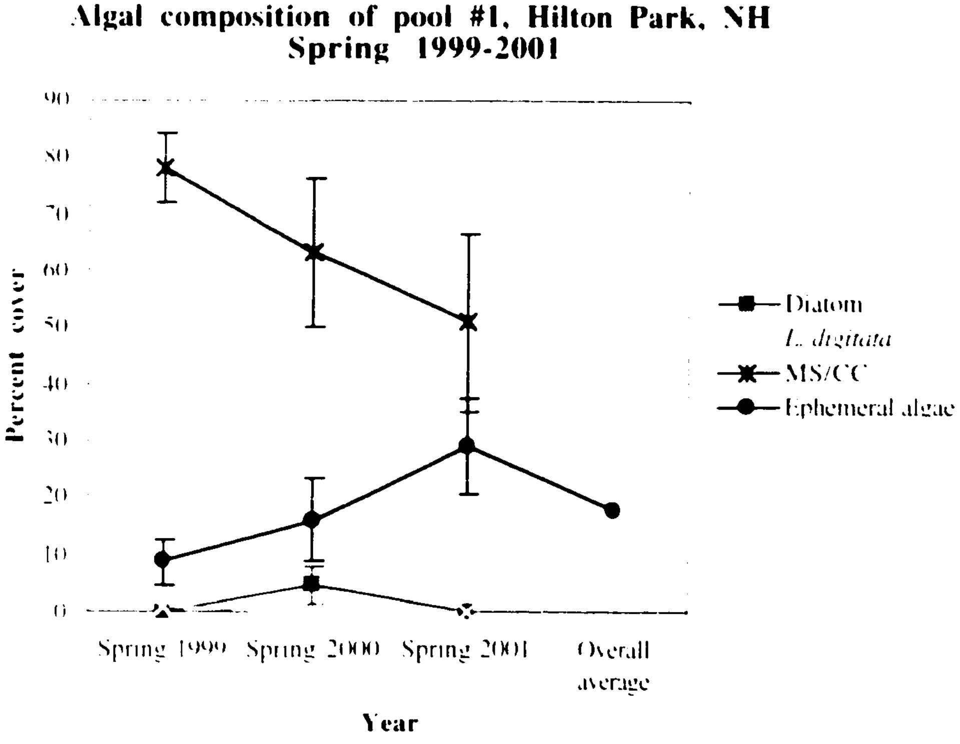


Figure 3.16b: Temporal variation in average percent cover (and standard error) of various groups of algae in an intertidal pool at Hilton Park, NH from Spring 1999 to Spring 2001. The overall mean percent cover of *Enteromorpha* sp. in spring is also shown. MS/CC is *M. stellatus* and *Chondrus crispus*.

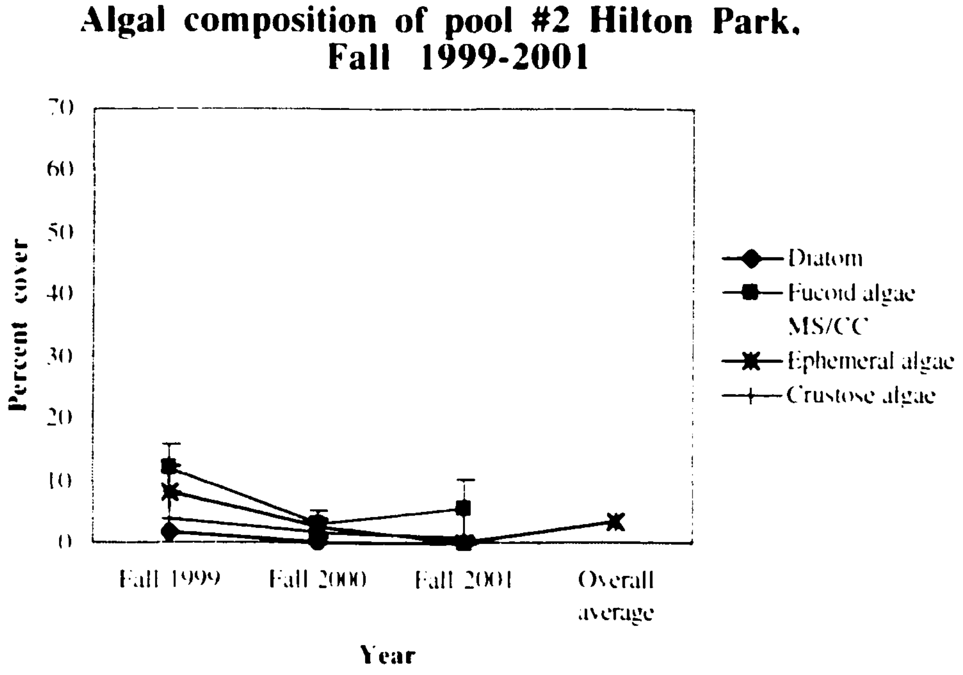


Figure 3.17a: Temporal variation in average percent cover (and standard error) of various groups of algae in an intertidal pool at Hilton Park, NH from Fall 1999 to Fall 2001. The overall mean percent cover of *Enteromorpha* sp. in fall is also shown. MS/CC is *M. stellatus* and *Chondrus crispus*.

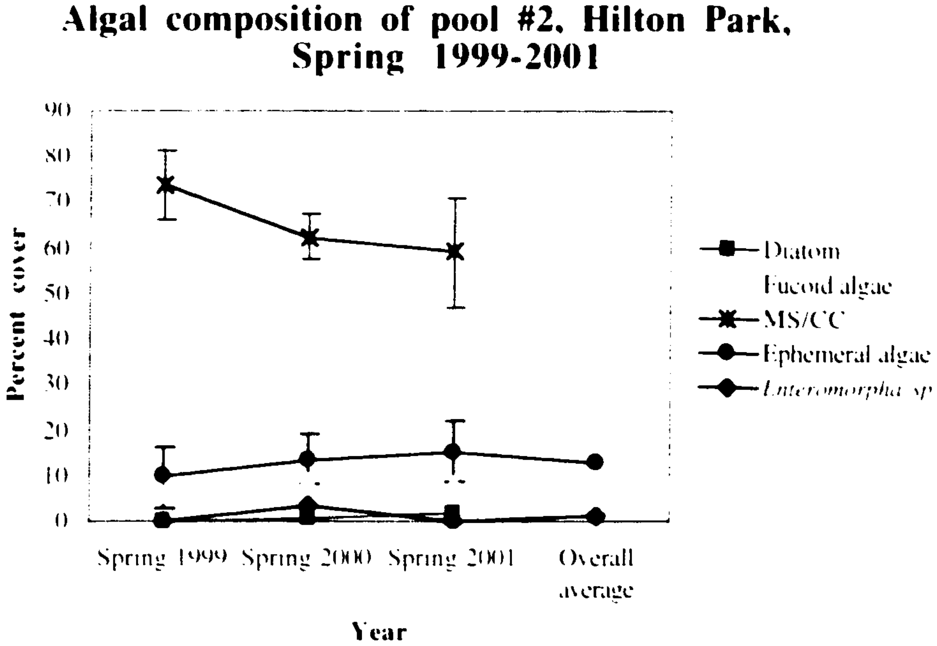

Algal composition of pool #2, Hilton Park, Spring 1999-2001

Figure 3.17b: Temporal variation in average percent cover (and standard error) of various groups of algae in an intertidal pool at Hilton Park, NH from Spring 1999 to Spring 2001. The overall mean percent cover of *Enteromorpha* sp. in spring is also shown. MS/CC is *M. stellatus* and *Chondrus crispus*.

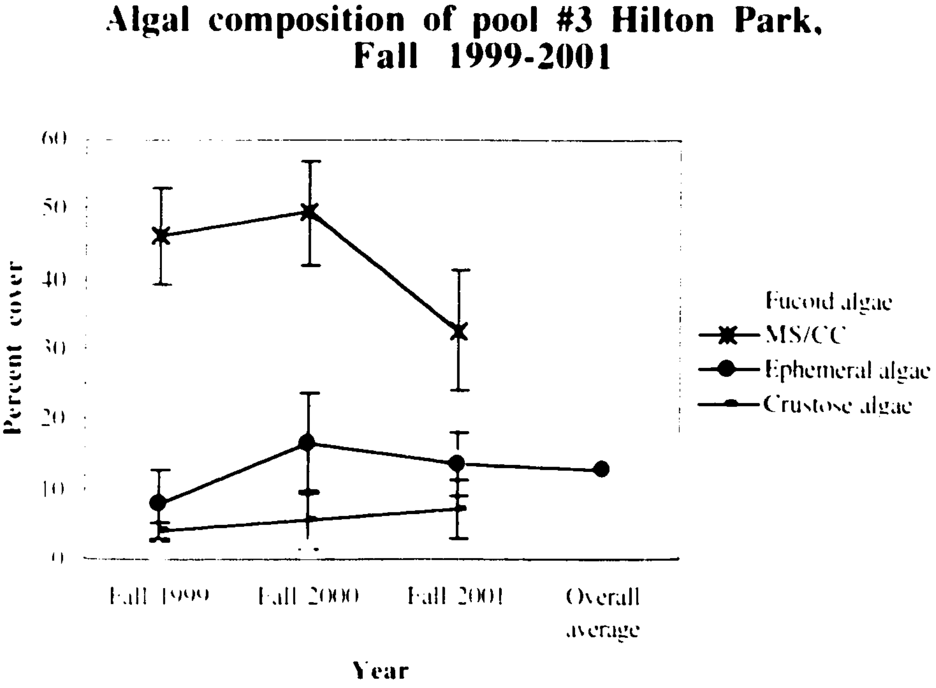


Figure 3.18a: Temporal variation in average percent cover (and standard error) of various groups of algae in an intertidal pool at Hilton Park, NH from Fall 1999 to Fall 2001. The overall mean percent cover of *Enteromorpha* sp. in fall is also shown. MS/CC is *M. stellatus* and *Chondrus crispus*.

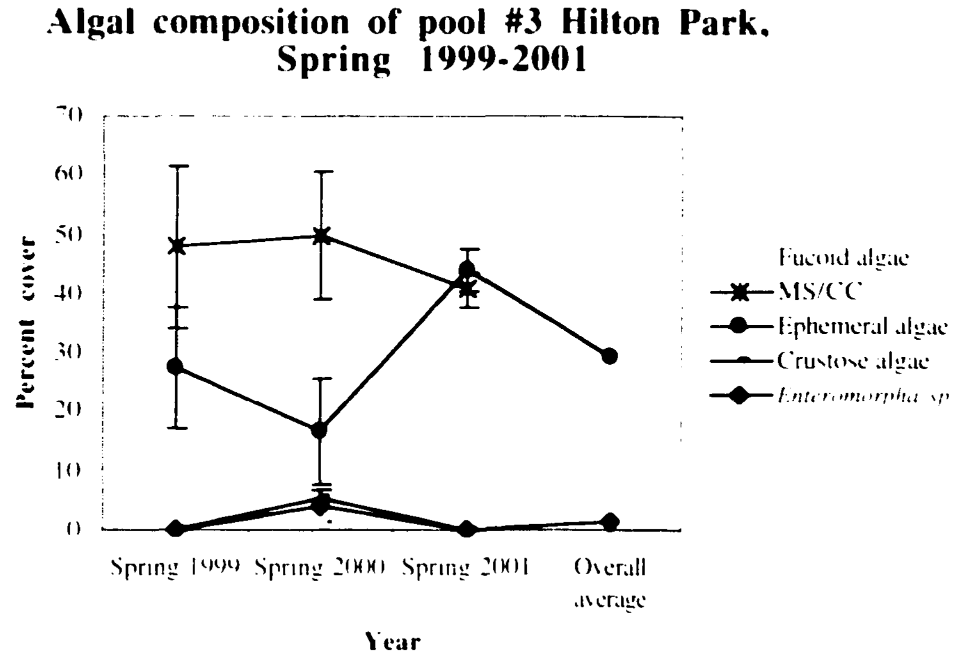


Figure 3.18b: Temporal variation in average percent cover (and standard error) of various groups of algae in an intertidal pool at Hilton Park, NH from Spring 1999 to Spring 2001. The overall mean percent cover of *Enteromorpha* sp. in spring is also shown. MS/CC is *M. stellatus* and *Chondrus crispus*.

CHAPTER IV

EFFECTS OF PREDATION BY TWO SPECIES OF INTRODUCED CRABS: INFERENCES FROM SHORT TERM MICROCOSM EXPERIMENTS

ABSTRACT

Two introduced crab species are currently established in northern New England, *Carcinus maenas* and *Hemigrapsus sanguineus*. *Carcinus maenas* has been in this region for at least 50 years, while *H. sanguineus* was first found in New Hampshire in 1998. In other regions where *C. maenas* has invaded, there has been speculation regarding the community-wide impacts of its introduction. In contrast, research into the impacts of *C. maenas* in northern New England has thus far been on a species by species basis. Based on the high densities of *H. sanguineus* in southern New England, where they are already well established, it is likely that the continued population growth of this crab in northern New England will have substantial consequences for potential competitors and prey. Microcosms of the rocky intertidal community were utilized to examine which organisms were consumed when each crab species was presented with a naturally occurring assemblage. The two crab species consumed similar prey including: *Semibalanus balanoides*, *Mytilus edulis*, *Spirorbis* sp. and various species of ephemeral algae. Interestingly, the feeding rate of *H. sanguineus* on *S. balanoides* was significantly higher than that of *C. maenas*. As populations of *H. sanguineus* continue to increase in northern

New England, these and other prey species are expected to decline due to increased *H. sanguineus* predation as they likely did following the establishment of *C. maenas*.

INTRODUCTION

Introduced species are being recognized as important components of marine communities due to their increasing abundance and roles in modifying these communities (Carlton, 1989; Carlton and Geller, 1993; Hedgepeth, 1993; Ruiz et al., 1997; 1999). The consequences of biological invasions are various and widespread; the homogenization of the planet's biota is considered by ecologists to be a major threat to ecosystem function (Baskin, 1996).

Introduced species can displace other species leading to a loss in biodiversity, numerically reduce native species, or even transform physical aspects of their new habitat. Several authors have speculated that the introduction of the European green crab, *Carcinus maenas* has the potential to cause a decline in biodiversity because of its predatory activities (in the Pacific: Cohen et al., 1995; Grosholz and Ruiz, 1995; Grosholz et al., 2000; in South Africa: Le Roux et al., 1990). The Asian clam, *Potamocorbula amurensis*, underwent a population explosion during a prolonged dry period in San Francisco which prevented recolonization by estuarine species (Nichols et al., 1990). In northern California estuaries, Byers (1999) documented declines of the native snail *Cerithidea californica* due to the establishment of the Asian mud snail, *Batillaria attramentaria*. Changes in the physical environment are other dramatic impacts of introduced species. The seagrass *Zostera japonica* colonizes mudflats in Oregon (Carlton, 1989) and grazing by the introduced snail *Littorina littorea* can transform marsh habitat to cobble beach in New England (Bertness, 1984). The impacts of an introduced species can even be so profound as to contribute to the collapse of an entire fishery. The ctenophore *Mnemiopsis leidyi*, introduced to the Azov and Black Seas, consumes larval fish and contributed to the collapse of the anchovy fishery (Zaitsev, 1992).

The United States Office of Technology Assessment concluded that the increasing frequency of introduced species and their cumulative impacts are creating a substantial economic and environmental burden for this country. Their estimates on economic losses from 79 non-indigenous species were 97 billion dollars from 1901 to 1991 (OTA Report Summary, 1993).

The northern New England (north of Cape Cod, MA) rocky intertidal zone is particularly suited to elucidate the community-wide impacts of introduced species because of its relatively low biological diversity. Guilds of higher trophic levels are composed of only 1 or 2 species in this region (Menge, 1976). Because there are few species to interact with each other, the community structure is relatively simple and therefore this habitat has been a model system for understanding community processes (Menge 1976; Lubchenco and Menge, 1978; Leonard et al., 1998). This habitat has already been impacted by several conspicuous introductions including, *C. maenas* (the European green crab) and *Littorina littorea* (the common periwinkle). The impacts of these two species on the rocky intertidal community have been considerable. *Littorina littorea* is the most abundant intertidal herbivore in the New England rocky intertidal zone with the ability to alter algal dominance patterns in this habitat (Lubchenco, 1978). Predation pressure by *C. maenas* has been implicated in the decline of the soft shell clam, *Mya arenaria*, fishery (Ropes, 1968) and has caused morphological changes in at least two species of intertidal snails, *Littorina obtusata* (Seeley, 1986) and *Nucella lapillus* (Vermeij, 1982).

While there is considerable information regarding the impacts of the establishment of *C. maenas* on selected individual species in northern New England, its broader impacts on the community have been comparatively neglected. In contrast, various authors have speculated on the possible impacts on community structure in other areas where *C. maenas* has been introduced (South Africa: Le Roux et. al. 1990, and the Pacific coast of the United States: Cohen et al., 1995; Grosholz and Ruiz, 1995; 1996; Grosholz et al., 2000). The omnivorous feeding habits of *C. maenas* (Ropes, 1968; P.A. Madigan, unpub. data) and its high densities in the rocky intertidal zone of this region (ca. 75/m^2, Tyrrell, 1999) suggest that it has an important ecological influence on the community.

Another introduced crab species has joined *C. maenas* in the northern New England rocky intertidal zone, *Hemigrapsus sanguineus*, the Asian shore crab (McDermott, 1999). *Hemigrapsus sanguineus* has recently been introduced to the Atlantic coast of the United States and has undergone rapid range extension (McDermott, 1998). This species was first recorded in New Hampshire in October, 1998 (McDermott, 1999) and since that time, at least 30 individuals have been found at a variety of locations in the state (Tyrrell, unpub. data). Both of these introduced crab species are general predators (for *C. maenas*: Ropes, 1968; for *H. sanguineus*: Lohrer and Whitlatch, 1997; Tyrrell, 1999). Because of their high trophic position, both species have the potential to exert top down control on prey populations which may result in cascading indirect effects on lower trophic levels.

Caging experiments have been used to determine the effects of predation by *C. maenas* on soft sediment organisms (Reise, 1977; Thrush, 1986; Raffaelli et al., 1989; Fernandes et al., 1999 and Richards et al., 1999) but comparatively little of this type of research has been done in hard substrate habitats. This study used a combination of laboratory and field experiments to investigate the feeding patterns of *H. sanguineus* and *C. maenas* on rocky intertidal assemblages. Microcosm experiments were conducted in the laboratory in the summer of 1999 and the winter of 2000, and field experiments were performed in the summer of 2000. There were three treatments: one consisting only of *C. maenas*, another consisting of *H. sanguineus*, and controls that did not have crabs. The results were used to extrapolate the potential community-wide impacts of both the "new", *H. sanguineus*, and "old", *C. maenas*, invader in the northern New England rocky intertidal zone.

