8-2003

Resilience of Green Sea Urchin (Strongylocentrotus droebachiensis) Populations Following Fishing Mortality: Marine Protected Areas, Alternate Stable States, and Larval Ecology

John Vavrinec III

RESILIENCE OF GREEN SEA URCHIN (*STRONGYLOCENTROTUS DROEBACHIENSIS*) POPULATIONS FOLLOWING FISHING MORTALITY: MARINE PROTECTED AREAS, ALTERNATE STABLE STATES, AND LARVAL ECOLOGY

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A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Doctor of Philosophy

(in Oceanography)

The Graduate School

The University of Maine

August, 2003

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The green sea urchin *Strongylocentrotus droebachiensis* has been aggressively fished in Maine since 1986 resulting in severe population declines throughout portions of the state. This research used Marine Protected Areas (MPAs) to evaluate the potential for recovery in depleted sea urchin populations. It was necessary to not only look at the direct impacts of the MPAs, but also at larval transport / supply and community interactions to gain a better understanding of the system.

We found that MPAs in the Gulf of Maine were of varied utility to restoring depleted sea urchin populations depending on location and community structure. MPAs established in coralline communities appeared to protect sea urchin populations from further declines and may have allowed some slow recovery. However, closures in areas that have undergone a community shift from coralline communities to fleshy macroalgal beds did not provide protection for the remaining sea urchins or appropriate habitat for

repopulation. Additionally, this macroalgal state appears stable over time so the potential for sea urchin recovery will probably remain low.

This study also determined the point at which sea urchins could no longer control macroalgal production and allowed the growth of fleshy macroalgal beds. This ecologically effective biomass declined exponentially with water depth and was inversely proportional to latitude. These patterns were probably caused by the factors that affect productivity (e.g. light, nutrients) and grazing rates (e.g. temperature, water movement).

Mechanisms driving sea urchin settlement were also examined. Competent echinoplutei were found higher in the water and advected onshore when northeast wind events created oceanographic downwelling conditions. Newly metamorphosed sea urchins were also found in the water column, suggesting that contact with the substrate is not needed to initiate metamorphosis. Sea urchin settlement was greatest in coralline communities with high micro-complexity and lowest in macroalgal beds. Survival through the summer, however, only averaged 50% regardless of community type or habitat micro-complexity. Lastly, this study identified adult sea urchins as a potential consumer of juvenile sea urchins, which may account for some of the relatively high mortality seen in sea urchin-dominated coralline communities

DEDICATION

For Katie,

who never stopped believing

ACKNOWLEDGEMENTS

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Chapter 1. Ecosystem shifts and the effectiveness of marine protected areas: a cautionary tale from the Maine sea urchin fishery.

Abstract

Marine protected areas (MPAs) are commonly considered to be a viable means of fisheries management, in part because they often result in increased population density and body size of harvested species. When MPAs do not work, the things most commonly blamed for their failure are poor site selection, pollution, inadequate enforcement, Allee effects, and unexpected trophic cascades after closure. We report that dramatic changes to the ecosystem occurring before MPA closure can also influence the results. In Maine, the green sea urchin *Strongylocentrotus droebachiensis* (Echinodermata, Echinoidea) is the dominant coastal benthic herbivore which has been widely depleted due to overfishing. As a result, benthic communities have moved to alternate stable equilibria from crustose coralline communities to fleshy macroalgal beds. In 1999, six small areas (< 0.15 km^2) along the coast were closed to sea urchin fishing to gauge resilience in sea urchin populations. Those areas that were grazed by sea urchins and dominated by coralline algae prior to closure appear to protect resident sea urchin populations from further degradation; sea urchin populations are also exhibiting signs of recovery. Areas dominated by fleshy macroalgal beds prior to closure, however, have shown no indications of sea urchin recovery or macroalgal reductions. We think that these areas represent an alternate stable state for the region, and that creating MPAs has little (or a very slow) effect on reversing the severe changes in the ecosystem. Managers need to be

aware of potential non-linear responses in their systems and take actions before long-lasting or irreversible changes occur.

Introduction

Natural fisheries are declining worldwide; sixty percent of the world's fisheries are fully or over exploited, and another six percent are depleted (total loss of the population) according to the FAO (1998). More recent data suggest global landings have been declining since 1988 (Watson and Pauly 2001). The questioning of traditional fisheries management has led to requests for alternative management methods (e.g. Botsford et al. 1997, Lubchenco et al. 2003). Marine protected areas (MPAs), where some or all fishing is prohibited, are increasingly becoming a mechanism commonly suggestioned to improve fisheries management.

The scientific community (see Ecological Applications 13(1) Supplement for example), environmental groups (e.g. Gell and Roberts 2002), non-government commissions (e.g. Palumbi 2002), and government councilors (National Research Council 2001) have been suggesting the use of MPAs for a number of reasons. They can protect critical habitat, provide a spatial refuge for exploited fish, conserve biodiversity, and facilitate tourism (for reviews see Gubbay 1995, Allison et al. 1998). These areas may provide new recruits to populations and serve as potential experimental plots for fisheries and ecological research (Dugan and Davis 1993b). While no one feels that MPAs alone can solve world fisheries problems, they can be a useful addition to a management plan (Dugan and Davis 1993a, Allison et al. 1998) and may help mitigate

some of the uncertainty in more traditional management options (Hall 1998, Lauck et al. 1998, Allison et al. 2003).

Numerous studies have validated the potential effectiveness of MPAs. Most MPAs have demonstrated increases in biomass, abundances, and densities of species (for reviews see Dugan and Davis 1993a, Palumbi 2001, Gell and Roberts 2002, Halpern 2003) and changes usually occur very quickly (Halpern and Warner 2002). Perhaps more importantly for fisheries management, there are studies that suggest MPAs can export target species into the surrounding fished areas (Russ and Alcala 1996, McClanahan and Mangi 2000, Roberts et al. 2001).

Not all MPAs function as designed, however. Kelleher et al. (1995) reported that only 31% of 1,306 MPAs surveyed worldwide met all their management objectives. They further reported that 29% failed to meet any of their management goals. MPA failure was usually attributed to improper siting of the reserve, Allee effects, poor enforcement, or unexpected trophic cascades once the MPA was established (for reviews see Palumbi 2001, Gell and Roberts 2002, Palumbi 2002). Jameson et al. (2002) recently stated that MPAs cannot be effective as long as managers fail to control stressors from outside the MPA (e.g. pollution), particularly from atmospheric, terrestrial, or oceanic sources.

Here we report on six areas in the Gulf of Maine closed to fishing of the green sea urchin, *Strongylocentrotus droebachiensis* (Muller), to determine its effects on abundances of this heavily exploited species. Our results varied, depending upon how much the ecosystem organization had changed prior to closure. We underscore the importance of understanding the ecology and successional processes within an ecosystem

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when trying to develop management plans. Directional changes in a community prior to closure may have resulted in a stable structure and confound expected rates of recovery.

Materials and Methods

Study Organisms

  S. droebachiensis is an important component of the coastal Gulf of Maine benthos (for review see Scheibling and Hatcher 2001). Economically, sea urchins are harvested for their gonads which are exported to Japan (Chenoweth 1994, Wilen and Wessells 1997). For almost a decade, sea urchins had been the second largest wild fishery in the State of Maine, second only to lobsters (DMR 1998). However, after rapid increases in the mid 1980s, sea urchin landings peaked in 1993 and have declined ever since (DMR 2000).

  Ecologically, the green sea urchin is the primary benthic herbivore in the Gulf of Maine (Steneck and Dethier 1994). Like many urchins worldwide (Lawrence 1975, Harrold and Pearse 1987, Pinnegar et al. 2000, Steneck et al. 2003), its population dynamics can control benthic community structure on hard substrates (Breen and Mann 1976, Lang and Mann 1976, Lawrence and Sammarco 1982, Scheibling 1986). When urchins are abundant, sea urchin grazing usually denudes the benthos of erect fleshy macroalgae, leaving behind a crustose coralline community (often called a "barrens"). Recently, however, fishing has reduced sea urchin populations in many areas to the point where their grazing can no longer control algal growth and high biomass fleshy macroalgal beds form (Steneck 1997, McNaught 1999). These algal beds provide a

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characteristic canopy for a much different community that can be beneficial for many different taxa (Steneck et al. 2003).

Algal beds in the Gulf of Maine can be complex but are easily broken down into assemblages having different canopy heights. The base consists of encrusting red algae such as *Lithothamnion* spp., *Phymatolithon laevigatum*, *Clathomorphum circumscriptum*, *Peyssonnelia* spp., and *Hildenbrandia rubra*. This assemblage is often characteristic of shallow productive environments with high sea urchin grazing. The small erect fleshy algae have a modest canopy height, usually less than 20 cm above the sea floor. These fleshy algae are composed of red, green, and brown algae. Common green algae include *Ulva lactuca, Chaetomorpha* spp. *Enteromorpha* spp., *Spongomorpha* spp., and the non-indigenous *Codium fragile*. Red alga representatives consist of *Chondrus crispus*, *Phycodrus rubens, Ceramium rubrum, Bonnemaisonia hamifera, Corallina officinalis*, *Palmaria palmata, Porphyra umbilicalis*, and *Polysiphonia* spp. Brown alga examples include *Desmarestia* spp., *Chordaria flagelliformis*, and sometimes *Fucus* spp. Kelp form the highest canopies and are usually dominated by *Laminaria saccharina, L. digitata, Agarum clathratum*, and *Alaria esculenta*.