MATERIALS and METHODS

Cobble covered by a characteristic assemblage of rocky intertidal organisms were used in all microcosms. Each replicate consisted of one cobble and the appropriate treatment. These rocks, large enough to contain a representative sample of the community but small enough to be transported to the lab, were selected from the mid to lower intertidal zone of Ft. Stark, Newcastle, NH (43 03.51N, 70 42.75W). A limited number of rocks that were used in the summer laboratory experiments were also taken from a nearby location, Odiorne State Park, Rye, NH (43 02.62N, 70 42.97W). Both of these sites are wave sheltered and have similar species composition and abundance (Tyrrell, 1999).

Laboratory Microcosms

There were two sets of laboratory microcosm experiments. One set was conducted during the summer from July 5, 1999 to September 5, 1999 and the other set during the winter from February 2, 2000 to February 25, 2000. A total of 38 rocks (10 controls, 14 *Hemigrapsus sanguineus* and 14 *Carcinus maenas* treatments) were examined for the summer microcosms and a total of 23 rocks were examined in winter (12 controls, 6 *H. sanguineus* and 5 *C. maenas*). The rocks used in summer microcosm experiments ranged in size from 7.5 to 18 cm long and 5 to 12.5 cm wide (minimum to maximum dimensions), while the rocks used in winter microcosm experiments ranged in size from 12 to 28 cm long to 9.5 to 19.5 cm wide. The time between collection of the rocks from the field and initiation of the experiments was less than 24 hours to limit changes due to snail grazing or other intrinsic factors.

After the rocks were collected, organisms on the sides and bottoms were removed by scraping. The rocks were rinsed to remove highly mobile species such as amphipods and isopods, which are difficult to quantify, and to ensure that observed changes were due only to consumption by the experimental crabs. All remaining animals, i.e. *Semibalanus balanoides* (barnacles) and *Spirorbis* sp. (the coiled worm), were counted before and after the experimental period. The number and shell length of *Mytilus edulis* (mussels) and Littorinids (snails) were recorded. Molluscs that were less than 2 mm shell length were not included in the analysis of results. The percent cover of sessile species (mostly foliose and encrusting algae) was also determined either by stretching a transparency or placing plexiglass with random points (15 points/49 cm^2) over a container. The species (or bare rock) under each point was recorded. A sketch and photograph were made of each rock so that it could be arranged in the same manner for percent cover analysis after the experiment, thus reducing error associated with this method.

The experiments were initiated by placing each rock into a container (38 L glass aquaria with a layer of sand and approximately 15 L of seawater for summer microcosm experiments and a 11 L dishpan filled with seawater for winter microcosms), along with its associated molluscs. Two similarly sized crabs that had been starved at least 48 hours were added to the experimental containers. The size range of *H. sanguineus* for the laboratory microcosm experiments was 13 - 27.9 mm carapace width, and *C. maenas* ranged in size from 14.2 - 47.6 mm carapace width. Control treatments did not have crabs added to the containers. There were Each container was covered with translucent plexiglass so that all of the organisms experienced a natural day/night cycle. Forty eight hours later, the crabs, rocks and associated organisms were removed and the previous analysis of the rocks was repeated.

Field Microcosms

Ten sets of field microcosm experiments were conducted at the Ft. Stark site at 0.5 m above mean lower low water. The first set of field microcosm experiments was initiated on August 8, 2000 and the last set was completed on September 30, 2000. Each set of experiments consisted of three rocks: a control treatment (no crabs), a *H. sanguineus* treatment and a *C. maenas* treatment. The field component of the experiments lasted for two days.

The enclosures were made from a 17 L translucent plastic storage bin (dimensions 41.2 cm long x 28.7 cm wide x 25.3 cm high) with a removable cover. The sides and bottom of the bin were cut out and plastic mesh (3 mm square) was glued over the openings. The bins were placed upside down (cover on the bottom) and they were secured to the substrate using tent stakes and bricks. Each bin was filled with coarse sand to 5 cm depth. A total of six bins were deployed.

Rocks used in field microcosm experiments were collected from the mid to lower intertidal zone of Ft. Stark. All analysis of prey assemblages on the rocks was done in the laboratory in the same manner used in the laboratory microcosm experiments, (same selection and preparation procedures). In some cases, the number of barnacles was very large (estimated at over 1000), and some barnacles were randomly scraped off of the rocks to facilitate counting them. The size range of rocks used in field microcosm experiments ranged from a minimum in each dimension of 13 cm long, 12 cm wide and 7 cm high and a maximum in each dimension of 29 cm long, 22 cm wide and 14 cm high.

The experiments were initiated during low tide by placing a rock and its associated organisms into one of the field enclosures. After several minutes, five similarly sized, starved, adult male crabs (either *C. maenas* or *H. sanguineus*) were placed into experimental enclosures. The stocking density of crabs corresponded to a density of 42 crabs per m^2, which is similar to ambient densities of *C. maenas* at this tidal height at this site (Tyrrell, unpub. data). The size range of *H. sanguineus* was 13.7 - 37 mm carapace width and the size range of *C. maenas* was 14.2 - 36.9 mm carapace width. The microcosms were checked daily and any drift algae that accumulated on the outside were removed. The experiment was concluded during low tide two days later, when the rocks, associated organisms and crabs were removed from the enclosures. The rocks and their associated organisms were returned to the laboratory for analysis, while the crabs were frozen and then transferred to alcohol. Once the cobble was transported to the lab, the percent cover analysis was repeated, the number of *S. balanoides* and *Spirorbis* sp. was determined and Littorinids and *M. edulis* were counted and measured. Other changes that had occurred during the experimental time period were also noted.

Analysis

After the experiments were completed, some algal species were combined into categories to facilitate the analysis of results. *Phymatolithon* sp. and *Lithothamniom glaciale* were combined to form a crustose algae category. In addition, a non-perennial, fleshy algae category (henceforth ephemeral algae) was created that included the species: *Scytosiphon simplicissimus*, *Rhizoclonium tortuosum*, *Chaetomorpha* sp., *Ulothrix flacca*, *Cladophora* sp., *Enteromorpha* sp., *Porphyra* sp., *Dumontia contorta* and diatoms. The algae comprising the ephemeral algae category (with the exception of *Chaetomorpha* sp.) were poorly represented between treatments and replicates. A fucoid algae category was also created; it was composed of *Fucus vesiculosus* and *Ascophyllum nodosum*.

The percent change in the abundance of all species after the experiment was determined to compare changes that occurred in the crab versus control treatments. In some cases, the percent changes were positive. This was due to some species (such as encrusting algae) being exposed as the crabs consumed foliose algae that had previously obscured it. The percent change was calculated for both count data and for percent cover data. The size frequency distributions of molluscs before and after the experiment were analyzed with Chi Square tests in Instat version 2.01 (Graphic software).

Results of the percent change data were analyzed using univariate ANOVA, Tukey's multiple comparison in Systat version 9.0 (SAS Institute). All data were checked for normality and homoscedasticity prior to analysis of variance (ANOVA). In several cases, (summer lab: *S. balanoides*, *Spirorbis* sp. crustose algae; winter lab: *S. balanoides*, *M. edulis*, bare rock, crustose algae, ephemeral algae; field: *M. edulis*, ephemeral algae, fucoid algae), the variance appeared to be heteroscedastic and so the data were square root arc sine transformed. For these cases, the results are reported for transformed data. Because several univariate ANOVA's were performed for each experiment, a sequential Bonferonni correction was used.

RESULTS

Both species of crabs consumed organisms on or associated with the rocks and the patterns of consumption were similar regardless of where (field or laboratory) or when (summer or winter) the microcosms were performed. Large changes were observed in the abundance of *Semibalanus balanoides*, *Mytilus edulis*, *Sprirobis* sp. and ephemeral algae in the microcosms that had crabs in them. It appeared that *Hemigrapsus sanguineus* had higher consumption rates than *Carcinus maenas*, because the absolute value of the percent change in the abundance of organisms was often higher in the *H. sanguineus* treatment than in the *C. maenas* treatments in each set of experiments. There were relatively few changes associated with control microcosms, with the exception that some organisms were lost during handling (i.e. some *S. balanoides* were accidently crushed during handling). Some primary consumers were eaten by crabs in experimental treatments, but did not occur in large enough numbers to be included in statistical analysis. These organisms included the limpet *Notoacmea testudinalis*, and the snails *Littorina obtusata* and *Lacuna vincta*.

The most noticeable difference between control and crab treatments in all of the microcosm experiments was the decline in *S. balanoides* (Table 4.1; Fig. 4.1). In the field microcosms, the decline of *S. balanoides* in the *H. sanguineus* treatments was significant when compared to both control and *C. maenas* treatments (Table 4.1; Fig. 4.1). Additionally, both *C. maenas* and *H. sanguineus* caused significant declines in *S. balanoides* as compared to controls in both sets of lab experiments (Table 4.1; Fig. 4.1). The reduction in the number of *Spirorbis* sp. in both crab treatments was significantly different from that of the controls in the summer lab experiments. *Spirorbis* sp. also declined in both crab treatments in the field experiments but the difference was not statistically significant from that of the controls (Table 4.1; Fig. 4.2). There were not enough *Spirorbis* sp. in the winter lab experiments to undergo this type of analysis. Although *M. edulis* declined in experimental treatments, this decline was not statistically significant in any of the experiments where this type of comparison was possible (Table 4.1; Fig.4.3). The changes in the abundance of ephemeral algae were variable between experiments and between crab species. It appeared that both species of crabs caused big declines in ephemeral algae in the summer lab experiments, but these differences were not statistically significant after the Bonferonni correction (Table 4.1; Fig. 4.4). However, the amount of ephemeral algae significantly increased in both crab treatments as compared to the controls in the winter lab experiments (Table 4.1; Fig. 4.4). In the field experiments, the changes in ephemeral algae were relatively minor (Table 4.1; Fig. 4.4). The significant difference between the *H. sanguineus* and control treatment in the crustose algae category in the summer lab experiments was due to the increased amount of algal crust that was exposed as the crabs consumed organisms that had previously obscured it (Table 4.1; Fig. 4.5). Similar to the crustose algae category, the amount of bare rock that was exposed increased in the crab treatments for lab experiments (Fig. 4.6), but in the field experiments, the changes in the bare rock category were mixed between crab treatments, and generally small in magnitude (Fig. 4.6). Finally, for both fucoid algae and the *Mastocarpus/Chondrus* category, the differences between the crab and control treatments were variable both between experiments and between species of crab (Figs. 4.7 and 4.8).

Size frequency

Figure 4.9 shows the size frequency distribution for *M. edulis* in the field and winter lab experiments. *Mytilus edulis* and *L. littorea* were the only two animal species that occurred in high enough densities to have their size frequency distributions compared. There were relatively low numbers of both species in the larger size classes. Therefore, all *L. littorea* larger than 26 mm shell length and all *M. edulis* larger than 31 mm shell length were grouped to achieve sufficient numbers to perform the Chi-square analysis. The Chi-square test showed that there were no differences between the size frequency distributions of *L. littorea* before and after in any of the treatments for any of the three sets of microcosm experiments (p values ranged from 1.0 to 0.5, results are not depicted graphically). The Chi-square test for trend indicated that there was a significant difference between size classes of *M. edulis* before and after for both the *C. maenas* ($\chi^2=7.33$, df=1, $p<0.01$) and *H. sanguineus* treatments ($\chi^2=4.83$, df=1, $p<0.05$) in the field microcosms. This difference was due to the high consumption of small size classes of *M. edulis* (Fig. 4.9a). The winter lab experiments did not have any significant differences (Fig. 4.9b) and there were not enough *M. edulis* in the summer lab microcosm experiments to analyze the changes in size frequency distributions.

DISCUSSION

Results from the three microcosm experiments can be used to infer impacts of both introduced crab species on the recipient community. It is apparent that both *Carcinus maenas* and *Hemigrapsus sanguineus* are capable of consuming a wide variety of prey from various trophic levels (algae to primary consumers). This omnivory among both invasive crab species may have contributed to their success in colonizing new environments with novel and/or variable prey assemblages. As populations of *C. maenas* became established in northern New England, it is likely that they influenced the structure of the community through their high trophic position. With the continued expansion and establishment of *H. sanguineus*, even higher predation pressure will be exerted on these same prey species.

The univariate statistical results indicated that both species of crabs caused significant changes in the assemblages of organisms on the cobble. The effect on *Semibalanus balanoides* was the greatest; we found that *S. balanoides* was consumed at high levels by both crab species, but *H. sanguineus* was responsible for a greater decline in barnacles than *C. maenas* (Table 4.1; Fig. 4.1). A similar result was found for long term microcosms; the changes in the *H. sanguineus* treatment were statistically significant from two types of control treatments as well as from the *C. maenas* treatment (Chapter V). It is also likely that the introductions of both crab species has already caused or may soon be responsible for additional predation pressure on *Spirobis* sp. (Fig. 4.2) and juvenile *Mytilus edulis* (Fig. 4.9a). A direct comparison of the feeding rates of the crabs in these microcosm experiments with the results from other feeding rates experiments are not warranted because the only other feeding rate experiments utilizing both crab species offered only juvenile *M. edulis* as the prey species (Lohrer and Whitlatch, 2002), rather than an assemblage of organisms.

The prey species that were reported to significantly decline in these microcosm experiments are not the only species that have been or will be affected by predation by introduced crabs. While the numbers of the gastropods *Littorina obtusata*, *Notoacmea testudinalis* and *Lacuna vincta* were too low to undergo statistical analysis, they were consumed by both species of crabs and it is possible that these species have also faced increased predation pressure with the arrival of *C. maenas* and *H. sanguineus*. In fact, it is possible that these gastropods and other prey were relatively uncommon in the microcosms because *C. maenas* predation has already influenced the community.

Although they have been previously documented to consume a wide variety of food items, *C. maenas* is generally perceived to be primarily a molluscan predator (Glude, 1955; Ebling et al., 1964; Ropes 1968, 1988; Hughes and Elner, 1979; Elner, 1981; Sanchez-Salazar, 1987; Cohen et al., 1995). The lack of statistically significant consumption of *M. edulis* in these experiments may have been due to the relatively low availability of this prey item, especially in sizes that are susceptible to crabs. However, when small *M. edulis* were present, they were consumed (Fig. 4.9a). Juvenile *C. maenas* have also been documented as barnacle predators (Rangeley and Thomas, 1987). This study adds to the body of literature on the diet breadth of *C. maenas* (significant consumption of *Spirorbis* sp.) as well as *H. sanguineus*, which was had previously been reported to be primarily herbivorous in its native range (Depledge, 1984).

This appears to be the first study that has utilized microcosms to determine some impacts of an "old" invader (*Carcinus meanas*) and to predict some impacts for a "new" invader (*Hemigrapsus sanguineus*) on the northern New England rocky intertidal community. This experimental design was beneficial because it utilized naturally occurring assemblages of organisms on the cobble, and therefore the microcosms represented a realistic community rather than one that is artificially constructed. However, the assemblage of organisms that was analyzed on the cobble was not representative of the rocky intertidal community as a whole. Several groups of organisms, including amphipods and isopods, were not included in the analysis due to their small size and mobility. The importance of these small crustaceans in the diet of *C. maenas* is unclear; Elner (1981) stated that they appeared to be of minor importance but Ropes (1988) found that they were one of the most commonly encountered food items in stomachs of juvenile (<20 cm carapace width) *C. maenas*. While generally the species composition on the cobble was similar to that of the adjacent rock bench, some species such as rockweed canopy algae and their associated organisms (i.e. *Littorina obtusata*) were underrepresented, as they are more common on rock bench substrates (M.C. Tyrrell and P.A. Madigan, pers. obs. and Tyrrell, 1999). Although the study sites are relatively wave sheltered, the differences in species composition between the cobble and the rock benches is likely due to the susceptibility of the cobble to wave action (Sousa, 1980). The effects of crab predation on species that are more strongly associated with rock benches may have been underestimated using this experimental design.

Artifacts associated with caging or microcosm experiments include: modified water movement, abnormal behavior of predators, shading and protection from desiccation, accumulation of debris on cages and have been discussed by many authors (e.g. Reise, 1977; Thrush, 1986; Hall et al., 1990; Fernandes et al., 1999). A potential problem with the experimental design for the field microcosms was the lack of cage control treatments. However, because the duration of the experiments was only forty-eight hours, some cage artifacts (shading, reduced water flow) probably only had minimal influence on the survival of organisms in the cages. Two factors that may have been important in affecting consumption rates in field microcosms may have been protection from predation (which could raise consumption rates) and increased agonistic interactions between crabs because of competition for refuge space under the rock (which could lower consumption rates).

Other artifacts particularly associated with this experiment, included different water temperatures between the lab and field experiments and the calculation of percent change rather than absolute change in abundance of each species. The consumption rates of the crabs in the laboratory microcosms could be expected to be higher than would be observed under natural conditions because of the elevated water temperatures and lack of tidal fluctuations. In addition, it was necessary to calculate percent change rather than absolute change in species abundance because each rock had different relative availability of prey species. A reduction from two individuals to one individual would be represented by the same percent change value as a reduction of two hundred to one hundred individuals. This issue was particularly relevant when comparing the abundances of *Spirorbis* sp. from the winter and summer microcosm experiments; the abundances of *Spirorbis* sp. were much lower in the winter microcosms than in the summer. In spite of this difference in the absolute availability of prey, the consumption patterns of the crabs were similar between seasons (Fig. 4.2).

Perhaps the most important artifact associated with these experiments was the fact that the rocks were taken from a community that was already influenced by *C. maenas* predation. As previously mentioned, the low abundance of some gastropods initially on the cobble may have been due to a high density of *C. maenas* in the study area. The conclusions from these experiments are limited by the fact that the community under investigation has already been impacted by one of the two introduced predators. Despite this limitation, many other researchers have used caging experiments to infer the impacts of *C. maenas* (Reise, 1978; Scherer and Reise, 1981; Jensen and Jensen, 1985; Raffaelli et al., 1989; Fernandes et al., 1999; Richards et al., 1999) predation in soft sediment environments in Europe. Caging experiments are the best option when working with a species whose mobility and ability to climb fencing make large scale, long term removal experiments untenable.

Tyrrell and Harris (2001) and Tyrrell (1999) predicted the effects of establishment by *H. sanguineus* on the northern New England rocky intertidal community. These authors found that *H. sanguineus* is most likely to have an omnivorous diet in northern

New England which could cause increased competition for food with both *C. maenas* and other herbivores. In addition, they showed that the mollusc feeding preferences of these two introduced crab species significantly overlapped which could lead to competition for food and/or disproportionate declines in the abundance of preferred prey. The results from this research support this conclusion. When presented with microcosms of the northern New England rocky intertidal community, *C. maenas* and *H. sanguineus* consume similar prey species, and it appears that *H. sanguineus* has higher consumption levels than *C. maenas* (Fig. 4.1 and on *M. edulis*, DeGraaf and Tyrrell, in prep.). If *H. sanguineus* reaches densities comparable to those in southern New England (ca. 70/m^2, Lohrer, 2000) and resources (i.e. prey, shelter) are limiting, we expect that these two introduced crab species will experience competitive overlap in northern New England. The introduction of *C. maenas* likely caused declines in the aforementioned prey populations, and we predict that the addition of *H. sanguineus* to this community will cause further declines in the populations of these and other prey species. Finally, declines in *C. maenas* abundance have been observed in southern New England where populations of *H. sanguineus* are high. This decline has been attributed to adult *H. sanguineus* consuming *C. maenas* as they recruit to rocky intertidal habitats (Lohrer and Whitlatch, 2002).