Maine Coastal Characteristics

The coast of Maine is generally characterized by two regions: east and west of Penobscot Bay. These sections vary in their physical oceanographic characteristics, primarily driven by the complex current systems in the Gulf of Maine (see Fig. 1.1 for diagram and Beardsley et al. 1997 for a full description). Tidally mixed water from the Bay of Fundy is rapidly transported southwest along the eastern part of the state by
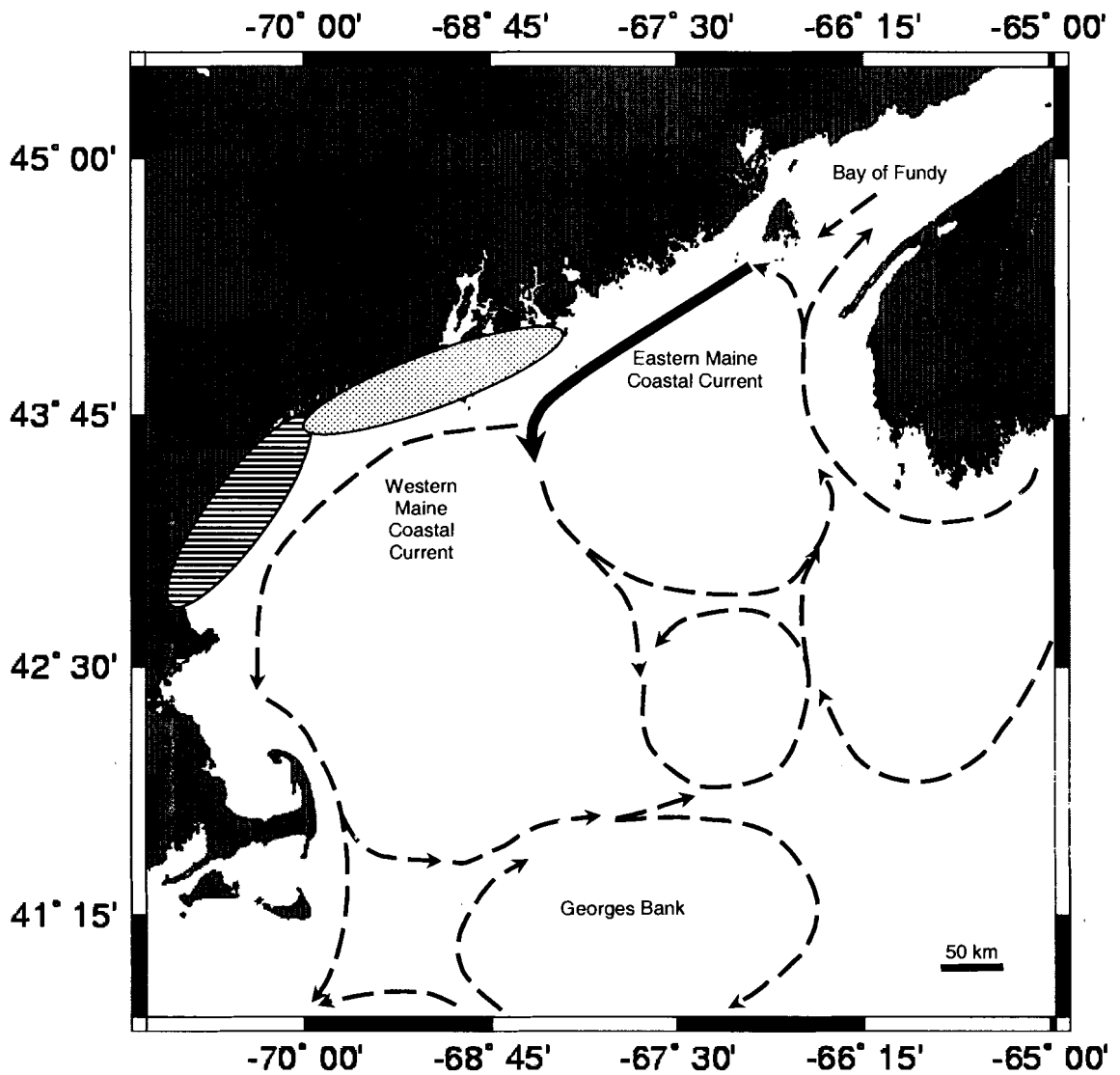
Figure 1.1. Prevailing surface currents in the Gulf of Maine (adapted from Beardsley et al. 1997). Dashed arrows show the generalized surface current patterns and the darker solid line represents the stronger and faster Eastern Maine Coastal Current. The location of where this current turns offshore can vary along the coast at different times. The shaded areas indicate either large-scale sea urchin depletion and predominance of macroalgal beds (≡) or patchy sea urchin extirpation with a mosaic of community types (⠿). Other coastal areas in Maine still have large urchin dominated coralline communities.

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the Eastern Maine Coastal Current (EMCC). The EMCC moves along the coast until the Penobscot Bay area where much of the water mass moves offshore. Some of the EMCC continues along the shore as part of the Western Maine Coastal Current (WMCC). In general, the EMCC is faster moving, less stratified, richer in nutrients, and colder than the WMCC (Townsend et al. 1987, Pettigrew et al. 1998).

There are also differences in the biotic communities these two sections of the coast (Fig. 1.1). Our observations and data indicate that most of the coastal hard substrate south of Casco Bay has shifted to fleshy macroalgal beds with greatly reduced populations of urchins remaining. The midcoast region, from Casco Bay to Penobscot Bay, has patchy urchin popluations and a mosaic of coralline communities and macroalgal beds exists. Both these areas were predominantly coralline communities before the 1990s (Steneck 1997), but intense localized sea urchin fishing has apparently forced a shift to the macroalgal stable point (McNaught 1999). Areas east of Penobscot Bay generally still have sea urchin populations and are characterized mostly by coralline communities.

Study Sites

Six sea urchin MPAs closed to sea urchin and scallop fishing were set up by the Maine Department of Marine Resources (DMR) in 1999 throughout the coast of Maine (Table 1.1, Fig. 1.2) at the request of the Sea Urchin Zone Council (SUZC). DMR and the SUZC designed these areas for research and thus they are much smaller (< 0.15 km^2) than most MPAs around the world. The state, with the help of the SUZC, held public hearings near each regional area to obtain input and support from the local fishers before

Table 1.1. Name, GPS coordinates, and years sampled for all the sites used in this study. Region is based on names given in Fig. 1.

Marine Protected Areas and Associated Controls		
Region	**MPA**	**Control**
York	East Point N 43° 8.0' W 70° 37.2' Data collected 1996 – 2002	Cow Beach N 43° 8.4' W 70° 37.2' Data collected 1996 – 2002
York	Seal Head Point N 43° 7.2' W 70° 37.9' Data collected 1996 – 2002	Stone's Rock N 43° 6.5' W 70° 38.4' Data collected 1996 – 2002
Pemaquid	Pemaquid Point N 43° 50.1' W 69° 31.0' Data collected 1996 – 2002	Thrumcap Island N 43° 49.0' W 69° 33.1' Data collected 1996 – 2002
Schoodic	Schoodic Peninsula N 44° 20.4' W 68° 02.5' Data collected 1996 – 2002	Little Moose Island N 44° 20.0' W 68° 02.6' Data collected 1998 – 2002
Jonesport	Outer Ram Island N 44° 29.5' W 67° 38.2' Data collected 1996 – 2002	Ram Island N 44° 29.5' W 67° 38.1' Data collected 1998 – 2002
Jonesport	Sea Duck Rock N 44° 29.1' W 67° 39.2' Data collected 1996 – 2002	Little Drisko Island N 44° 29.0' W 67° 39.8' Data collected 1998 – 2002