This study demonstrates that the impacts of an introduced species on a naturally occurring assemblage of organisms can be assessed using microcosms to gain a more comprehensive understanding of the feeding biology of the introduced species. The effects of these two introduced crab species on the rocky intertidal community appear to be similar in that they consume similar prey, and as the abundance of *H. sanguineus* increases in northern New England, the initial impact on the community is likely to be increased pressure from the crab guild. If *H. sanguineus* displaces *C. maenas* in northern New England, as it appears to have done in southern New England, prey populations will remain low and particular species may even decline further than they did when *C.*

maenas became established because of *H. sanguineus*' high feeding rate. The negative consequences of the introductions and establishment of these two introduced crab species are likely to be experienced by a wide variety of potential prey and competitors in the rocky intertidal zone and the potential impact of the "new" crab invader on prey and competitors may exceed that which *C. maenas* posed when it invaded New England's rocky shores.

Table 4.1: Results from one -way ANOVA of abundance in each microcosm experiment. Values in bold indicate statistical significance after sequential Bonferonni correction for multiple comparisons. HS= *Hemigrapsus sanguineus*, CM= *Carcinus maenas*.

Experiment	Source	df	Mean Square	F value	p value	Tukey's post hoc
Field	*Semibalanus balanoides*	2	2720.903	14.624	**0.000**	HS < Control, p=**0.000**, HS < CM, p=**0.006**
	Spirorbis sp.	2	3340.339	2.858	0.091	
	Mytilus edulis	2	0.713	0.470	0.634	
	Bare rock	2	7.938	0.282	0.756	
	Crustose algae	2	26.651	0.759	0.478	
	Ephemeral algae	2	0.017	0.451	0.651	
	Fucoid algae	2	0.014	0.365	0.699	
	Mastocarpus/Chondrus	2	3.990	0.170	0.845	
Lab- summer	*Semibalanus balanoides*	2	3.124	11.199	**0.001**	HS < Control, p=**0.001** CM < Control, p=**0.014**
	Spirorbis sp.	2	2.146	25.112	**0.000**	HS < Control, p=**0.000**, CM < Control, p=**0.000**
	Bare rock	2	30.958	0.867	0.432	
	Crustose algae	2	0.462	9.527	**0.001**	HS > Control, p=**0.000**
	Ephemeral algae	2	315.155	3.437	0.054	
	Fucoid algae	2	24.977	3.215	0.065	
	Mastocarpus/Chondrus	2	203.471	2.740	0.079	
Lab- winter	*Semibalanus balanoides*	2	2.253	21.792	**0.000**	HS < Control, p=**0.000**, CM < Control, p=**0.002**
	Mytilus edulis.	2	1.259	3.544	0.053	
	Bare rock	2	0.103	1.928	0.172	
	Crustose algae	2	0.017	0.208	0.814	
	Ephemeral algae	2	0.159	10.139	**0.002**	CM > Control, p=**0.004** HS > Control, p=**0.021**
	Fucoid algae	2	31.294	0.729	0.496	
	Mastocarpus/Chondrus	2	6.400	1.566	0.249	

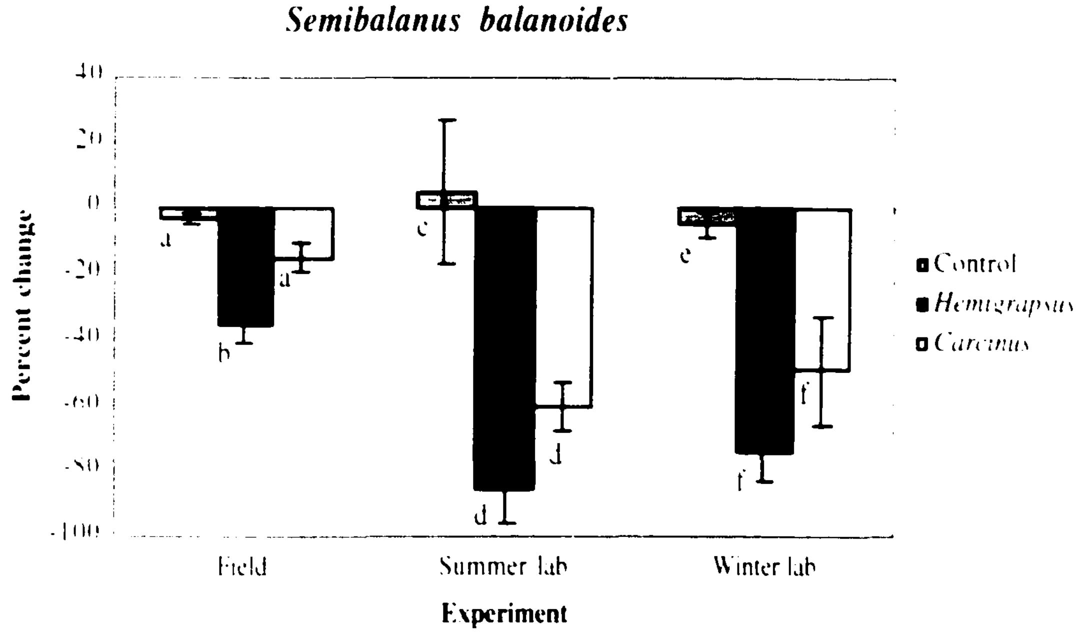


Figure 4.1: Average percent change of *Semibalanus balanoides* in each treatment in each microcosm experiment. Different letters denote treatments that were statistically significant from each other after a sequential Bonferonni correction.

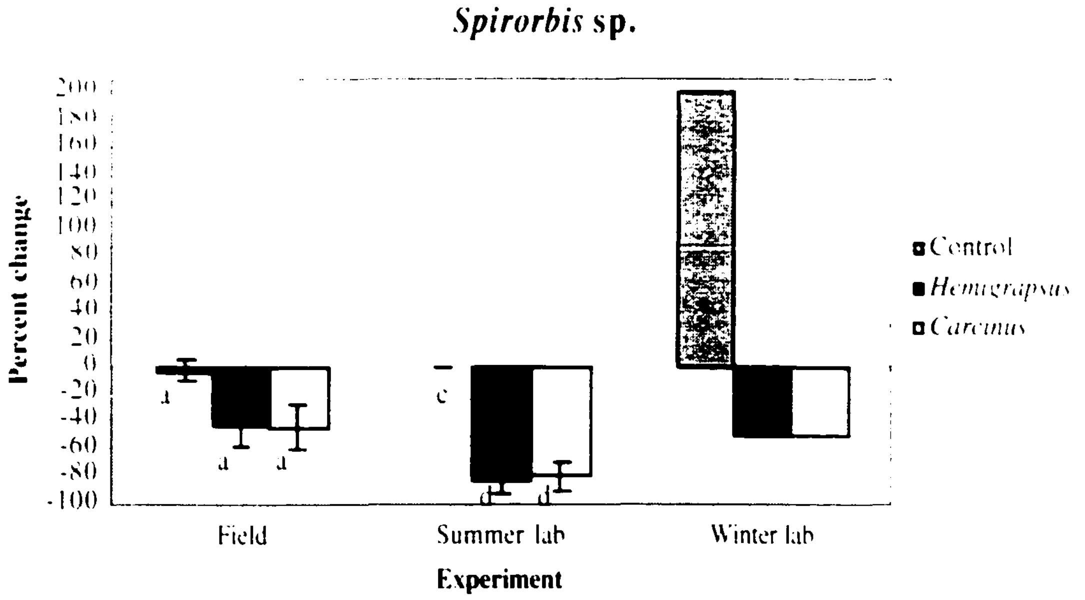


Figure 4.2: Average percent change of *Spirobis* sp. in each treatment in each microcosm experiment. Different letters denote treatments that were statistically significant from each other after a sequential Bonferonni correction.

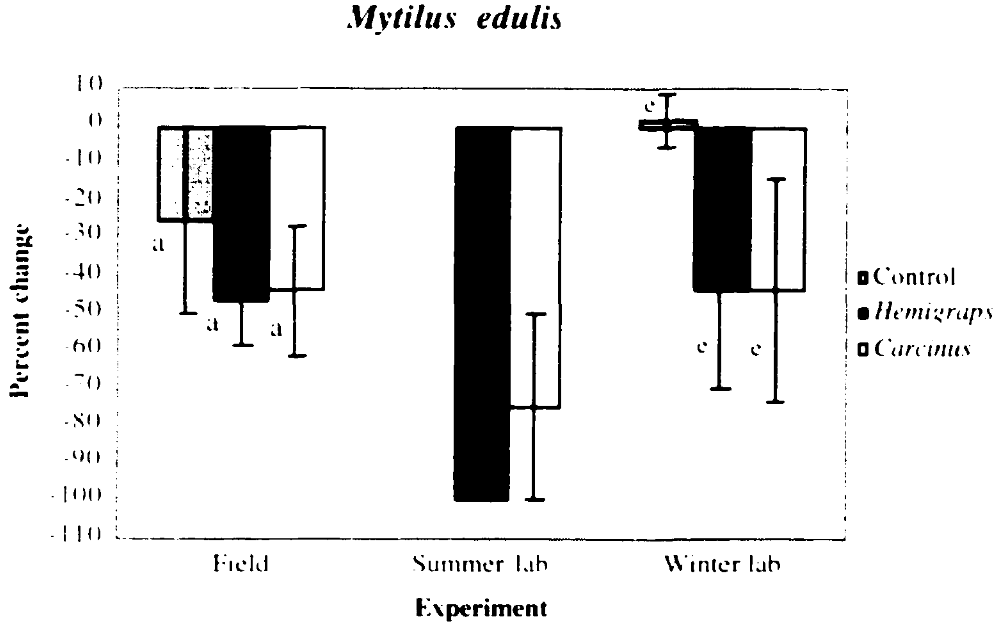


Figure 4.3: Average percent change of *Mytilus edulis* in each treatment in each microcosm experiment.

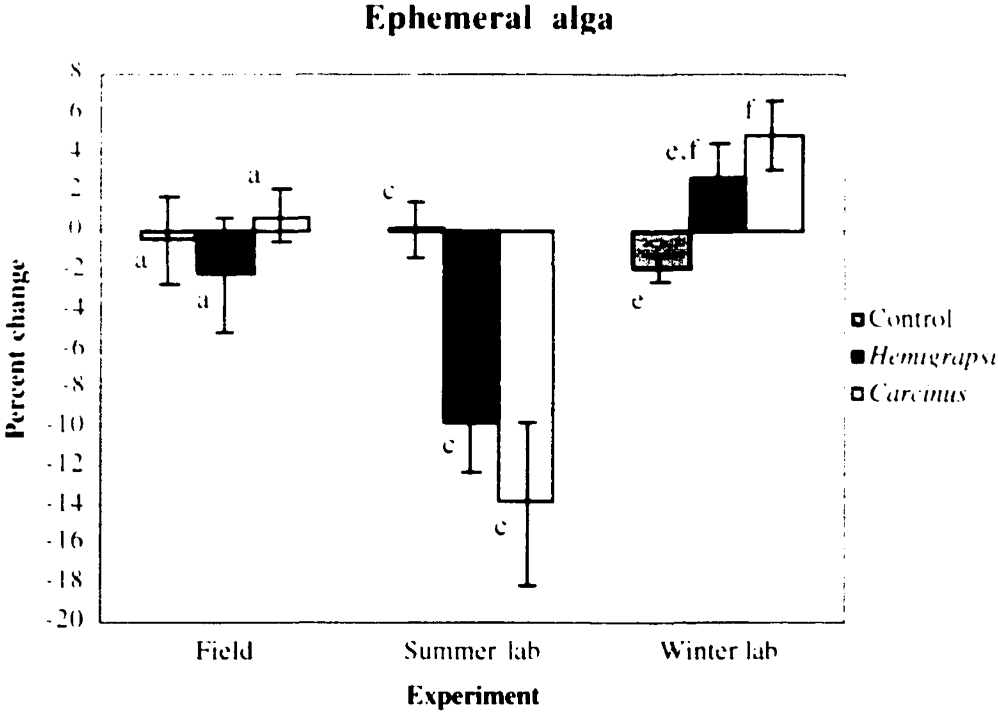


Figure 4.4: Average percent change of ephemeral algae in each treatment in each microcosm experiment. Different letters denote treatments that were statistically significant from each other after a sequential Bonferonni correction.

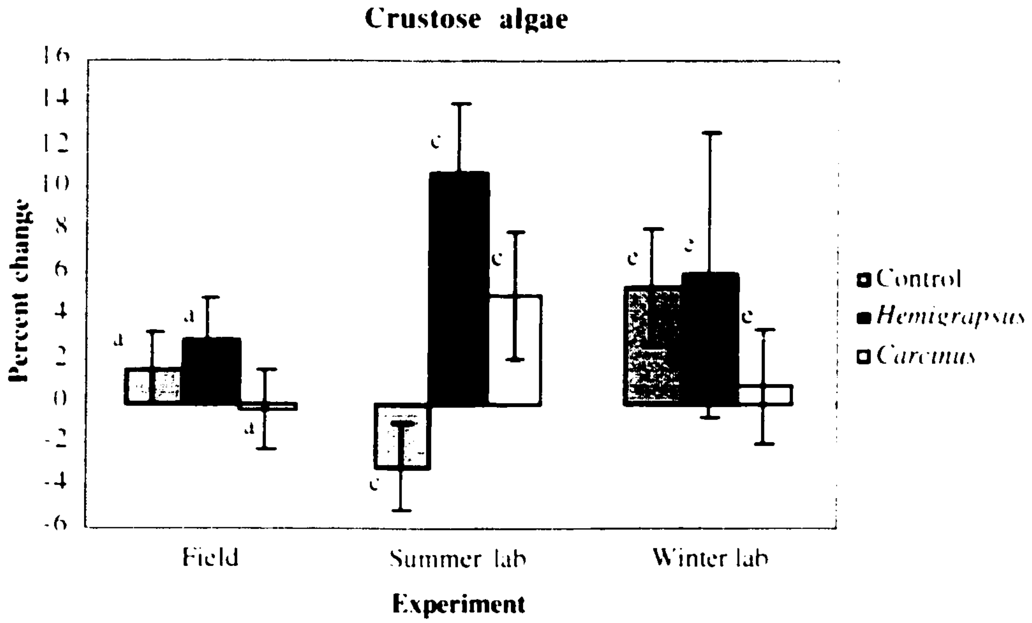


Figure 4.5: Average percent change of crustose algae in each treatment in each microcosm experiment. Different letters denote treatments that were statistically significant from each other after a sequential Bonferonni correction.

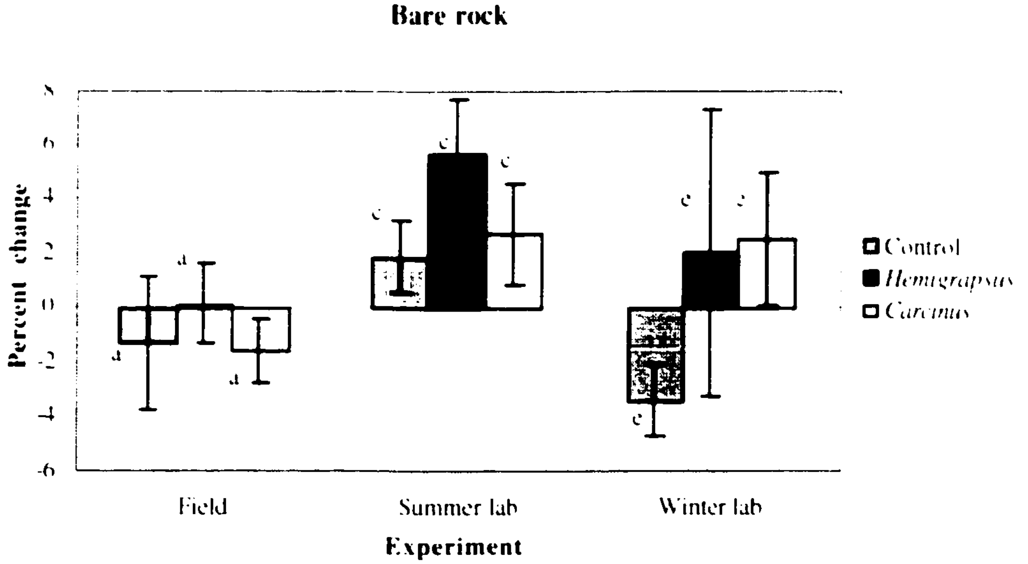


Figure 4.6: Average percent change of bare rock in each treatment in each microcosm experiment.

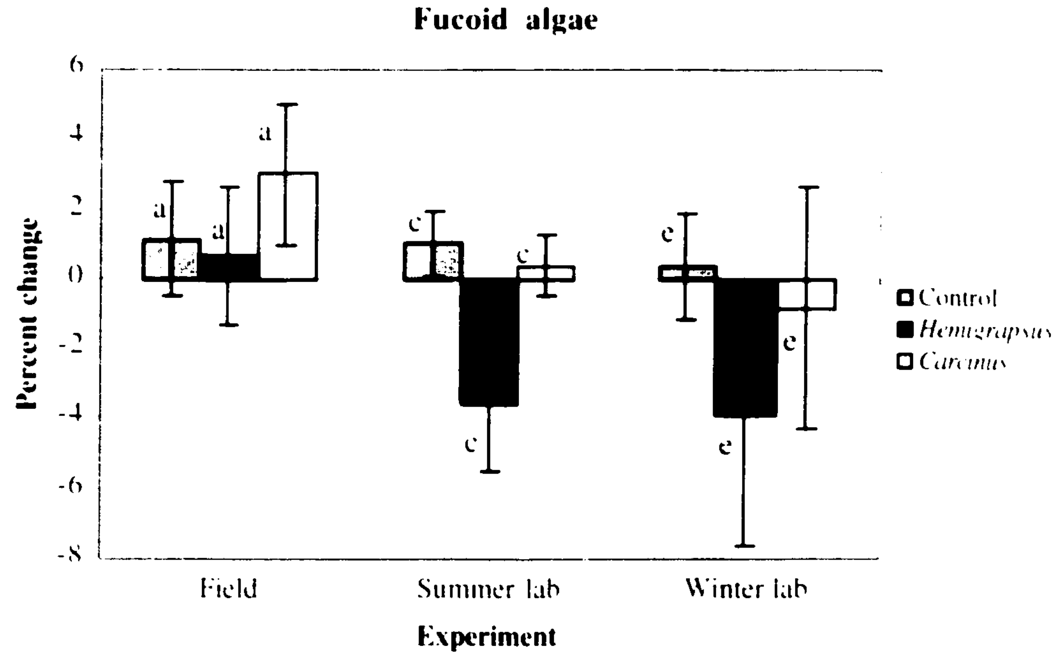


Figure 4.7: Average percent change of fucoid algae in each treatment in each microcosm experiment.

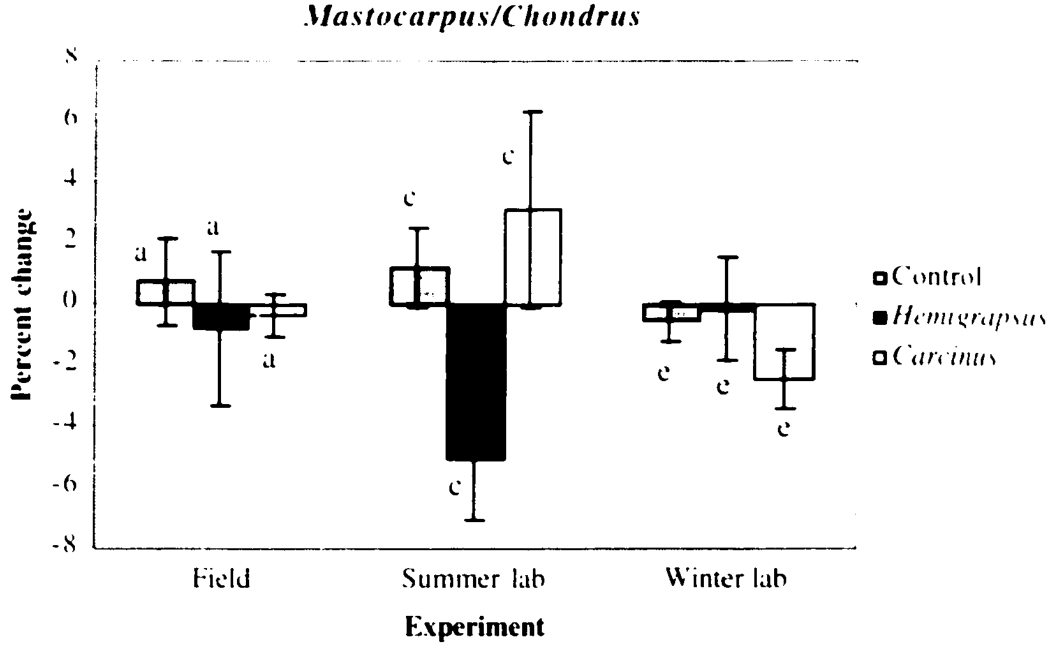
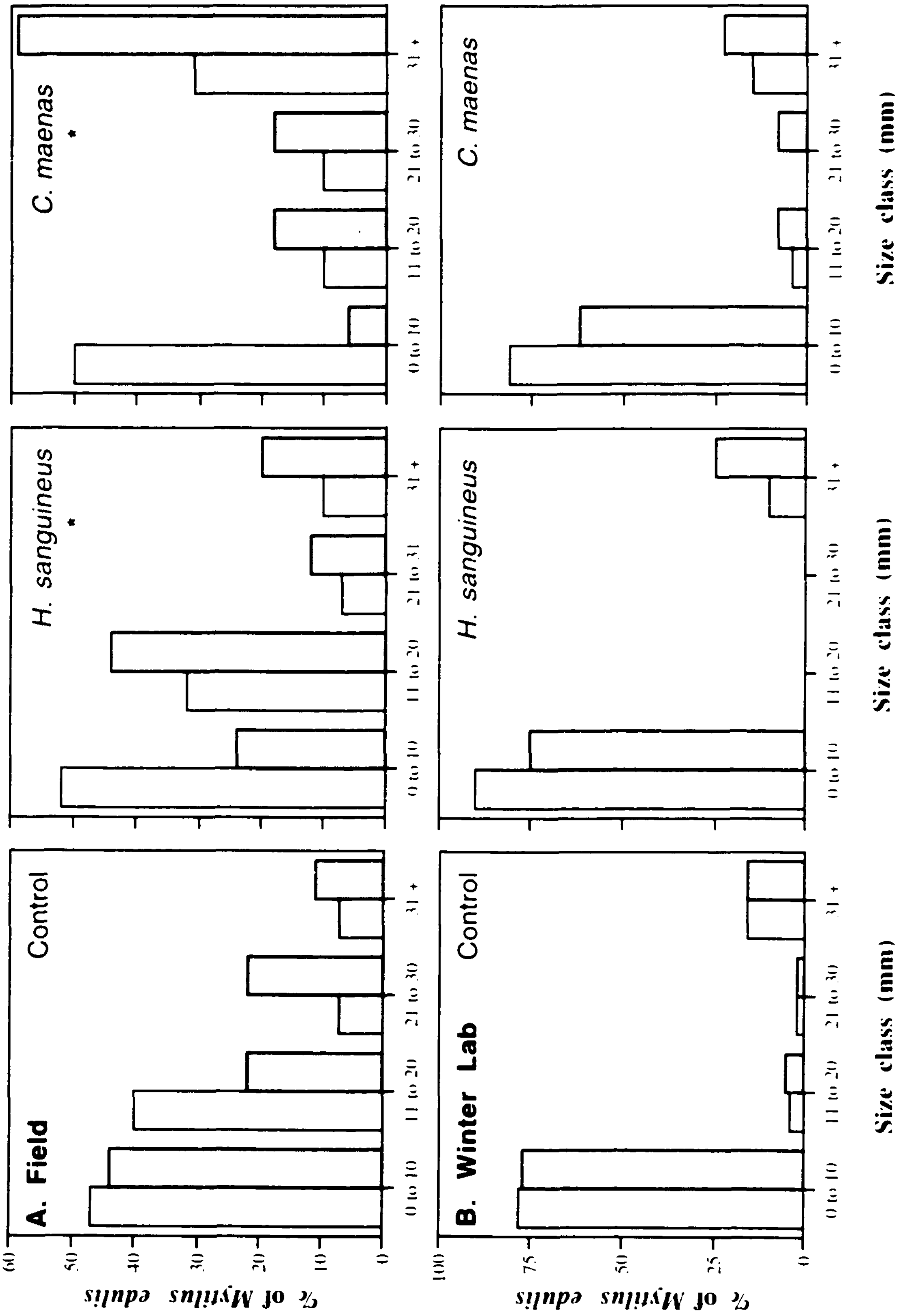


Figure 4.8: Average percent change of *Mastocarpus/Chondrus*, in each treatment in each microcosm experiment.

Figure 4.9: Size frequencies of *Mytilus edulis* in each treatment in the a) summer field and b) winter lab experiments. Open bars are before and shaded bars are after the experimental trial was completed. Asterisks denote statistical significance ($p<0.05$).


A. Field
Control
H. sanguineus
*
C. maenas
*
B. Winter Lab
Control
H. sanguineus
C. maenas
% of Mytilus edulis
0
10
20
30
40
50
60
0
25
50
75
100
0 to 10
11 to 20
21 to 30
31 +
Size class (mm)

CHAPTER V

EFFECTS OF PREDATION BY TWO SPECIES OF INTRODUCED CRABS: INFERENCES FROM LONG TERM MICROCOSM EXPERIMENTS

ABSTRACT

Two introduced crab species currently inhabit the northern New England rocky intertidal zone, *Carcinus maenas* and *Hemigrapsus sanguineus*. *Carcinus maenas* has been established in this region for many years, while *H. sanguineus* is just beginning to establish populations in New Hampshire. The objective of this study was to examine the feeding patterns of these two crab species when presented with microcosms of the rocky intertidal community. Five adult male crabs of each species were placed into enclosures that contained cobble that roughly represented the rocky intertidal community as a whole. Control enclosures did not contain crabs and cage control treatments were only partially enclosed to assess the effects of caging. After fourteen days, the changes that took place in each crab treatment were compared to changes in both types of control treatments.

There was evidence of high aggression between crabs in the cages; many crabs were missing legs or claws and some were apparently killed by conspecifics. Very high consumption of *Semibalanus balanoides* was recorded for the *H. sanguineus* treatment, the decline in *S. balanoides* was statistically significant in the *H. sanguineus* treatment versus all other treatments. The data gathered from these long term microcosm experiments was used to infer some of the possible impacts *C. maenas* had when it was introduced and to predict some of the changes that might take place as populations of *H. sanguineus* continue to increase in this region.

INTRODUCTION

The role of introduced species in influencing the communities they inhabit varies from alteration of food webs to alteration of ecosystem function. When the introduced species is a generalized predator, such as the European green crab, *Carcinus maenas*, both the direct and indirect effects of the introduction can influence the entire community to some extent. For example, *C. maenas* has been introduced to soft substrate habitats on the Pacific coast of the United States (Cohen et al. 1995; Grosholz and Ruiz, 1995; Grosholz et al., 2000) and has caused significant declines in some bivalve and crustacean species (Grosholz et al., 2000). These authors suggested that heavy predation by this crab on burrowing bivalves may have allowed non-prey species such as polychaetes and tube- building tanaids to dramatically increase because of competitive release.

Carcinus maenas has also been found to have considerable impacts on the prey community in Europe. In soft substrate habitats, several authors have found that predation by *C. maenas* can cause statistically significant declines in the abundance of common molluscs (Raffaelli et al., 1989; Fernandes et al., 1999; Richards et al., 1999). In the western Atlantic, where it is also an introduced species, research into the impacts of *C. maenas* has tended to focus on individual prey species (e.g. *Mya arenaria*, Ropes, 1968; *Nucella lapillus*, Vermeij, 1982 and *Littorina obtusata*, Seeley, 1986; Trussell, 1996). In contrast to research on the west coast of the U.S. (e.g. Cohen et al., 1995; Grosholz and Ruiz, 1995; Grosholz et al., 2000), the community wide impacts (direct, indirect effects, potential changes in species richness etc.) of the introduction of *C. maenas* to New England have been neglected.

Currently, another introduced crab species is becoming increasingly abundant in the rocky intertidal zone of northern New England. *Hemigrapsus sanguineus* is now the most abundant crab in rocky habitats in the U.S. mid-Atlantic (New York: Gerard et al., 1999; New Jersey: McDermott, 1998) and southern New England (Connecticut: Lohrer et al., 1997; Ahl and Moss, 1999; southeastern Massachusetts: Ledesma and O'Connor, 2001). There has been much speculation about the impacts of the introduction of this species because it can reach very high densities (estimated at up to 320/m^2, McDermott, 1998) and because it appears to have a high feeding rate (J. DeGraaf and M. C. Tyrrell, in prep.).

In the rocky intertidal zone of temperate regions, predators notoriously have strong effects on their prey. In these regions, predation, either directly or indirectly, has a substantial influence on the structure of the community as a whole (Paine, 1974; Menge, 1976; 1978; Petraitis, 1987; Janke, 1990). However, previous investigations into the impacts of predators in northern New England have not fully accounted for predation by crabs. To date, there have been no studies that have focused on assessing the impacts of *C. maenas* predation in hard substrate communities of northern New England. In addition, the studies that have attempted to assess the impacts of *H. sanguineus* predation have been based on laboratory experiments (Lohrer and Whitlach, 1997; McDermott, 1998; Gerard et al., 1999; Brousseau et al., 2001) with one exception (Lohrer and Whitlatch, 2002).

The objective of this research was to further investigate the feeding patterns of both *C. maenas* and *H. sanguineus* when they were presented with a microcosm of the rocky intertidal community. This research complimented similar previous investigations of the feeding patterns of both crab species in short term (forty-eight hour) lab and field microcosm experiments (Chapter IV; Tyrrell and Madigan, in prep.). The results from the short term microcosm experiments revealed that both *C. maenas* and *H. sanguineus* caused qualitatively similar changes in the abundance of prey, but that *H. sanguineus* had a higher feeding rate on *S. balanoides*. These long term microcosm experiments were designed to determine if the feeding patterns of each species would be similar on a longer time scale and to determine if the difference in feeding rates that was observed in short term experiments persisted. The results from the microcosm experiments were used to retroactively infer impacts of the introduction of *C. maenas* and to predict the impacts of the establishment of *H. sanguineus* in northern New England.

MATERIALS and METHODS

Microcosm experiments were conducted at Ft. Stark, Newcastle, NH (43 03.51N, 70 42.75W). The first set of field microcosm experiments was begun on August 16, 2001 and the last set was completed on September 6, 2001. Each set of experiments consisted of four treatments: a control (no crabs in the cage), a cage control (the bottom half of the mesh covering the openings was removed), a *Hemigrapsus sanguineus* treatment and a *Carcinus maenas* treatment. Preparation for the experiments consisted of two parts: analysis of the community composition on the cobble before being exposed to one of the four treatments, and a repeat of the community composition analysis after the fourteen day experimental period.

Cobble analysis

Cobble covered by a characteristic assemblage of rocky intertidal organisms was selected from the mid to lower intertidal zone of Ft. Stark. The rocks were selected for inclusion in the experiments based on their assemblage of organisms; the cobble were large enough to contain a representative sample of the community but small enough to be transported to the lab. The size range of cobble used in field microcosm experiments ranged from 20 – 28 cm long, 13 – 28 cm wide and 6 – 16 cm high. All mobile organisms (mostly gastropods) associated with the cobble were also collected and placed into a plastic bag.

After being transported to the lab, the rocks were rinsed to insure that all mobile organisms (juvenile crabs, amphipoids, isopods) had been removed. Sessile organisms attached to the rock (*Semibalanus balanoides* [barnacle] and *Spirorbis* sp. [coiled worm] were counted. All molluscs (*Mytilus edulis* [mussels], Littorinid snails and *Notoacmea testudinalis* [limpet]) were measured (shell length) as well as counted. Molluscs that were less than 3 mm shell length were not included in the analysis of results.

The percent cover of sessile species (mostly foliose and encrusting algae) was determined by placing the cobble in a dishpan and filling the dishpan with seawater so that the canopy algae were floating. Plexiglass marked with a grid of random points (15 points/49 cm^2) was then placed over the dishpan. The species (or bare rock) under each point was recorded; the number of points recorded for each cobble ranged from 63 to 193 depending on the size of the rock. A sketch and digital photograph were made of each rock so that the canopy algae could be arranged in the same manner for the post treatment percent cover analysis, thus reducing error associated with this method.

Experimental crabs

Thirty-seven male *Hemigrapsus sanguineus* and sixty-two male *Carcinus maenas* were measured and weighed to determine the carapace width/biomass relationship. This was done in order to utilize crabs with comparable biomass in the microcosm experiments. All *C. maenas* used for the experiments were between 20 –25 mm carapace width (2.03 – 3.39 g; mean weight 2.69 g, SE 0.21 g) and all *H. sanguineus* were 17 – 20 mm (2.25 to 4.08 g; mean weight 3.16 g, SE 0.20 g). Although the average weight of *H. sanguineus* was slightly heavier than *C. maenas*, the overall biomass of each species was roughly comparable. All of the crabs used in the experiments had been maintained on clam meat in the laboratory but were starved for at least two but not more than six days prior to being used in the experiments.

Field microcosms

After initial analysis in the laboratory, the cobble and all mobile organisms associated with it were returned to the Ft. Stark collection site and placed in cages at 0.5 m above mean lower low water. Cages were made from a 17 L translucent plastic storage bin (dimensions 41.2 x 28.7 x 25.3 cm) with a removable cover. The sides and bottom of the bin were cut out and 3 mm plastic mesh was glued over the openings. The bins were placed cover side down and were secured to the substrate using tent stakes and bricks. Each cage was filled with coarse sand to 5 cm depth; the cobble and associated organisms were placed on top of the sand. A total of twenty cages were deployed.

Several minutes after the cobble and associated organisms were placed in to the cages, five similarly sized starved male crabs (of a single species) were placed into experimental enclosures. The stocking density of crabs corresponded to a density of 42 crabs/m^2, which is similar to ambient densities of *C. maenas* at this tidal height at this site (Chapter II).

The microcosms were checked (by looking through the mesh on the top and sides) at least every two days in order to find dead crabs or other potential problems. Drift algae that accumulated on the outside of the cages were removed. Only one dead *H. sanguineus* was discovered during these checks and this crab was replaced the following day with a similarly sized starved male crab.

The experiments were concluded after fourteen days by removing the cobble, associated organisms and crabs from the cages. In many cases, only some of the experimental crabs were initially recovered while the cage was located in the field and in those cases, all of the sediment in the cage was sieved through a 0.5 cm mesh to retrieve the remaining crabs. The cobble and their associated organisms were returned to the laboratory and the percent cover analysis was repeated, the number of barnacles and *Spirorbis* sp. was determined and snails and mussels were counted and measured. Other changes (such as the disappearance of species) that had occurred during the experimental time period were also noted.

Analysis

The percent change in the abundance of organisms on or associated with the cobble was calculated to compare the two types of control treatments with the two crab treatments. The percent change was calculated for both count data and for percent cover data. The size frequency distributions of organisms before and after the experiment were analyzed with Chi Square tests in Instat version 2.01 (Graphic software).

To facilitate the analysis of results for the percent cover data, some types of algae were combined into categories because they have similar functional roles within the community. The crustose algae category included: *Phymatolithon laevigatum, Lithothamnion glaciale* and *Clathomorphum circumscriptum, Hildenbrandia rubra, Verrucaria* sp. and *Ralfsia verrucosa.* The fucoid algae category was composed of *Fucus vesiculosus* and *Ascophyllum nodosum.* In addition, an ephemeral algae category was created to incorporate several non-perennial species that were found on the cobble including: *Chaetomorpha* sp., *Cystoclonium purpureum*, *Ahnfeltia plicata*, *Enteromorpha* sp., diatoms and one unidentified red and brown ephemeral algae species each. All data were checked for normality and homoscedasticity prior to analysis of variance (ANOVA). The percent change data were subjected to ANOVA and Tukey's HSD post hoc test using Systat version 9 (SAS institute). Because seven univariate ANOVA's were performed, a sequential Bonferonni correction was used. Exploratory data analysis was also done using Discriminant analysis in Systat version 9 (SAS institute). The same seven categories that were tested using ANOVA were the predictor variables for the Discriminant analysis. The groups for the Discriminant analysis were the four types of treatments.

RESULTS

Unexpected results of these caging experiments were that there were high levels of aggression between the crabs within the cages. Two juvenile non-experimental crabs were also recovered from the cages at the end of the experiment. Many of the crabs that were recovered at the end of the experiment were missing multiple limbs and there were other signs of aggression: four *C. maenas* and two *H. sanguineus* were eaten by conspecifics (Appendix A). The average mortality in the *C. maenas* treatment was 20% while in the *H. sanguineus* treatment, the average mortality was 10%. Fragments of exoskeleton were often found in the cages, indicating that the missing crabs were presumably eaten and did not escape. In addition, several of the *C. maenas* that were recovered at the end of the experiment had molted. Two juvenile crabs (one *H.*

sanguineus and one *C. maenas*) that were not intended to be included in the experiments were recovered while sieving the sediment from the cages at the end of the experiment (see Appendix A for details). It is unlikely that these small crabs crawled into the cages during the course of the experiment because the cages were secure and checked often to insure that crabs could not escape.