Other Sites Used For Regional Studies (data collected 1996-2002)	
Region	**Site**
Pemaquid	Damariscove Island N 43° 46.0' W 69° 36.8'
Pemaquid	Fisherman's Island N 43° 47.6' W 69° 36.1'
Mount Desert Island	Long Island N 44° 6.2' W 68° 20.6'
Mount Desert Island	Great Duck Island N 44° 8.8' W 68° 15.1'
Mount Desert Island	Little Duck Island N 44° 10.4' W 68° 14.9'
Mount Desert Island	Baker Island N 44° 14.3' W 68° 12.4'
Jonesport	Brownie Ledges N 44° 29.1' W 67° 37.7'
Jonesport	Outer Sand Island N 44° 27.7' W 67° 40.7'
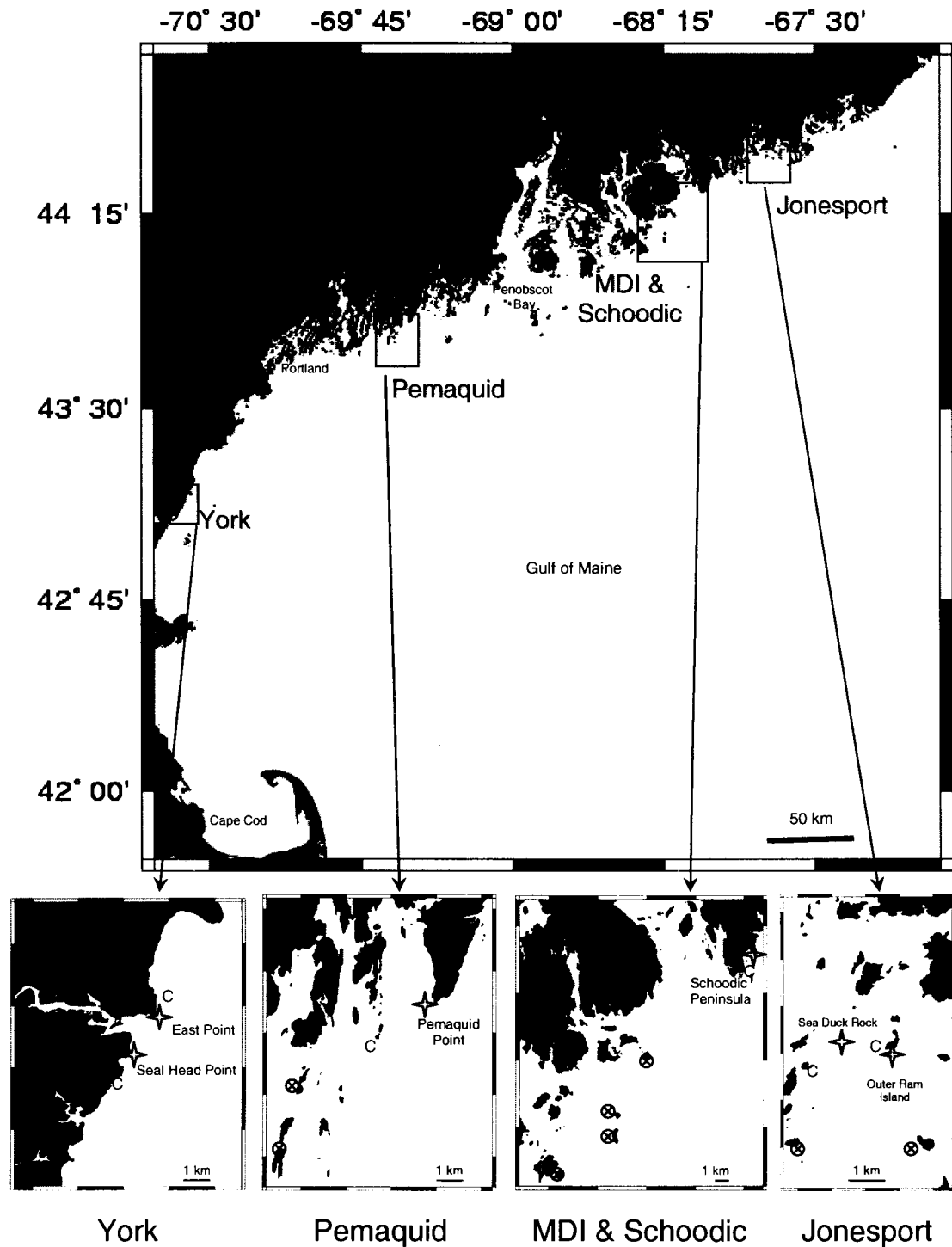
Figure 1.2. Regions and study sites located within the Gulf of Maine. Each marine protected area is designated by a star (✦) and labeled by name. Each control site is marked with a "C". All other sites used for benthic surveys and urchin settlement are shown by the symbol ⊗. MDI abbreviates Mt. Desert Island.

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closing it. We positioned closed areas according to a standardized set of criteria including ledge substrate, southwest exposure, previous history of dense sea urchin populations currently overfished, the existence of previous scientific data, and high visibility for enforcement. We used at least two sites per region for replication wherever possible politically. Each MPA had 300 m of coastline and generally extended down to the 20 to 30 m isobath (which is usually beyond ledge substrate and urchin populations; J. Vavrinec pers. obs.). Buoys marked the boundaries and licensed sea urchin fishers were notified by mail with charts of the closed areas. Local marine patrol officers also provided marked charts for fishermen as an additional reminder.

A control site open to fishing was established for each research MPA (Table 1.1, Fig. 1.1). Seven years of data were available in some cases for both the MPA and control for the comparisons (e.g. East Point, Seal Head, and Pemaquid). The other MPAs (Schoodic Peninsula, Sea Duck Rock, and Outer Ram Island) did not have a control among the sites already being studied. For these, we established controls in 1999. Therefore, in these sites we have seven years of data in the MPA but only four years of data from the control (i.e. one before the MPA establishment, three after closure), a necessary limitation of the system with which we worked. All data collected prior to 1998 were derived from McNaught (1999).

In addition to the MPAs and their controls, we collected data at nine other sites (Table 1.1, Fig.1.1). These sites allowed for some replication in the four larger regions (York, Pemaquid, Mount Desert Island, and Jonesport) studied by McNaught (1999). Schoodic is considered a separate region for the settlement data since it is not close to any other MPAs.

Benthic Surveys

All benthic surveys were conducted in late July or early August of each year. We did this firstly because the sea urchin fishing season is in the winter (approximately October to March) and summer sampling makes sure our data are collected after a full fishing season. Additionally, algal populations are generally fully established mid-summer after the winter dieback (J. Vavrinec pers. obs.) facilitating accurate estimates of cover and composition. Also we wanted to avoid possible seasonal variations in the sea urchin populations (Konar 2001). Lastly, the weather is usually calmer during the late summer with less surge underwater allowing divers to work more easily and efficiently on data collection.

SCUBA divers conducted all benthic surveys at approximately 10 m depth for consistency. We haphazardly threw 1 m^2 quadrats on ledge substrate. At least 20 quadrats were surveyed at each site to meet the minimum sample size.

Sea urchin surveys were conducted using a telescoping quadrat design (after McNaught 1999). This design scales the quadrat dimensions with the size class (test diameter – TD) of the sea urchin so all sizes can be adequately sampled. The 1 m^2 quadrat is subdivided into four smaller divisions and we quantified a particular size range of urchins in each. Urchins $\leq$ 10 mm TD were surveyed in a 1/64 m^2 area, urchins > 10 mm and $\leq$ 30 mm in a 1/16 m^2 area, urchins > 30 mm and $\leq$ 50 mm in a 1/4 m^2 area, urchins > 50 mm and $\leq$ 70 mm in a 9/32 m^2 area, and urchins >70 mm were surveyed in the entire 1 m^2 area. We counted all urchins in the appropriate quadrat and categorized them into 5 mm size bins. We took particular care when searching for small urchins

since they could hide under algal and shell debris, in cracks, and within the branches of the *Lithothamnion* spp. We included only those urchins more than halfway in the appropriate quadrat.

We also conducted algal surveys, estimating the percent-cover for each species within the same 1 m^2 used for the sea urchin surveys. Algae that could not be identified to species were quantified by functional group (Steneck and Dethier 1994). We estimated the percent of the substrate covered by each the algal type (i.e. 100% each possible for crusts, small erect fleshy macroalgae, and kelp) for a potential total of 300% cover.

Settlement Collectors

To test for differences in settlement, we monitored sea urchin settlement at all 20 study sites (Table 1.1, Fig. 1.2). We constructed the 9 x 20 cm collectors from artificial turf (Astroturf™ Monsanto Corp., St. Louis, MO) attached to flat PVC plates for rigidity since other studies in the area successfully used this material (Harris et al. 1994, McNaught 1999). Four collectors were placed at each site at approximately 10 m depth secured ~3 cm above the substrate on a stainless steel bolt cemented to ledge substrate with an underwater epoxy (Kopcoat Splash Zone Compound A-788, Carboline Co., St. Louis, MO). We deployed the collectors in May and retrieved them in late July and early August to cover the reported settlement period for *S. droebachiensis* in the region (Harris et al. 1994, McNaught 1999, Chapt. 3).

We followed the methods of McNaught (1999) for the collection and sorting of the settlement panels. SCUBA divers carefully placed the collectors in plastic bags, and

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then placed in a second bag back on the boat to prevent leaks. Samples were kept in a

cooler with ice packs until they could be sorted at the laboratory. Samples not sorted

within 24 hours were frozen for later processing. At the laboratory, panels were soaked

in a 7% MgCl solution (to relax the urchins) and thoroughly rinsed with 10 μm filtered

seawater. The water was then filtered through at a 300 μm sieve and the remaining

sample carefully sorted under a dissecting compound microscope for newly settled

urchins.

Data Analysis

We processed the sea urchin survey data two different ways. First, because

McNaught (1999) found sea urchin biomass was a good predictor of herbivory (and

therefore community control), we converted numbers of urchins into biomass per quadrat

(grams wet weight per m^2). We multiplied the number of urchins per 1 m^2 in each size

class by the mean wet weight for that size class (calculated from the regression log

biomass = 2.84 (log test diameter in cm)-0.23 [McNaught 1999]) to estimate the biomass

for each size bin. Total biomass was then summed for the quadrat, and all quadrats were

averaged for a site average biomass. All data reported for 1994 and 1995 are means and

SE from McNaught (1999) and were not used in statistical analyses. The data for the

remaining years could not be transformed to meet the ANOVA assumption requiring

homogeneity of variances (Sokal and Rohlf 1981), so Kruskal-Wallis tests were used to

determine changes within sites. We also used a *post hoc* Multiple Comparison Test of

Mean Ranks to compare different years within sites when there was a significant

Kruskal-Wallis value. All statistical tests were performed via Statistica (StatSoft Inc., Tulsa, OK) or SigmaPlot (SPSS Inc., Chicago, IL) with an $\alpha=0.05$.