In addition to the high levels of aggression between crabs in the experiments, there was also high consumption of *Semibalanus balanoides* by *H. sanguineus*. The decline in the number of *S. balanoides* was statistically significant for the *H. sanguineus* treatment versus both types of control treatments and versus the *C. maenas* treatment (Table 5.1; Fig. 5.1). In one *H. sanguineus* treatment, the number of *S. balanoides* declined from 221 to 71 and all of the remaining barnacles were relatively large (estimated to be >5 mm test diameter). Although it appeared that *S. balanoides* also declined in the *C. maenas* treatments relative to the controls, none of these differences were statistically significant (Fig. 5.1). The numbers of *Spirorbis* sp. declined in all of the treatments over the two weeks of the experiment, but there were not any statistically significant differences between the treatments (Fig. 5.2). The amount of rock that was exposed was not significantly different between any of the treatments (Fig. 5.3) and the changes in the amount of crustose algae were also not significantly different between any of the treatments (Fig. 5.4). It appeared that the amount of ephemeral algae declined in the *H. sanguineus* treatment relative to changes in the control treatments, but again, this difference was not statistically significant (Fig. 5.5). The change in cover by fucoid algae was significantly higher in the *C. maenas* treatment versus the control and cage control treatments (Fig. 5.6) and there were no significant differences between the treatments for changes in *Mastocarpus stellatus* (Fig. 5.7).

To examine differences between treatments when all of the seven categories of data are considered simultaneously, a discriminant analysis was performed. The discriminant analysis requires a value in every cell even when a particular organism was not recorded for the cobble. There were fifteen cases (out of a possible 140) where a zero had to be filled in for one of the predictor values. The effect of this requirement is to make the results of the discriminant analysis conservative. The discriminant analysis revealed that the differences between the four treatments were statistically significant (p=0.041) and the classifications for each treatment were relatively high (Table 5.2). The canonical discriminant functions are listed in Table 5.3. They show that the changes in the *S. balanoides* treatment were most important in discriminating between the groups.

The composition of the cobble community was generally similar between all of the replicates, but several species that were consumed in the crab treatments did not occur in high enough numbers to be included in statistical analysis. These uncommon species included: the chiton, *Tonicella rubra* and the jingle shell, *Anomia simplex*. In addition, the alga *Cystoclonium purpureum* was recorded on two rocks that were *H. sanguineus* treatments; in both cases, this species was not present after the fourteen day experimental period (these data are included in the ephemeral algae category).

<u>Size frequency</u>

Littorina littorea was the only species that occurred in high enough numbers to undergo Chi-Square tests for changes in size frequency distribution. In order to achieve sufficient numbers of *L. littorea* in particular size categories, all snails larger than 26 mm shell length were grouped and some of the smaller size categories also were grouped. The Chi-Square test showed that there were no significant differences between the population structure of *L. littorea* before and after for the *C. maenas*, *H. sanguineus* and control treatments (all p values > 0.67; Fig. 5.8). However, there was a significant difference in size frequency distributions for the cage control treatment (χ^2 =35.86, df=5, p<0.0001) and a Chi-Square test for trend also indicated that the size frequency distribution of snails left in the cage control treatment was composed of bigger snails (χ^2 for trend= 28.11, df=1, p<0.001; Fig. 5.8).

DISCUSSION

Results from these long term microcosm experiments provide insight into some of the changes that may have occurred in the rocky intertidal community following the establishment of *Carcinus maenas* and some of the changes that may occur as *Hemigrapsus sanguineus* becomes common in northern New England. The most striking result from these experiments was the decline in the number of *Semibalanus balanoides* in the *H. sanguineus* treatments, especially versus the *C. maenas* treatment. Based on the results from similar short term microcosm experiments (Chapter IV; Tyrrell and Madigan, in prep.) and from previous observations of *C. maenas* in England (Rangely and Thomas, 1987) it also seems likely that *S. balanoides* may have experienced increased predation pressure when *C. maenas* was introduced. The results from the discriminant analysis support the conclusion that a decline in the abundance of *S.*

balanoides may be expected when crabs are abundant in a community. As populations of *H. sanguineus* continue to expand in northern New England, the abundance of *S. balanoides* may decrease even further than it likely did when *C. maenas* was introduced.

Similar studies that have examined the impacts of *C. maenas* predation in soft substrate habitats have revealed significant reductions in bivalve densities when enclosed with naturally occurring *C. maenas* densities (Richards et al., 1999) and with enhanced *C. maenas* densities (Raffaelli et al., 1989; Fernandes et al., 1999). The differences in results between caging studies in soft sediment habitats (i.e. *C. maenas* caused large reductions in bivalve densities) and this study (large reductions in *S. balanoides*, changes in *Chaetomorpha* sp. important in discriminating between crab and control treatments) are likely due to the different species compositions of the two habitats. There is strong evidence from examinations of gut contents that *C. maenas* in the northwest Atlantic are primarily molluscan predators (Ropes, 1968; Elner, 1981; Raffaellei et al., 1989), but in this study, there was little evidence of predation on any of the mollusc species (with the exceptions noted above, *Tonicella rubra, Anomia simplex*). It is likely that the majority of the *Mytilus edulis* that were present in the microcosms were too large to be eaten by the *C. maenas*. In addition, *Littorina littorea*, the only other mollusc that was common in the microcosms, was lowest on a preference hierarchy in laboratory feeding preference studies with *C. maenas* and *H. sanguineus* (Tyrrell and Harris, 2001). Therefore, it is likely that the high predation levels on *S. balanoides* that were observed in this study could be due to the lack of other prey that are preferred by the crabs or the lack of prey in size ranges that were accessible to the crabs. The lack of small *M. edulis* and other prey organisms that are preferred by the crabs may be due to the fact that the cobble were taken from a community that is already affected by *C. maenas* predation.

The increase in the amount of fucoid algae in the *C. maenas* treatment relative to the control and cage control treatments was unexpected and could be due to several factors. Although none of the declines in the abundance of other prey species in *C. maenas* treatments were statistically significant (*S. balanoides*, *Spirorbis* sp. and a smaller increase in ephemeral algae than in either type of control treatment), the collective effect of these changes in relative abundance may have resulted in an apparent increase in the amount of fucoid algae. Alternatively, the significant difference may simply be an artifact of the method to assess changes in algal abundance (percent cover) and low replication. A small shift in the position of a clump of fucoid algae could result in many more points being intersected and therefore, this method is not optimal for assessing the abundance of algae. A preferable method to assess changes in algae would be to measure biomass, but this would have required removing the algae from the cobble and the objective of this experiment was to present the crabs with realistic microcosms of the rocky intertidal community.

The potential consequences of the invasions of these two crabs species extend beyond decreased abundance of *S. balanoides* to indirect effects on other predators and other potential prey species. For example, *Semibalanus balanoides* is an important food source for the intertidal predatory snail, *Nucella lapillus* (Menge and Lubchenco, 1981). The high levels of consumption of *S. balanoides* by *H. sanguineus* could not only cause competition for food with *N. lapillus*; but the presence of crabs also appears to alter the predatory behavior of this gastropod (Matthews- Cascon, 1997). In addition, a potential decline in *S. balanoides* could have indirect consequences for many other species that interact with it. For example, the physical structure of barnacle tests may provide sufficient heterogeneity to enhance the recruitment and survival of both algae and animals. Lubchenco (1983) found that the microtopography created by barnacle tests could enhance survival of *Fucus* sp. germlings and Petraitis (1987) also suggested that the presence of barnacles could positively influence mussel recruitment.

Mytilus edulis is a superior competitor for space and may be kept from monopolizing space on in the low zone of sheltered rocky shores because of heavy predation pressure (Menge, 1976). This species is preferred by both crab species (Tyrrell and Harris, 2001), and heavy predation pressure on small mussels may account for their relative absence in the microcosms. As *H. sanguineus* becomes more common in northern New England, there may be a precipitous decline in mussel abundance due to the combined effects of direct predation along with the indirect effect of reduced recruitment because of a reduced abundance of barnacle tests and ephemeral algae (which also enhances mussel recruitment).

The high levels of mortality in the crab treatments, apparently due to cannibalism, were surprising. It is impossible to determine if the crabs that were eaten by conspecifics were molting or hard shelled, because the cages were not continually monitored. Compared to *H. sanguineus*, twice as many *C. maenas* were eaten and showed signs of intraspecific aggression. This may indicate that *C. maenas* are more aggressive toward conspecifics. However, the fact that two *C. maenas* successfully molted during the experimental period may indicate that at the time the experiments were conducted, many *C. maenas* were molting, thus leaving them more susceptible to cannibalism. Several other caging experiments with *C. maenas* have revealed comparable average mortalities ranging from 20% to 40% after month long experiments (Raffaelli et al. 1989; Fernandes et al., 1999; Richards et al., 1999). Lohrer and Whitlatch (2002) conducted the only other study where *H. sanguineus* and *C. maenas* were placed in cages in the field. They found low mortality of adult crabs of both species during the seven day experiments and that *H. sanguineus* significantly reduced the abundance of 0-year *C. maenas* when compared to control treatments. Cages inhibit the movement of the experimental animals and may inflate the level of conspecific aggressive encounters versus what may be expected under natural conditions.

A potential artifact of using caging experiments to assess predation levels is the fact that cages hinder both prey and predator movement, thus artificially inflating the effects of predation. The stocking density of crabs that was used for these experiments was based on the density of *C. maenas* (averaged for three years) at the same tidal height at the Ft. Stark site. These density data were collected at low tide when the majority of crabs are not foraging but resting in shelters. The high levels of consumption of prey (and possibly the high levels of aggression) that were observed in this study could be due to unnaturally high densities of foraging crabs in the cages. However, other authors that have investigated the impacts of predation by *C. maenas* have used densities that were ten times naturally occurring densities (Richards et al., 1999). The emigration of small *L. littorea* out of the cage control treatment may reflect their apparent vulnerability to predation by *C. maenas* (Lubchenco, 1978) even though this species is low on their preference hierarchy (Tyrrell and Harris, 2001). In quantitative community sampling, I found that proportion of small *L. littorea* (0-10 mm shell length) increases with increasing tidal height at Ft. Stark (Chapter II). Small *L. littorea* may have diminished survival in the lower intertidal zone where these experiments were conducted.

The low replication of treatments in this study as well as the high variability in relative abundance of species associated with the cobble could reduce power to detect differences between the treatments (Cohen, 1977). However, a large effect size was anticipated based on previous microcosm experiments (Chapter IV; Tyrrell and Madigan, in prep). In addition, the number of replicates used in this experiment (five) equaled or exceeded that of other authors that used cages to examine the impacts of *C. maenas* predation on community structure (Thrush, 1986; Raffaelli et al., 1989; Fernandes et al., 1999; Richards et al., 1999). The sequential Bonferonni correction of the experimental alpha caused a loss of statistical significance for the ephemeral algae and crustose algae categories (all p values were less than 0.05 but greater than 0.007) and is considered a conservative method to reduce the chance of committing a type I error. Rafaelli et al. (1989) also performed seven univariate ANOVA's on various prey species in their *C. maenas* caging experiments and did not do the Bonferonni correction, however, Fernandes et al. (1999) did fifteen ANOVA's and they did use the Bonferonni correction. I chose to take a conservative route, following Fernandes et al. (1999), but I may have raised the probability of committing a type II error by using such a low p value.

Englund (1997) noted that the rate of prey movement could potentially confound interpretation of the effects of predators in caging experiments where some prey are allowed to move in and out of cages. In the present study, the mesh size excluded movements of all but the smallest potential prey items such as amphipods and isopods. Previous examination of the gut contents of *C. maenas* (Ropes, 1968; Elner, 1981;

Raffaellei et al., 1989) did not indicate that these crustaceans form a major part of the diet of *C. maenas* and the same holds true for *H. sanguineus* (Lohrer, 2000; Tyrrell and Harris, 2001). However, Lesdesma and O'Connor (2001) found that crustacean parts were the most commonly encountered food item in the guts of *H. sanguineus* collected from various locations in Buzzards Bay, Massachusetts. In order to include these prey in the microcosm experiments, the mesh size on the cage would have had to have been very small (ca. 1 mm) which may have inhibited water flow and enhanced other caging artifacts (shading, etc.). In addition, amphipods and isopods are extremely difficult to quantify because of their small size and high mobility. Therefore, these microcosm experiments do not account for crab predation on small crustaceans, but the evidence that these organisms are important in their diet is inconclusive.

Tyrrell and Harris (2001) created two schematic models of the potential impacts of the establishment of *H. sanguineus* in northern New England. One of these models focused on potential competitive interactions with *C. maenas* and the other model proposed several scenarios regarding potential changes in community structure depending on the diet of *H. sanguineus*. They suggested that *H. sanguineus* is most likely to have an omnivorous diet in northern New England, and the results from microcosm experiments (this study, Chapter IV) support this assertion. In addition, Tyrrell and Harris (2001) proposed that *H. sanguineus* was likely to outcompete *C. maenas* for food and shelter. The results from these microcosm experiments suggest that potential competition for food could occur between the two crab species because of similar feeding patterns, but the microcosm experiments were not designed to address competitive interactions specifically. However, the evidence that *H. sanguineus* has a higher feeding rate than *C. maenas* is mounting (results from *S. balanoides* in this study and short term field microcosm experiments, on *M. edulis*: DeGraff and Tyrrell, in prep.). It is possible that one mechanism by which this new invader could suppress the old invader is via reducing the availability of food. However, it should be noted that the mean biomass of *H. sanguineus* used in these experiments was slightly larger than that of *C. maenas*. Further experimentation to compare the feeding rates of these two crab species would clarify if apparent pattern of *H. sanguineus* having a significantly higher feeding rate than *C. maenas* persists. If *H. sanguineus* has an omnivorous diet and its high feeding rate causes a decline in the availability of food for *C. maenas*, the result could be declines in the abundance of *H. sanguineus*' preferred foods (see Tyrrell and Harris, 2001; Figure 8, Community 2) as well as in populations of *C. maenas* (see Tyrrell and Harris, 2001; Figure 7).

In conclusion, it appears increasing densities of *H. sanguineus* have the potential to cause declines in the abundance of the barnacle *Semibalanus balanoides* in northern New England. The lack of statistically significant declines in the abundance of other prey species in these experiments does not imply that other prey organisms are immune to the effects of crab predation. As demonstrated by this study and other studies of the effects of *C. maenas* predation, the introduction of a generalist predator can cause significant changes in the abundance or morphology of particular prey species (*L. obtusata* [Seeley, 1986], *Nucella lapillus* [Vermeij, 1982]). The community-wide impacts of crab predation may include increased relative abundance of perennial algae due to the consumption of epiphytic algae by crabs (especially *H. sanguineus*), altered gastropod activity due to the presence of crabs, (for *L. littorea*: Jacobsen and Stabell, 1999; for *N. lapillus*: Palmer, 1990; Vadas et al., 1994) and myriad indirect effects of these shifts in relative abundance or behavior. The changes in the microcosms caused by *C. maenas* and *H. sanguineus* were similar overall, indicating that these two introduced species could compete for food, if this resource is limiting. The apparent higher feeding rate of *H. sanguineus* on *S. balanoides* and the fact that it dominates *C. maenas* under other conditions (Lohrer and Whitlatch 2002; B. Hull and M. Tyrrell, unpub. data, pers. obs.) indicates that this new invader may have a greater overall effect on the rocky intertidal community, and that it could even cause a decline in the abundance of the previously introduced *C. maenas*.

Table 5.1: One-way analysis of variance of abundance in all treatments, significant values (after sequential Bonferonni correction) are in bold.

Source	**df**	**MS treatment**	**F**	**P**	**Tukey's post hoc**
Semibalanus balanoides	3	5923.178	19.502	**0.000**	*H. sanguineus* > *C. maenas*, p=**0.003** *H. sanguineus* > cage control, p=**0.000** *H. sanguineus* >control, p=**0.000**
Spirorbis sp.	3	1049.194	0.836	0.507	
Bare rock	3	54.922	0.874	0.476	
Crustose algae	3	44.237	0.858	0.483	
Ephemeral algae	3	163.943	2.763	0.081	
Fucoid algae	3	98.786	6.541	**0.007**	*C. maenas* > control, p=**0.006** C. maenas > cage control, p=**0.019**
Mastocarpus stellatus	3	72.579	1.837	0.181	

Table 5.2: Results from discriminant analysis of long term microcosm experiments. HS= *Hemigrapsus sanguineus*, CM= *Carcinus maenas*.

Wilk's lambda	Approximate F	df	p value	% classified correctly	Jackknifed classification
0.077	2.009	21, 29	**0.041**	Control 60	Control 40
				Cage control 80	Cage control 60
				HS 100	HS 60
				CM 100	CM 60

Table 5.3: Canonical discriminant functions standardized by within variances for long term microcosm experiments..

Factor 1	Canonical discriminant function	Factor 2	Canonical discriminant function
Semibalanus balanoides	-1.056	Fucoid algae	2.148
Mastocarpus stellatus	0.682	Bare rock	1.734
Bare rock	0.560	Ephemeral algae	1.459
Ephemeral algae	-0.268	*Mastocarpus stellatus*	1.092

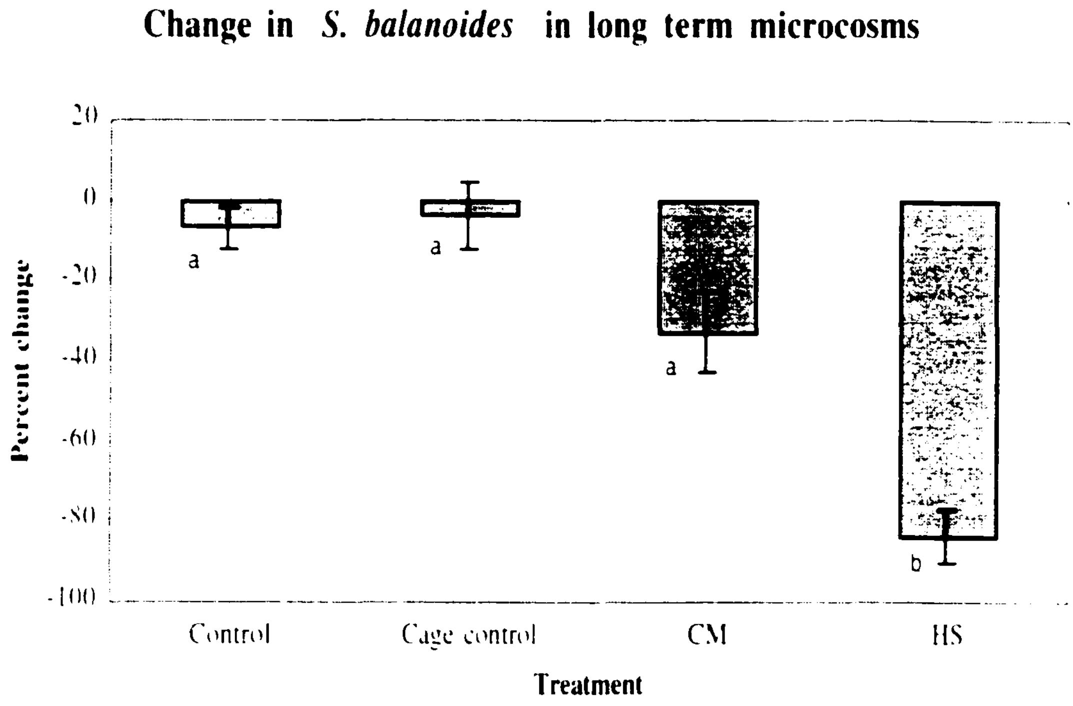


Figure 5.1: Average percent change (and standard error) in the abundance of the barnacle, *Semibalanus balanoides*, in long term field microcosm experiments with *Carcinus maenas* and *Hemigrapsus sanguineus*. Different letters denote treatments that were significantly different from each other after a sequential Bonferonni correction. CM=*C. maenas* and HS=*H. sanguineus*.