Second, sea urchin surveys were also used to calculate size frequency curves. Each sea urchin was assigned the mean TD in each size bin (e.g. an urchin classified as 10 to 15 mm was labeled 12.5 mm) for the calculations and estimates were done per 1 m^2. The primary goal of the MPAs was to promote the recovery of sea urchin populations and variations in settlement can skew smaller size classes; therefore we focused primarily on urchins larger than legal size (51mm TD). We also calculated the average size of the legal urchins for each site during each year. However, we observed no significant changes or patterns in size frequency distributions with Student's t-tests and Kolmogorov-Smirnov tests and we therefore do not present those data.

Algal data were similarly tested to compare results from different years within a site. We combined the values of the species from the small erect macroalgae and kelp to create one average of total percent cover of all fleshy macroalgae for a given year in different sites. The data did not meet the assumptions of ANOVA, so Kruskal-Wallis and (when F was significant) Multiple Comparison tests were performed on the datasets. Data from Sea Duck Rock and Little Drisko were also analyzed via ANOVA using a square root transformation $[(a+0.5)^{1/2}]$. We also calculated a regional average percent cover by averaging all site (MPAs, controls, and regional sites) values within a region for each year. The Schoodic Region only had two sites, but the other four regions each had four sites to average.

The most effective way to evaluate the effects of MPA implementation is through a BACI (Before-After-Control-Impact) design (Stewart-Oaten et al. 1986). This design

takes the difference in value (e.g. sea urchin biomass) between the MPA and its associated control site for each year. It is not necessarily important that difference be zero since the change in the difference over time is tested. The differences are then grouped into before and after closure categories and tested for similarity with a Student's t-test (Stewart-Oaten et al. 1986). We performed these BACI tests on all the MPA datasets for years with data from both sites (MPA values – control values) and, while we did not find significant differences, many of the patterns suggest trends and are therefore included in the results.

Lastly, we calculated regional averages for sea urchin settlement. The number of urchins per plate was averaged for each site. We then calculated the mean of all the site averages in each region for an annual regional average. Regional averages in Jonesport were not calculated with exact same sites through all the years. Prior to 1999, collectors were placed at Outer Sand Island and the Brownie Ledges (in addition to the proposed MPAs). Due to sea urchin populations and macroalgal cover differences these two sites were not appropriate for controls and new sites were chosen (Little Drisko Island and Ram Island). Due to logistics, we moved all data collection including settlement monitoring to these new sites. We were concerned that this change affected the settlement numbers, so we placed collectors again at Outer Sand Island in 2001 for comparison and obtained similar results to the new control sites.

Results

Regional Sea Urchin Settlement

Averages in regional settlement differed greatly between regions, with highest

numbers consistently recorded in the southwestern parts of the state and the lowest in the

northeastern sections (Fig. 1.3). Settlement within regions was variable over time. With

the possible exception of Jonesport, there did not appear to be any trends in continued

decreases within a region over the duration of the study. Settlement in York and

Pemaquid decreased until 1999, but increased until 2001 (which had settlement numbers

similar to 1997). In 2002 settlement again decreased. Schoodic and the Mt. Desert

Island region have remained relatively constant over time except for a small decrease in

1998. Jonesport never received much settlement, the highest only being 54 settlers m^{-2}

(in 1997), and no settlers have been in our collectors in the last four years.

Regional Macroalgal Percent Cover

We also determined the average total percent cover of macroalgae for each of the

regions over time (Fig. 1.4). These numbers were usually a mixture of estimates from

coralline communities and macroalgal beds as each site can be different, but the average

can give an idea of overall trends in the different regions. The shift from coralline

communities to fleshy macroalgal beds appears to be moving from west to east along the

coast. By 1996, all York sites had converted to algal beds but all the other regions were

largely coralline communities. Over the next couple of years, the Pemaquid Region
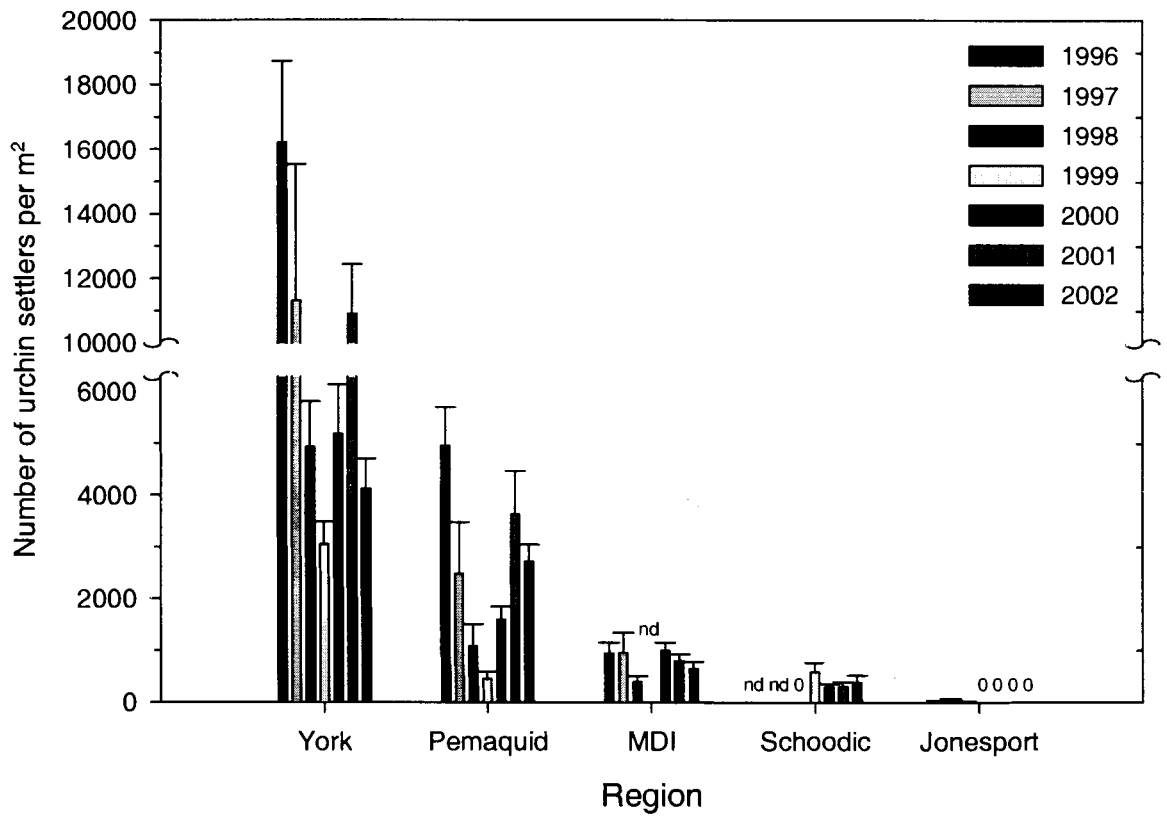
Figure 1.3. Average annual number of urchin settlers per m^2 ($\pm$ SE) 1996 through 2002. Regions are based on those shown in Fig. 1. Years without settlement data are designated with 'nd' and '0' indicates no settlement was observed for that year.
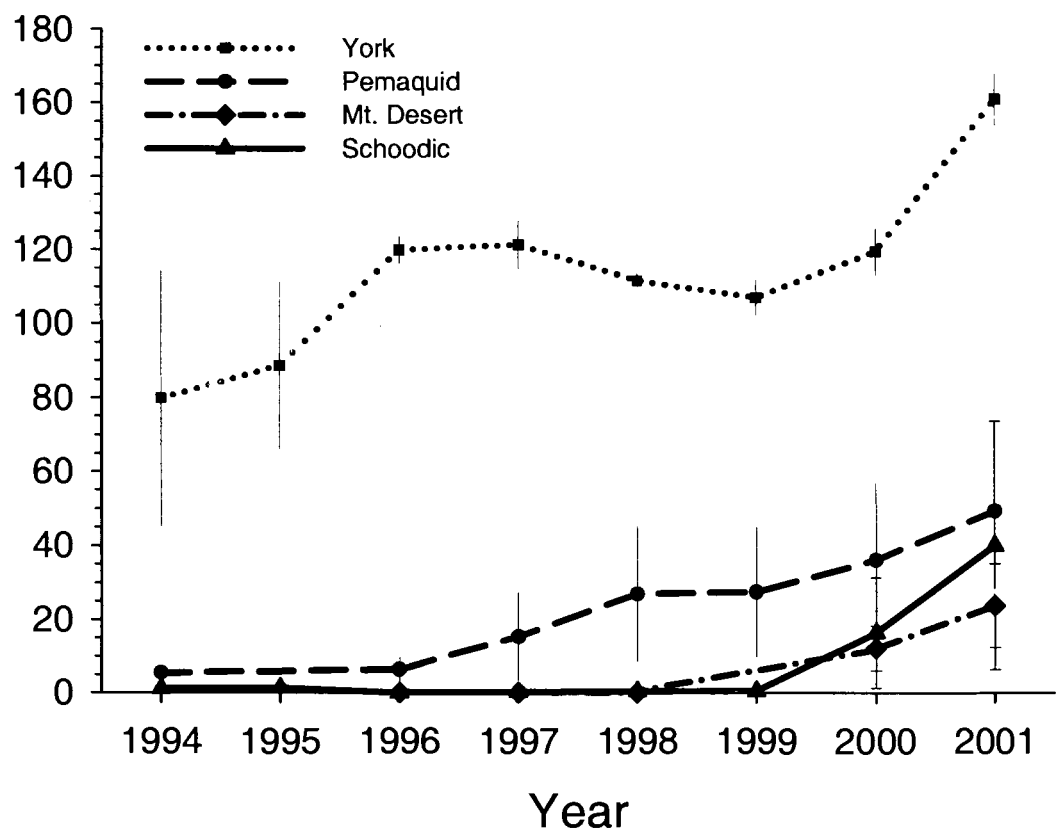
Figure 1.4. Average regional percent cover of fleshy macroalgae over time for the York, Pemaquid, Mt. Desert, and Schoodic regions. Error bars are ± 1SE

exhibited more macroalgae, and in the last three years even sites around MDI and Schoodic have started to increase in macroalgal cover.

MPA Case Studies

<u>East Point, York</u>

At the initiation of this study, the East Point MPA was as a macroalgal bed with very low sea urchin biomass and has remained that way for seven years (Fig. 1.5). Sea urchin populations have been functionally absent during the whole time, with the highest average biomass recorded being 2.4 g m^{-2} in 1996. No urchins were found in 1997 or 1999-2002. Macroalgal cover remained over 100% for the entire time between 1995 and 2002 and actually increased in the last two years (Figure 1.5, Table 1.2).