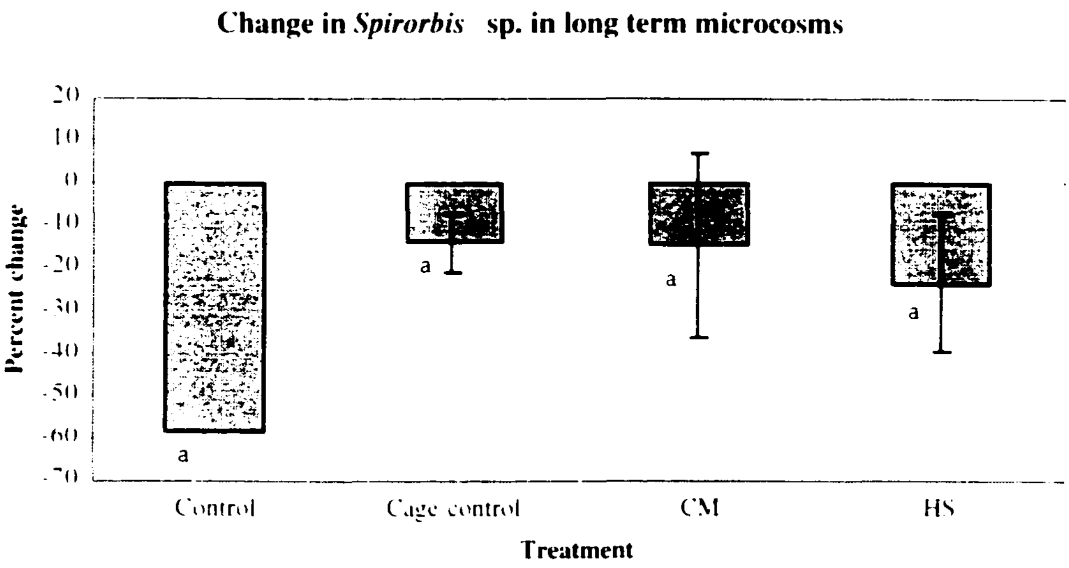


Figure 5.2: Average percent change (and standard error) in the abundance of the coiled worm, *Sprirorbis* sp., in long term field microcosm experiments with *Carcinus maenas* and *Hemigrapsus sanguineus*. CM=*C. maenas* and HS=*H. sanguineus*.

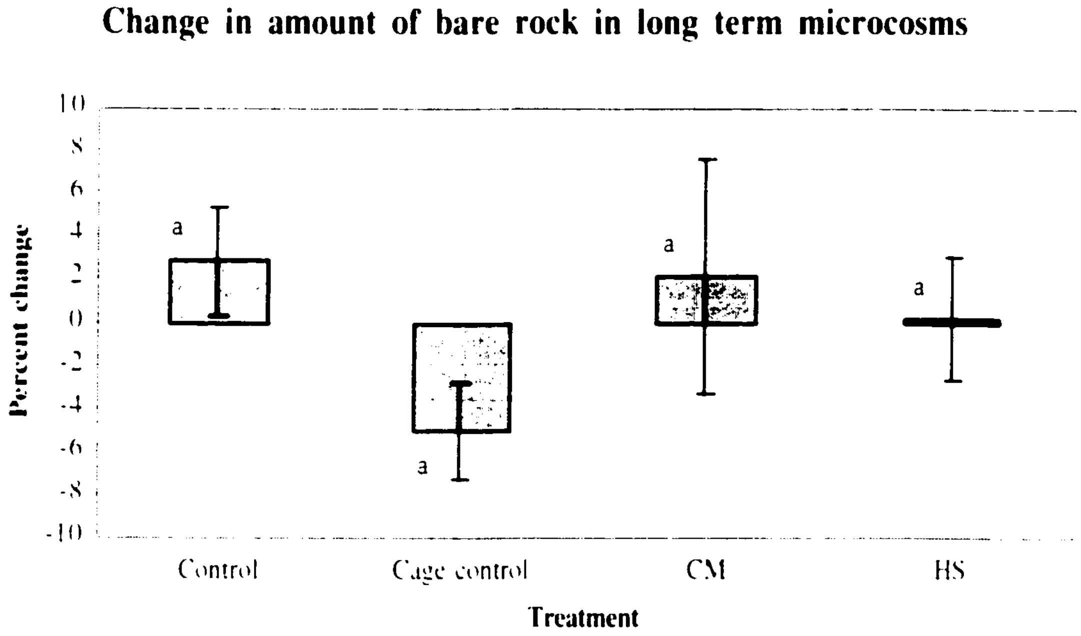


Figure 5.3: Average percent change (and standard error) in the abundance of bare rock that was exposed in long term field microcosm experiments with *Carcinus maenas* and *Hemigrapsus sanguineus*. CM=*C. maenas* and HS=*H. sanguineus*.

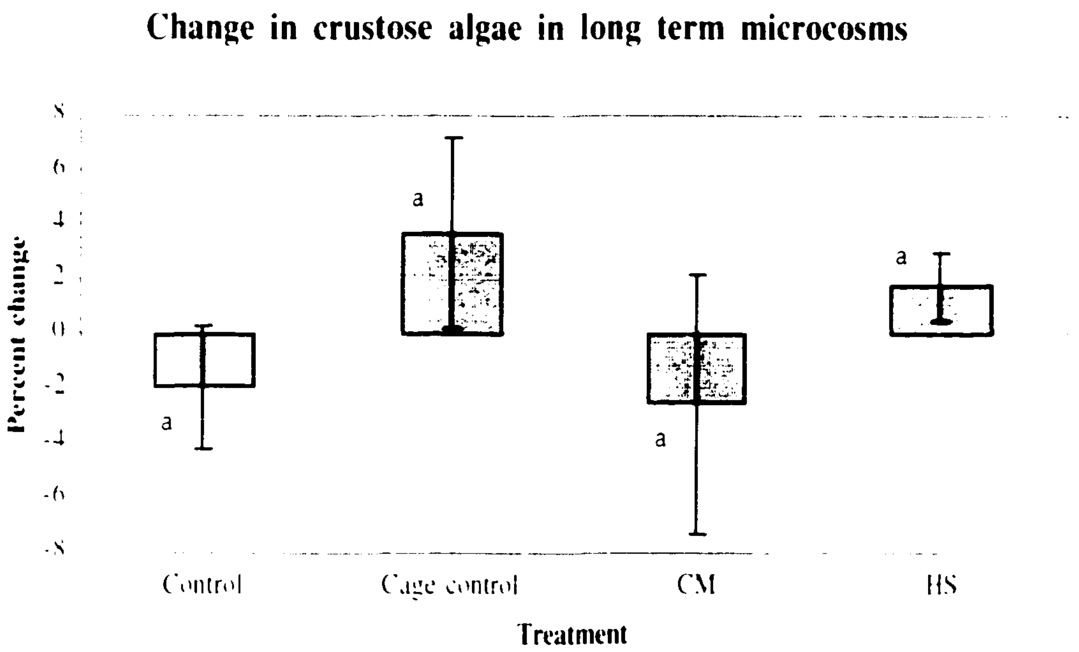


Figure 5.4: Average percent change (and standard error) in the abundance of crustose algae in long term field microcosm experiments with *Carcinus maenas* and *Hemigrapsus sanguineus*. CM=*C. maenas* and HS=*H. sanguineus*.

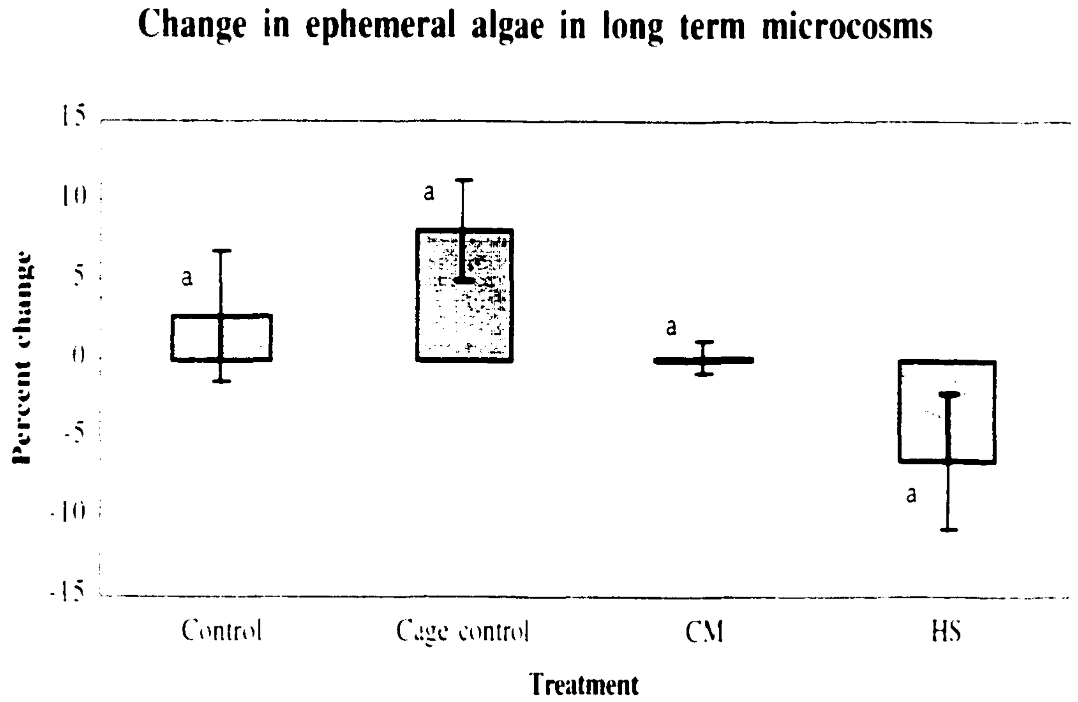


Figure 5.5: Average percent change (and standard error) in the abundance of ephemeral algae in long term field microcosm experiments with *Carcinus maenas* and *Hemigrapsus sanguineus*. CM=*C. maenas* and HS=*H. sanguineus*.

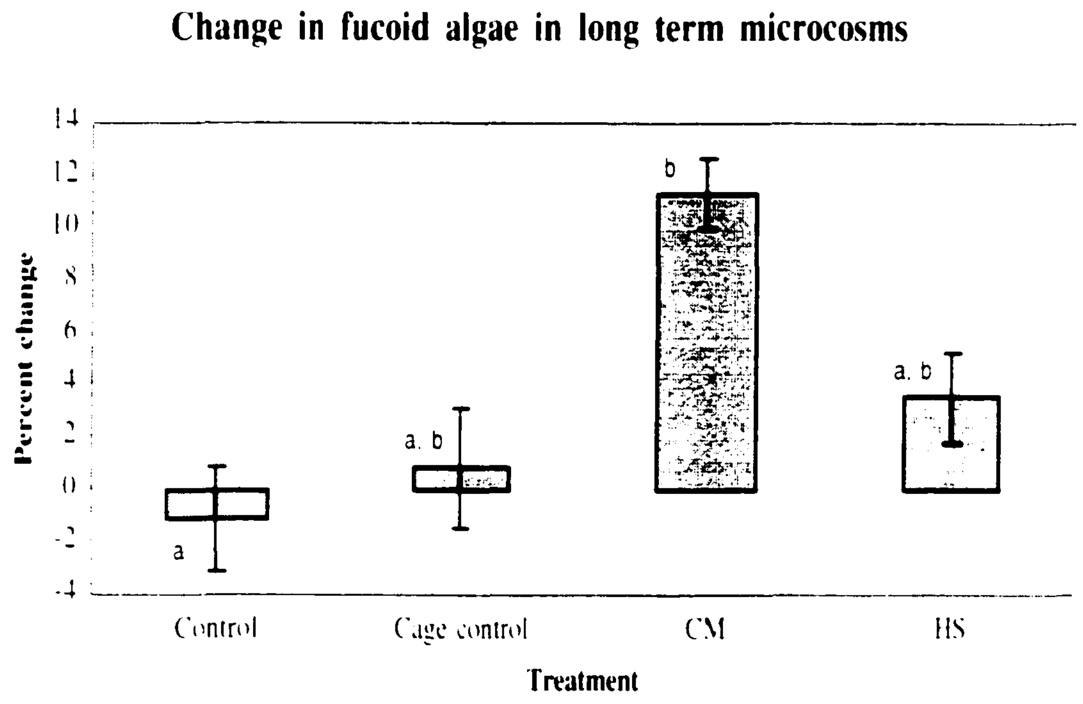


Figure 5.6: Average percent change (and standard error) in the abundance of fucoid algae in long term field microcosm experiments with *Carcinus maenas* and *Hemigrapsus sanguineus*. Different letters denote treatments that were significantly different from each other after a sequential Bonferonni correction. CM=*C. maenas* and HS=*H. sanguineus*.

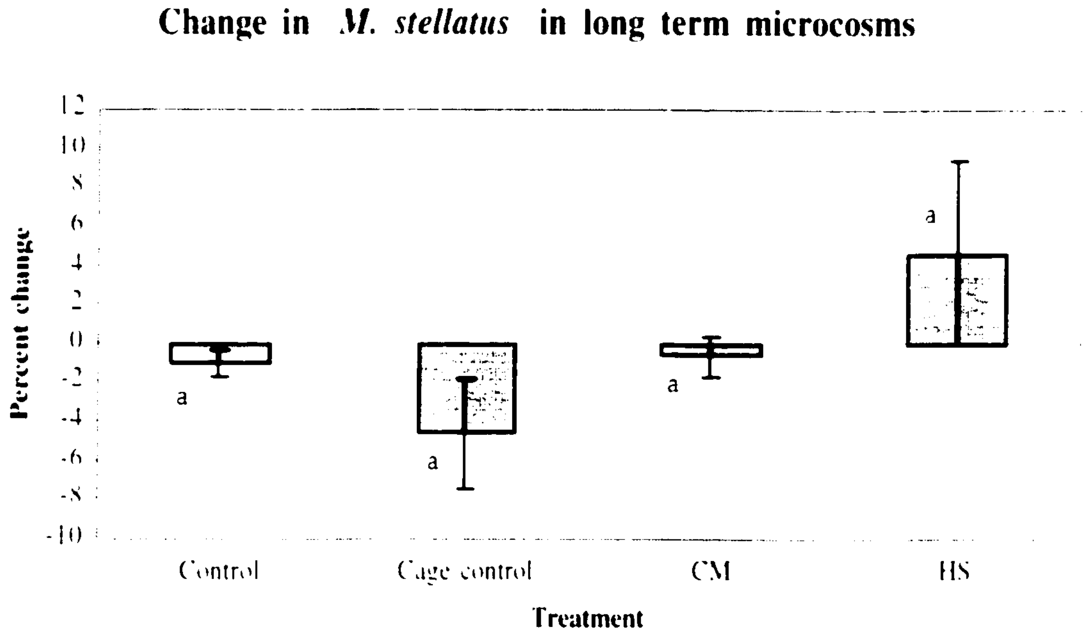


Figure 5.7: Average percent change (and standard error) in the abundance of *M. stellatus* in long term field microcosm experiments with *Carcinus maenas* and *Hemigrapsus sanguineus*. CM=*C. maenas* and HS=*H. sanguineus*.

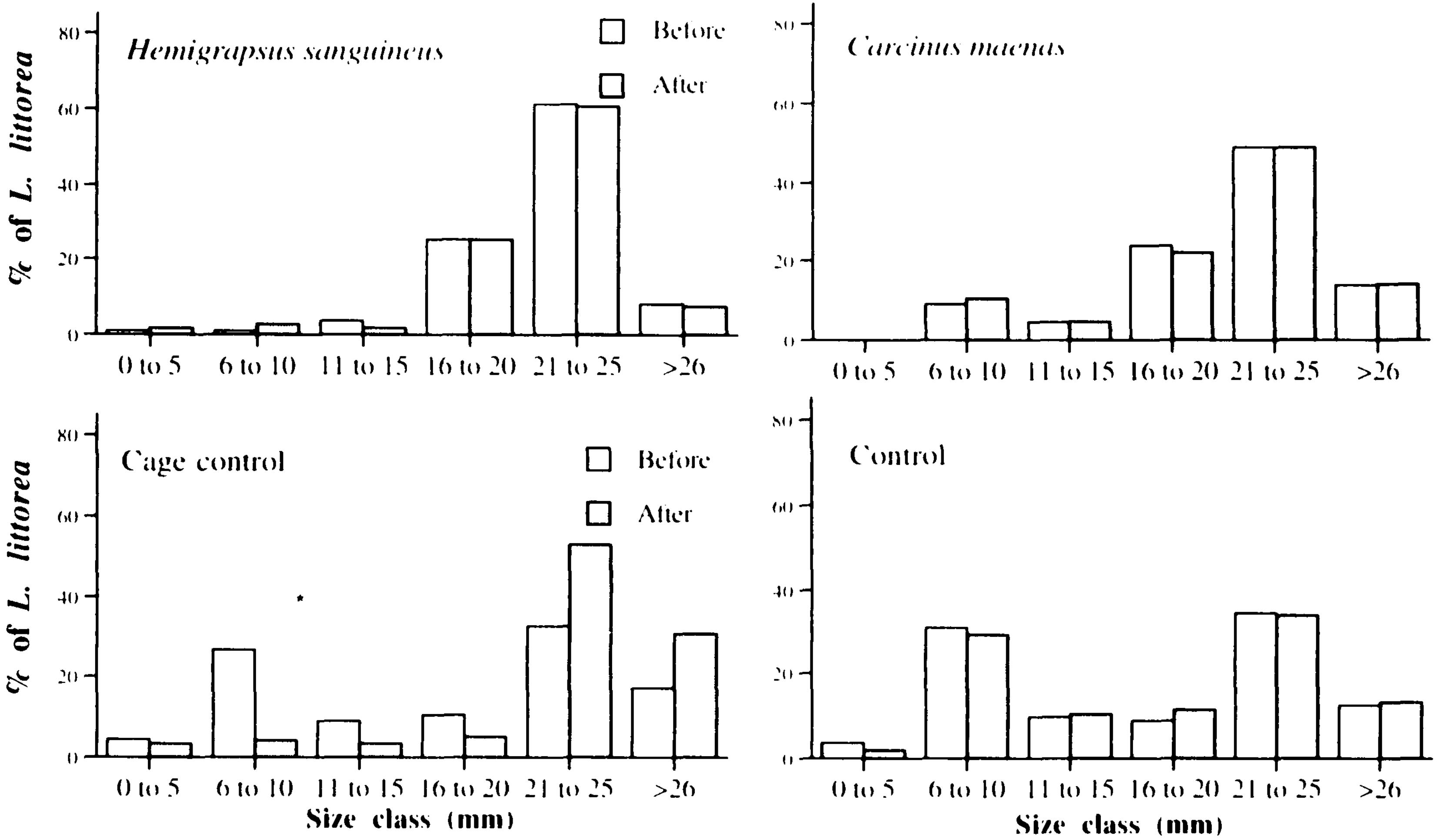


Figure 5.8: Size frequency distributions of *Littorina littorea* in various treatments in long term field microcosm experiments. Asterik denotes statistical significance (Chi Square for trend = 28.11, df = 1, p< 0.001).

Appendix A: Observations of *Carcinus maenas* (CM) and *Hemigrapsus sanguineus* (HS) in long term microcosm experiments.

Replicate	**Treatment**	**Observations**
101	HS	1 crab missing 1 left leg
108	HS	1 crab found dead (eaten) on 8/22/01 and replaced on 8/23/01, 1 crab missing 2 right legs, 1 crab missing 1 left and 1 right leg
109	HS	1 crab missing and presumed eaten, 1 small HS found during sieving
116	HS	1 crab missing 2 right legs
103	CM	1 crab missing 1 left leg, 1 crab missing 3 right legs, 2 crabs presumed eaten (found carapaces)
107	CM	1 crab molted during experiment (new size=30.67 mm carapace width)
112	CM	1 crab missing and presumed eaten, 1 small CM found during sieving
113	CM	1 crab missing 2 left legs, 1 crab with carapace damage, 1 crab molted during experiment (new size=31.7 mm carapace width)
118	CM	1 crab missing and presumed eaten, 1 crab missing both claws and 1 right leg, 1 crab missing 1 left leg

Summary: Two *Hemigrapsus sanguineus* eaten by conspecifics, four *H. sanguineus* showed signs of intraspecific aggression, 1 small *H. sanguineus* found that accidently was included in experiment. Four *Carcinus maenas* eaten by conspecifics, four *C. maenas* showed signs of intraspecific aggression, two *C. maenas* successfully molted and one small *C. maenas* found that accidently was included in experiment. Average mortality of *C. maenas* was 20%, average mortality of *H. sanguineus* was 10%.

GENERAL CONCLUSIONS

The original objective of this dissertation was to try to predict the potential impacts of *H. sanguineus* if it became established in northern New England. At the time that I started collecting data for this dissertation, no *H. sanguineus* had been found north of the Cape Cod Canal in Massachusetts. Since that time, the species has rapidly expanded its range northwards and in the summer of 2001, it was reported at several locations in Maine.

Based on research conducted in its native range of Japan, Lafferty and Kuris (1996) suggested that *H. sanguineus* would not interfere with native crabs because of its putative upper intertidal distribution. Reports on the diet of *H. sanguineus* in Japan also indicated that this species has primarily herbivorous habits in that region (Depledge, 1984). In addition, one of the first reports of *H. sanguineus* on the Atlantic coast of the U.S. stated that this species was maintained on a diet of *Enteromorpha* sp. (McDermott, 1991). This early information regarding the general ecology of *H. sanguineus* spurred me to conduct the surveys of ephemeral algae in upper intertidal pools in anticipation that *H. sanguineus* may be able to colonize these pools.

In its invaded range, *H. sanguineus* quickly became the dominant crab species in the rocky intertidal zone of several locations (southern New Jersey, McDermott [1998]; Long Island Sound, Lohrer and Whitlatch [2002], Greenwich Point, CT, Ahl and Moss [1999]). Contrary to the early predictions that *H. sanguineus* was not likely to have a substantial impact on the rocky intertidal community (Lafferty and Kuris, 1996), many researchers (e.g. Lohrer and Whitlatch, 1997; McDermott, 1998, Ahl and Moss, 1999; Gerard et al., 1999; Lesdesma and O'Connor, 1999) have become interested in this species because its range expansion has been rapid, because it has reached numerical dominance within a short time and because it has been estimated to reach densities as high as several hundred/m^2 (McDermott, 1998). *Hemigrapsus sanguineus* was most recently reported in France and the Netherlands (Breton et al., 2002) and there is concern about its potential impact on shellfish populations in the Netherlands. Obviously, this species has attracted much research interest but thus far, all of the research aimed at documenting the impacts of *H. sanguineus* has been conducted after this species has become conspicuous in the community. This dissertation is unique in that it encompasses both monitoring and experimental research aimed at *predicting* the impacts of *H. sanguineus* if it becomes established in northern New England.

Northern New England is unique from other regions where the impacts of *H. sanguineus* have been examined. Fucoid algae dominate wave sheltered rocky shores in this region, and the biota is a mix of boreal and warm-temperate species. South of Cape Cod, rocky shore habitats are less common, canopy forming fucoid algae are much less abundant and the biota is mostly composed of warm-temperate species. Aside from the differences in community structure, another distinguishing characteristic of my research from that of others working south of Cape Cod is the differences in densities of *H. sanguineus*' primary potential competitor, *Carcinus maenas*. The densities of *C. maenas* in Long Island Sound are estimated to be less than 10/m^2 (Lohrer and Whitlatch, 2002) while at my northern New England study sites, the densities of *C. maenas* are approximately six times higher.

The results from Chapter I indicate that while the timing of peak settlement of *C. maenas* is predictable on a yearly basis, the timing of peak recruitment of juvenile *C. maenas* varies more substantially between years. In addition, at Ft. Stark it appears that the lowest tidal heights harbor the highest densities of juvenile *C. maenas*, while at Odiorne Park, the spatial pattern is less clear. Despite the high variability in the *C. maenas* recruitment data, they are still valuable because they provide information about the timing of critical life history stages of an important member of the rocky intertidal community. In addition, these data may become more valuable to compare future recruitment densities of

C. maenas in the presence of adult *H. sanguineus* that consume newly recruited *C. maenas* (Lohrer and Whitlatch, 2002).

Chapter II illustrated that the three long term monitoring sites were largely composed of similar suites of species and that the fluctuations in the populations of these species were not linked between sites. If the population dynamics had appeared to be strongly correlated between these three sites, it would have reduced their utility as replicates to infer the impacts of *H. sanguineus*. Unfortunately, the Hilton Park site has the highest densities of *H. sanguineus*, but is also the site with the least amount of monitoring (only three years of pre-*H. sanguineus* data). Nevertheless, even the abundance of *H. sanguineus* at the Hilton Park site in 2001 was low enough relative to *C. maenas* (1:11) that the community could still be considered only moderately affected by *H. sanguineus* as compared to *C. maenas*.

A potential criticism of both Chapters II and III is that they are composed of monitoring data and that no specific hypotheses were tested. While this criticism has some validity, long term monitoring data is essential in order to decisively determine the effects of any environmental perturbation (Stewart-Oaten et al. 1986). Monitoring data is essential to document the pre-invasion temporal variability within a community, without it, one can only infer what the structure of a particular community was prior to an invasion. For example, a problem with using microcosms to infer the impacts of the introduced *C. maenas* is that because *C. maenas* has been present in the community for decades, it has doubtless already affected both the behavior and abundance of potential prey. In spite of these types of drawbacks, removal experiments have historically been used to infer the impacts of introduced species in New England rocky shores (e.g. *L. littorea*, Lubchenco, 1978; Bertness, 1984). The combination of monitoring and experimental research focused on predicting the impacts of an introduced crab species before it becomes abundant in a community make this dissertation unique.

In spite of the potential complications associated with inferring the impacts of *C. maenas* using an assemblage of organisms from a community where this introduced crab is already abundant, both the short and long term microcosms provided some interesting insights into the ecology of *C. maenas* and *H. sanguineus*. The fact that both crab species consumed similar prey but that *H. sanguineus* had a significantly higher feeding rate on *S. balanoides*, indicates that this "new" invader could have a higher per capita impact on the recipient community. This assertion is further supported by the significantly higher feeding rate of *H. sanguineus* on *M. edulis* in laboratory feeding trials (DeGraaf and Tyrrell, in prep.). In addition, the significant predation by *C. maenas* on *Spirorbis* sp. that was observed for the summer lab microcosms widens the extent of prey species that may have declined following the establishment of this crab in northern New England. Finally, there was evidence from both the short and long term microcosms that *C. maenas* may positively influence the abundance of algae. In the winter short term experiments, there was a significant increase in ephemeral algae in the *C. maenas* treatment relative to controls and in the long term experiments, fucoid algae in the *C. maenas* treatment significantly increased relative to both types of control treatments. It is possible that the chemical cues of *C. maenas* were sufficient to inhibit herbivore activity enough so as allow ephemeral algae to increase in a two day time frame and the more slowly growing fucoid algae to increase over the two week experimental period. The fact that there were no increases in the abundance of algae in the *H. sanguineus* treatments could be due to the fact that this crab is more herbivorous than *C. maenas* (Tyrrell, 1999) or that the herbivores did not respond to its chemical cues because it is a novel predator. It should be noted that the replication in the winter lab and long term microcosm experiments was relatively low (minimum of 5 for each treatment) and therefore, further experimentation is necessary to verify these observations.

The potential impacts of introduced crabs in northern New England extend beyond declines in prey abundance. As detailed in Chapters IV and V, the indirect effects of crabs could affect multiple trophic levels as well as species that create habitat for other species (fucoid algae, *Mytilus edulis*). Prior to the introduction of *C. maenas* in northern New England, there probably wasn't any other crab species that was abundant in the intertidal zone, particularly the mid or upper intertidal zone. In fact, in an early paper that examined predation in New England, Menge (1976) did not account for crab predation because of their low densities ($4/m^2$) and small sizes (<30 mm) at his study sites. In contrast, the average density of *C. maenas* over all of my sites was $61.4/m^2$ at the 1.0 m tidal height and $64.8/m^2$ at the 2.0 m tidal height. It is possible that the differences in density estimates between the two studies are due to a real increase in *C. maenas* densities for the last 20 years. There is evidence that populations of *C. maenas* benefited from increased water temperatures and spread northwards during the middle part of the last century (Glude, 1955). However, variation in search technique could also effectively account for the lower density estimates obtained by Menge (1976). Nevertheless, the high abundance of *C. maenas* at my three study sites study testifies to the present necessity of accounting for their predatory activities when examining factors that contribute to the community structure.

Prior to the establishment of *C. maenas*, the only other generalized invertebrate predators that were common in the rocky intertidal zone were *Nucella lapillus* and *Asterias* sp. The changes in shell morphology that have been observed for *N. lapillus* (Vermeij, 1982) and *L. obtusata* (Seeley, 1986; Trussell, 1996) following the establishment of *C. maenas* testify to their influence on the community. Crab predation is fundamentally different from that of seastars or predatory gastropods because crab chelae are capable of crushing or peeling shells. Defense against the predatory activities of crabs requires different behavioral or structural compensation than defense against slow moving predators such as snails or seastars. For these reasons, the rocky intertidal prey community of northern New England was particularly susceptible to the negative effects of an introduced intertidal crab.

Tyrrell (1999) and Tyrrell and Harris (2001) created schematic models that predicted the impact of *H. sanguineus*' predatory activities as well as with its potential competition with *C. maenas* in northern New England. One of their most salient predictions was that a decline in the abundance and recruitment of *C. maenas* would occur in the rocky intertidal zone due to the superior competitive abilities of *H. sanguineus* for shelter and food. This prediction was validated shortly thereafter for southern New England by other researchers. In Long Island Sound, Lohrer and Whitlatch (2002) reported a 90% decline in *C. maenas* abundance that coincided with a 10 fold increase in *H. sanguineus* abundance. In addition, Tyrrell and Harris (2001) predicted that the establishment of *H. sanguineus* in northern New England would lead to declines in the abundance of their preferred prey species. In the same paper, Tyrrell and Harris reported the results from pairwise feeding preference trials with *C. maenas* and *H. sanguineus* that utilized the four common rocky intertidal mollusk species of northern New England. The results from these laboratory trials indicated that *M. edulis* was the most preferred species followed by *L. obtusata* and *L. saxatilis*. *Littorina saxatilis* may be the most susceptible to increased populations of *H. sanguineus* in northern New England. This species has direct development and Lohrer (2001) has noted that it declined markedly in southern New England in the past several years. Although they were not subjected to feeding preference trials per se, the results from the microcosm experiments indicate that *S. balanoides* is also readily consumed by both crab species, particularly *H. sanguineus*, and barnacles could decline as *H. sanguineus* becomes more common in northern New England. Interestingly, the study site that has the highest density of *H. sanguineus*, the Hilton Park 1.0 m site, also experienced a decline in the density of *S. balanoides* from 1999 to 2001. The decline in *S. balanoides* at the Hilton Park 1.0 m site continued into 2002, (M.C. Tyrrell, unpub. data) but the density of *H. sanguineus* was slightly lower in 2002 as compared to 2001. Further monitoring will be required to determine whether the trend of declining *S. balanoides* with increasing *H. sanguineus* continues at Hilton Park and the other study sites.

As *H. sanguineus* continues to increase in northern New England, its high feeding rate on *S. balanoides* may lead to severe reductions in the abundance of this prey species. A reduction in *S. balanoides* is likely to lead to cascading effects on lower trophic levels and changes in the abundance of its competitors and predators. *Semibalanus balanoides* is an important prey item for the gastropod *Nucella lapillus* (Menge and Lubchenco, 1981) and *S. balanoides* and *M. edulis* compete for space (Menge, 1976). If the abundance of *S. balanoides* is a limiting resource for its predator, *N. lapillus*, diminished populations of *S. balanoides* could cause *N. lapillus* to shift to consuming more *M. edulis*. Interestingly, Petraitis (1987) suggested that the microtopography provided by barnacle tests enhances the recruitment success of *M. edulis* and Lubchenco (1983) suggested that *Fucus* sp. germlings also benefit from the presence of barnacle tests. The consequences of diminished *S. balanoides* populations could negatively affect both species that consume it as well as species that benefit from the physical structure created by its test.

Large populations of *H. sanguineus* could both directly and indirectly lead to reductions in the abundance of a suite of intertidal species. However, because *H. sanguineus* has a generalist diet (Tyrrell and Harris, 2001) and because its maximum size (44 mm CW-New Jersey, McDermott, 2001) is small compared to that of *C. maenas* (82 mm CW- Maine, Berrill, 1982), the overall effect of this newly introduced crab species could be that of a juvenile filter for both algae and other animal species. The high feeding rate of *H. sanguineus* as compared to *C. maenas* suggests that *H. sanguineus* could have a larger per capita impact than *C. maenas* even though the maximum size of *H. sanguineus* is half of that of *C. maenas*.

While the increasing abundance of *H. sanguineus* may have negative implications for lower trophic levels, the effects of *H. sanguineus* on higher trophic levels are less clear. To date, there is no published research that addresses the impacts of the introduction of *H. sanguineus* to its potential predators. Predators of *H. sanguineus* are likely to include larger crustaceans, birds and fish. In a nine year examination of the impacts of the invasion of *C. maenas* on the U.S. Pacific coast, Grosholz et al. (2000) found that the increasing abundance of *C. maenas* did not have bottom-up effects on birds but that *C. maenas* did exert strong top-down control on the prey community. These authors predicted that bottom-up control of *C. maenas* on birds will occur as *C. maenas* expands its population within the study site and its range over the entire region. It is reasonable to expect that a similar phenomenon may occur for the *H. sanguineus* invasion on the U.S. Atlantic coast; therefore, changes in higher trophic levels may lag behind changes in prey and competitor populations.

Previous research into the impacts of *C. maenas* on the U.S. Atlantic coast has been undertaken on a species by species basis. This dissertation is the first effort to infer some of the community-wide impacts of the introduction of *C. maenas* and to predict some of the potential impacts of *H. sanguineus* in northern New England. It appears that the establishment of *H. sanguineus* is imminent in this region and therefore it may be possible to test some of the predictions of this research in the near future. If *H. sanguineus* has similar behavior in northern New England as it did in the microcosms and in southern New England, the rocky intertidal community could soon be dominated by a "new" introduced crab species that has a higher per capita impact than the "old" introduced crab species.

LITERATURE CITED

Ahl, R. S. and S. P. Moss. 1999. Status of the nonindigenous crab, *Hemigrapsus sanguineus*, at Greenwich Point, Connecticut. Northeast Naturalist 6(3): 221-224.

Ballantine, W. J. 1961. A biologically- defined exposure scale for the comparative description of rocky shore. Field Studies 1: 1-19.

Baskin, Y. 1996. Curbing undesirable invaders. BioScience 46(10): 732-736.

Berrill, M. 1982. The life cycle of the green crab *Carcinus maenas* at the northern end of its range. Journal of Crustacean Biology 2(1): 31-39.

Bertness, M. D. 1984. Habitat and community modification by an introduced herbivorous snail. Ecology 65(2): 370-381.

Bertness, M. D. 1999. The ecology of Atlantic shorelines. Sinauer Associates, Inc. Sunderland, Massachusetts. 417 pp.

Beukema, J. J. 1991. The abundance of shore crabs *Carcinus maenas* (L.) on a tidal flat in the Wadden Sea after cold and mild winters. Journal of Experimental Marine Biology and Ecology 153: 97-113.

Brenchley, G. A. and J. T. Carlton. 1983. Competitive displacement of native mud snails by introduced periwinkles in the New England intertidal zone. Biological Bulletin 165: 543-558.

Brown, J. H., T. G. Whitham, S. K. Morgan Ernest and C. A. Gehring. 2001. Complex species interactions and the dynamics of ecological systems: Long term experiments. Science 293: 643-650.

Brousseau, D. J., A. Filipowicz and J. A. Baglivo. 2001. Laboratory investigations of the effects of predator sex and size on prey selection by the Asian crab, *Hemigrapsus sanguineus*. Journal of Experimental Marine Biology and Ecology 262: 199-210.

Byers, J. E. 1999. The distribution of an introduced mollusc and its role in the long-term demise of a native confamilial species. Biological Invasions 1(4): 339-353.

Carlton, J. T. 1989. Man's role in changing the face of the ocean: biological invasions and implications for conservation of near-shore environments. Conservation Biology. 3(3): 265-273.

Carlton, J. T. and J. B. Geller. 1993. Ecological roulette: the global transport of nonindigenous marine organisms. Science 26: 78-82.

Clarke, K. R. and R. M. Warwick. 1994. *Change in marine communities: an approach to statistical analysis and interpretation.* Plymouth Marine Laboratory, UK. 120 pp.

Cohen, A. N., J. T. Carlton, and M. C. Fountain. 1995. Introduction, dispersal and potential impacts of the green crab *Carcinus maenas* in San Francisco Bay, California. Marine Biology 122: 225-237.

Cohen, J. 1977. *Statistical power analysis for the behavioral sciences.* Academic Press, New York, 2nd edition, 474 pp.

Cubit, J. D. 1984. Herbivory and the seasonal abundance of algae on a high intertidal rocky shore. Ecology 65(6): 1904-1917.

Culotta, E. 1991. "Superbug" attacks California crops. Science 254: 1445.

Depledge, M. H. 1984. Cardiac activity in the intertidal crab, *Hemigrapsus sanguineus*, (De Haan). Asian Marine Biology 1: 115-123.

Dye, A. H. 1993. Recolonization of intertidal macroalgae in relation to gap size and molluscan herbivory on a rocky shore on the east coast of Southern Africa. Marine Ecology Progress Series 95: 263-271.

Ebling, F. J., J. A. Kitching, L. Muntz and C. M. Taylor. 1964. The ecology of Lough Ine. XIII. experimental observations of the destruction of *Mytilus edulis* and *Nucella lapillus* by crabs. Journal of Animal Ecology 33: 73-82.

Elner, R.W. 1981. Diet of the green crab *Carcinus maenas* (L.) from Port Hebert, Southwestern Nova Scotia. Journal of Shellfish Research 1(1): 89-94.

Englund, G. 1997. Importance of spatial scale and prey movements in predator caging experiments. Ecology 78(8): 2316-2325.

Enserink, M. 1999. Biological invaders sweep in. Science 285: 1834-1836.

Einav, R., S. Breckle and S. Beer. 1995. Ecophysical Adaptation Strategies of Some Intertidal Marine Macro algae of the Israeli Mediterranean Coast. Marine Ecology Progress Series 125: 219-228.

Epifanio, C. E., A. I. Dittel, S. Park, S. Schwalm and A. Fouts. 1998. Early life history of *Hemigrapsus sanguineus*, a non-indigenous crab in the Middle Atlantic Bight (USA). Marine Ecology Progress Series 170: 231-238.

Eriksson, S. and A. M. Edlund. 1977. On the ecological energetics of 0- group *Carcinus maenas* (L.) from a shallow sandy bottom in Gullmar Fjord, Sweden. Journal of Experimental Marine Biology and Ecology 30: 233-248.

Field, J. G., K. R. Clarke and R. M. Warwick. 1982. A practical strategy for analyzing multispecies distribution patterns. Marine Ecology Progress Series. 8: 37-52.

Fernandes, T. F., M. Huxham and S. R. Piper. 1999. Predator caging experiments: a test of the importance of scale. Journal of Experimental Marine Biology and Ecology. 241: 137-154.

Fukui, Y. 1988. Comparative studies on the life history of the grapsid crabs (Crustacea, Brachyura) inhabiting intertidal cobble and boulder shores. Publications of the Seto Marine Biological Laboratory 33(4/6): 121-162.

Gaines, S. and J. Roughgarden. 1985. Larval settlement rate: A leading determinant of structure in an ecological community of the marine intertidal zone. Proceedings of the National Academy of Science, USA 82: 3707-3711.

Gerard, V. A., R. M. Cerrato and A. A. Larson. 1999. Potential impacts of a western Pacific grapsid crab on intertidal communities of the northwestern Atlantic Ocean. Biological Invasions 1(4): 353-361.

Glude, J. B. 1955. The effects of temperature and predators on the abundance of the soft-shell clam, *Mya arenaria*, in New England. Transactions of the American Fisheries Society 84: 13-26.

Grosholz, E. D. and G. M. Ruiz. 1995. Spread and potential impact of the recently introduced European green crab, *Carcinus maenas*, in central California. Marine Biology 122: 239-247.

Grosholz, E. D. and G. M. Ruiz. 1996. Predicting the impact of introduced marine species: lessons from the multiple invasions of the European green crab *Carcinus maenas*. Biological Conservation 78: 59-66.

Grosholz, E. D., G. M. Ruiz, C. A. Dean, K. A. Shirley, J. L. Maron and P. G. Connors. 2000. The impacts of a nonindigenous marine predator in a California bay. Ecology 81(5): 1206-1224.

Hall, S. J., D. Raffaelli and W. R. Turrell. 1990. Predator-caging experiments in marine systems: a reexamination of their value. American Naturalist 136(5): 657-672.

Harris, L. G. and C. M. Chester. 1996. Effects of location, exposure and physical structure on juvenile recruitment of the sea urchin, *Strongylocentrotus droebachiensis* in the Gulf of Maine. Journal of Invertebrate Reproduction 30:(1-3): 207-215.

Harris, L. G., M. C. Tyrrell, C. Williams, C. Chester, C. Sisson and S. Chavanich. 2000. Declining sea urchin recruitment in the Gulf of Maine: Is overfishing to blame?. *Proceedings of the 10th International Echinoderm Conference*. Dunedin, New Zealand. pp. 439-444.

Harris, L. G. and M. C. Tyrrell. 2001. Changing community states in the Gulf of Maine: Synergism between invaders, overfishing and climate change. Biological Invasions 3: 9-21.

Hedgpeth, J. W. 1993. Foreign invaders. Science 261: 34-35.

Hughes, R. N. and R. W. Elner. 1979. Tactics of a predator, *Carcinus maenas* and morphological responses of the prey, *Nucella lapillus*. Journal of Animal Ecology 48: 65-78.

Jacobsen, H. P. and O. B. Stabell. 1999. Predator-induced alarm responses in the common periwinkle, *Littorina littorea*: dependence on season, light conditions, and chemical labeling of predators. Marine Biology 134(3): 551-557.

Jensen, K.T. and J.N. Jensen. The importance of some epibenthic predators on the density of juvenile benthic macrofauna in the Danish Wadden Sea. Journal of Experimental Marine Biology and Ecology 89: 157-174.

Janke, K. 1990. Biological interactions and their role in community structure in the rocky intertidal of Helgoland (German Bight, North Sea). Helgolander Meeresuntersuchungen 44: 219-263.

Keough, M. J. and B. J. Downes. 1982. Recruitment of marine invertebrates: the role of active larval choices and early mortality. Oecologia (Berlin): 54: 348-352.

Kimmerer, W. J., E. Gartside and J. J. Orsi. 1994. Predation by an introduced clam as the likely cause of substantial declines in zooplankton of San Francisco Bay. Marine Ecology Progress Series 113: 81-93.

Klein-Breteler,W. C. M. 1976. Settlement, growth and production of the shore crab, *Carcinus maenas*, on tidal flats in the Dutch Wadden Sea. Netherlands Journal of Sea Research 10(3): 354-376.

Lafferty, K. D. and A. M. Kuris. 1996. Biological control of marine pests. Ecology 77(7): 1989-2000.

Ledesma, M. E. and N. J. O'Connor. 2001. Habitat and diet of the non-native crab *Hemigrapsus sanguineus* in southeastern New England. Northeastern Naturalist 8(1): 63-78.

Leonard, G. H., J. M. Levine, R. M. Schmidt and M. D. Bertness. 1998. Flow-driven variation in intertidal community structure in a Maine estuary. Ecology 79(4): 1395-1411.

LeRoux, P. J., G. M. Branch and M. A. P. Joska. 1990. On the distribution, diet and possible impact of the invasive shore crab, *Carcinus maenas* (L.) Along the South African coast. South African Journal of Marine Science 9: 85-93.

Lohrer, A.M. 2001. The invasion by *Hemigrapsus sanguineus* in eastern North America: A review. Aquatic Invaders, the digest of the National Aquatic Nuisance Species Clearinghouse. 12(3): 1-11.

Lohrer, A. M. 2000. Mechanisms and consequences of an exotic crab species invasion. PhD. Dissertation. University of Connecticut. 147 pp.

Lohrer, A. M. and R. B. Whitlatch. 1997. Ecological studies on the recently introduced Japanese shore crab (*Hemigrapsus sanguineus*), in Eastern Long Island Sound. In N. C. Balcom (ed.)*Proceedings of the Second Northeast Conference on Nonindigenous Aquatic Nuisance Species*. Connecticut Sea Grant College Program. April 18-19. Burlington, VT.

Lohrer, A. M. and R. B. Whitlatch. 2002. Interactions among aliens: apparent replacement of one exotic species by another. Ecology 83(3): 719-732.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. American Naturalist 112(983): 23-39.

Lubchenco, J. 1983. *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity, and plant escapes during succession. Ecology 64(5): 1116-1123.

Lubchenco, J. and B. A. Menge. 1978. Community development and persistence in a low rocky intertidal zone. Ecological Monographs 48: 67-94.

Magurran, A. E. 1992. *Ecological diversity and its measurement*. Princeton University Press, Princeton, NJ. 179 pp.

Mascaro, M. and R. Seed. 2001. Foraging behavior of juvenile *Carcinus maenas*(L.) and *Cancer pagurus* (L.). Marine Biology 139: 1135-1145.

Matthews-Cason, H. 1997. Predation by *Nucella lapillus* on *Littorina obtusata* and *Mytilus edulis*. PhD. Dissertation. University of New Hampshire, Durham, NH, USA. 79 pp.

McDermott, J. J. 1991. A breeding population of the Western Pacific crab *Hemigrapsus sanguineus* (Crustacea: Decapoda: Grapsidae) established in the Atlantic coast of North America. Biological Bulletin 181: 195-198.

McDermott, J. J. 1992. Biology of the Western Pacific crab, *Hemigrapsus sanguineus*, living along the Mid-Atlantic coast of the United States. American Zoologist 32(5): 73A.

McDermott, J. J. 1994. Geographical distribution of a Western Pacific brachyuran crab, *Hemigrapsus sanguineus*, along the East coast of the United States. Chesapeake Research Consortium Publication (149): 708.

McDermott, J. J. 1998. The Western Pacific Brachyuran (*Hemigrapsus sanguineus*: Grapsidae), in its new habitat along the Atlantic Coast of the United States: geographic distribution and ecology. ICES Journal of Marine Science 55: 289-298.

McDermott, J. J. 1999. A review of the natural history of the Asian shore crab, *Hemigrapsus sanguineus* in the western Atlantic with additional information on its biology. In: First National Conference on Marine Bioinvasions; 1999 January 24-27; Cambridge, MA.

McDermott, J. J. 2001. Natural history and biology of the Asian shore crab *Hemigrapsus sanguineus* in the Western Atlantic: A review, with new information. In: Pederson J (ed) Proceedings of the First National Conference on Marine Bioinvasions. Cambridge, MA, January 24-27, 1999. MIT Press, Cambridge. pp. 193-199.

McDonald, P. S., G. C. Jensen and D. A. Armstrong. 2001. The competitive and predatory impacts of the nonindigenous crab *Carcinus maenas* (L.) on early benthic phase Dungeness crab *Cancer magister* Dana. Journal of Experimental Marine Biology and Ecology 258: 39-54.

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

Menge, B. A. 1978. Predation intensity in a rocky intertidal community -relation between predator foraging activity and environmental harshness. Oecologia (Berlin) 34: 1-16.

Menge, B. A. 1983. Components of predation intensity in the low zone of the New England rocky intertidal region. Oecologia (Berlin) 58: 141-155.

Menge, B. A. 1991. Relative importance of recruitment and other causes of variation in rocky intertidal community structure. Journal of Experimental Marine Biology and Ecology 146: 69-100.

Menge, B.A. and J. Lubchenco. 1981. Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. Ecological Monographs 51(4): 429-450.

Moksnes, P-O., L. Pihl and J. van Montfrans. 1998. Predation on postlarvae and juveniles of the shore crab *Carcinus maenas*: importance of shelter, size and cannibalism. Marine Ecology Progress Series 166: 211-225.

Moksnes, P-O. and H. Wennhage. 2001. Methods for estimating decapod larval supply and settlement: importance of larval behavior and development stage. Marine Ecology Progress Series 209: 257-273.

Morgan, S.G., R.K. Kimmer-Faust, K.L. Heck and L.D. Coen. 1996. Population regulation of blue crabs *Callinectes sapidus*in the northern Gulf of Mexico: postlarval supply. Marine Ecology Progress Series 133: 73-88.

Nichols, F. H., J. K. Thompson and L. E. Schemel. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the Asian Clam *Potamocorbula amurensis* II. Displacement of a former community. Marine Ecology Progress Series 66: 95-101.

Paine, R. T. 1974. Intertidal community structure: Experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia 15: 93-120.

Palmer, A. R. 1990. Effect of crab effluent and scent of damaged conspecifics on feeding, growth, and shell morphology of the Atlantic dogwhelk, *Nucella lapillus* (L.). Hydrobiologia 193: 155-182.

Petraitis, P. S. 1987. Factors organizing rocky intertidal communities of New England: herbivory and predation in sheltered bays. Journal of Experimental Marine Biology and Ecology 109: 117-136.

Pihl, L. and R. Rosenberg. 1982. Production, abundance, and biomass of mobile epibenthic marine fauna in shallow waters of western Sweden. Journal of Experimental Marine Biology and Ecology 57: 273-301.

Raffaelli, D., A. Conacher, H. McLachlan and C. Emes. 1989. The role of epibenthic crustacean predators in an estuarine food web. Estuarine, Coastal and Shelf Science 28: 149-160.

Rangeley, R. W. and M. L. H. Thomas. 1987. Predatory behaviour of the juvenile shore crab, *Carcinus maenas*. Journal of Experimental Marine Biology and Ecology 108: 191-197.

Reid, D. G. 1996. *Systematics and Evolution of Littorinids.* The Dorset Press, Dorchester, UK. 463 pp.

Reise, K. 1977. Predator exclusion experiments in an intertidal mud flat. Helgolander Wiss. Meeresuntersuchungen 30: 263-271.

Reise, K. 1978. Experiments on epibenthic predation in the Wadden Sea. Helgolander Wiss. Meeresunters 31: 55-101.

Richards, M. G., M. Huxham and A. Bryant. 1999. Predation: a causal mechanism for variability in intertidal bivalve populations. Journal of Experimental Marine Biology and Ecology 241: 159-177.

Richardson, J. 2001. Boy spies Maine's latest invader: Casey Gillespie, 10, found the Asian shore crab, a critter scientists fear will be bad news for native tidepool species. Portland Press Herald, Portland, Maine. June 30, 2001.

Ropes, J. W. 1968. The feeding habits of the green crab, *Carcinus maenas* (L.). Fishery Bulletin 67(2): 183-203.

Ropes, J. W. 1988. The food habits of five crab species at Pettaquamscutt River, Rhode Island. Fishery Bulletin 87: 197-204.

Ruiz, G. M., J. T. Carlton, E. D. Grosholz and A. H. Hines. 1997. Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent and consequences. American Zoolgist 37: 621-632.

Ruiz, G. M., P. Fofonoff and E. D. Grosholz. 1999. Non-indigenous species as stressors in estuarine and marine communities: assessing invasion impacts and interactions. Limnology and Oceanography 44(3): 950-972.

Sanchez-Salazar, M. E., C. L. Griffiths and R. Seed. 1987. The interactive roles of predation and tidal elevation in structuring populations of the edible cockle, *Cerastoderma edule*. Estuarine, Coastal and Shelf Science 25: 245-260.

Scherer, B. and K. Reise. 1981. Significant predation on micro- and macrobenthos by the crab, *Carcinus maenas* L. in the Wadden Sea. Kieler Meerforschungen Sonderheft 5: 490-500.

Schwindt, E., A. Bortolus and O.O. Iribarne. 2001. Invasion of a reef-builder polychaete: direct and indirect impacts on the native benthic community structure. Biological Invasions **3**: 137-149.

Seeley, R. H. 1986. Intense natural selection caused a rapid morphological transition in a living marine snail. Proceedings of the National Academy of Science, USA 83: 6897-6901.

Siagusa, M. and O. Kawagoye. 1997. Circatidal rhythm of an intertidal crab, *Hemigrapsus sanguineus*: synchrony with unequal tide height and involvement of a light-response mechanism. Marine Biology 129: 87-96.

Stewart-Oaten, A., W. M. Murdoch and K.R. Parker. 1986. Environmental impact assessment: "Pseudoreplication" in time?. Ecology 76: 929-940.

Sousa, W. P. 1980. Experimental investigations of disturbance and ecological succession in a rocky intertidal community. Ecological Monographs 49(3): 227-254.

Takada, Y. 1999. Influence of shade and number of boulder layers on mobile organisms on a warm temperate boulder shore. Marine Ecology Procress Series 189: 171-179.

Takada, Y. and T. Kikuchi. 1991. Seasonal and vertical variation of the boulder shore fauna in Amakusa. Publications of the Amakusa Marine Biology Lab 11(1): 1-17.

Thiel, M. and T. Dernedde. 1994. Recruitment of shore crabs, *Carcinus maenas* on tidal flats: mussel clumps as an important refuge for juveniles. Helgolander Meeresuntersuchungen 48: 321-332.

Thrush, S. F. 1986. Community structure on the floor of a sea-lough: are large epibenthic predators important? Journal of Experimental Marine Biology and Ecology. 104: 171-183.

Trussell, G. C. 1996. Phenotypic plasticity in an intertidal snail: the role of a common crab predator. Evolution 50(1): 448-454.

Tyrrell, M. C. 1999. Predicted impacts of the introduced crab, *Hemigrapsus sanguineus*, in northern New England. Master's thesis, University of New Hampshire, Durham, NH. 114 pp.

Tyrrell, M. C. and L. G. Harris. 2001. Potential impact of the introduced Asian shore crab, *Hemigrapsus sanguineus*, in northern New England: Diet, feeding preferences, and overlap with the green crab, *Carcinus maenas*. In: Pederson J (ed) *Proceedings of the First National Conference on Marine Bioinvasions*. Cambridge, MA, January 24-27, 1999. MIT Press, Cambridge. pp. 208-220.

Tyrrell, M. C. and P. A. Madigan. 2001. Impacts of a "new" and "old" crab invader in northern New England inferred from microcosms. (submitted to Journal of Shellfish Research, May 2002)

U.S. Congress, Office of Technology Assessment 1993. Harmful non-indigenous species in the United States. OTA-F-565. Washington, D.C., U.S. Congress Government Printing Office.

Vadas, R. L., M. T. Burrows and R. N. Hughes. 1994. Foraging strategies of dogwhelks, *Nucella lapillus* (L.): interacting effects of age, diet and chemical cues to the threat of predation. Oecologia 100: 439-450.

Vermeij, G. J. 1982. Phenotypic evolution in a poorly dispersing snail after the arrival of a predator. Nature 229: 349-350.

Villalard-Bohnsack, M. 1995. *Illustrated key to the seaweeds of New England.* Rhode Island Natural History Survey. 143 pp.

Vitousek, P. M., C. M. D'Antonio, L. L. Loope and R. Westerbrooks. 1996. Biological invasions as global environmental change. American Scientist 84: 468-478.

Wahle, R. A. and R. S. Steneck. 1991. Recruitment habitats and nursery grounds of the American lobster *Homarus americanus*: a demographic bottleneck? Marine Ecology Progress Series 69: 231-243.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips and E. Losos. 1998. Quantifying threats to imperiled species in the United States. BioScience 48(8): 607-615.

Williams, A. B. and J. J. McDermott. 1990. An Eastern United States record for the Western Indo-Pacific crab, *Hemigrapsus sanguineus* (Crustacea: Decapoda: Grapsidae). Proceedings of the Biological Society of Washington 103(1): 108-09.

Wolcott, D. L. and N. J. O'Connor. 1992. Herbivory in crabs: adaptations and ecological considerations. American Zoologist 32: 370-381.

Young, C.M. 1994 Marine larval ecology gets a meeting of its own. Trends in Ecology and Evolution 9(3): 84-85.

Zaitsev, Y. P. 1992. Recent changes in the trophic structure of the Black Sea. Fisheries and Oceanography 1(2): 180-189.