The Cow Beach control showed similar trends to the MPA. While early data from McNaught (1999) indicated the site went through a phase shift between 1995 and 1996, the area has remained an algal bed since 1996. Again, sea urchin biomass over time remained low (no urchins were found in the last two years) and not changed according to the Multiple Comparison of Mean Ranks test (Fig. 1.5C) and differences were on the order of tens of g m^{-2}. Algae varied over time (Table 1.2) but patterns showed similar to the East Point MPA (Fig. 1.5A).

The BACI differences show slightly different results. The differences in sea urchin biomass were variable within a small range but leveled out to zero as no urchins were seen in the sites (Fig. 1.5D). There were not significant differences in the annual
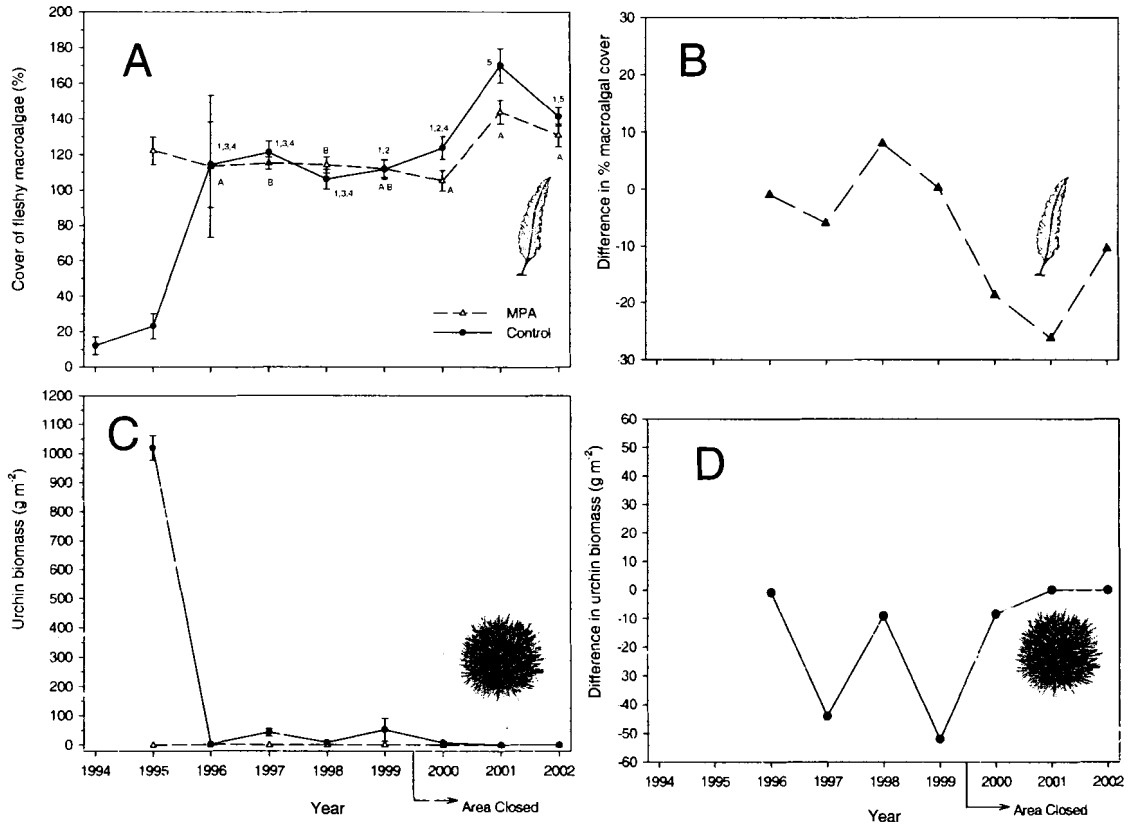
Figure 1.5. Data for the East Point MPA and Cow Beach control site in York, Maine.
A) Average percent cover of all fleshy macroalgae at both sites over time. The total possible percent cover can be 200% since we quantified two levels of macroalgae (see text). Different letters by the data point indicate statistical difference in MPA data as determined by a Multiple Comparison of Mean Ranks test ($\alpha=0.05$), numbers are used for the control site. No statistical notations are used where the test found no difference.
B) Difference in the percent cover of fleshy macroalgae between the two sites (MPA – control site) for each year.
C) Average urchin biomass in g m^{-2} for both sites over time. Statistical notations are the same as A.
D) Difference in the urchin biomass between the two sites as is B.
All error bars are $\pm$ 1 standard error. All data before 1998 is from McNaught (1999).

Table 1.2. Results of Kruskal-Wallis tests on average sea urchin biomass and percent cover of fleshy macroalgae for all sites studied. Site names correspond with those in Table 1 and Fig. 1. Categories include the site name, classification of study site, years studied, and the measurements taken.

Site	Class.	Years	Measure	df	n	p value
East Point	MPA	'96-'02	urchins	6	210	$p > 0.05$
			algae	6	210	$p < 0.0001$***
Cow Beach	Control	'96-'02	urchins	6	168	$p > 0.05$
			algae	6	168	$p < 0.0001$***
Seal Head Point	MPA	'96-'02	urchins	6	195	$p = 0.02$*
			algae	6	195	$p < 0.0001$***
Stone's Rock	Control	'96-'02	urchins	5	168	$p = 0.0001$***
			algae	5	168	$p < 0.0001$***
Pemaquid Point	MPA	'96-'02	urchins	6	280	$p = 0.0016$**
			algae	6	280	$p = 0.039$*
Thrumcap	Control	'96-'02	urchins	6	228	$p < 0.0001$***
			algae	6	228	$p < 0.0001$***
Schoodic Peninsula	MPA	'96-'02	urchins	5	156	$p < 0.0001$***
			algae	5	156	$p < 0.001$**
Little Moose Island	Control	'98-'02	urchins	3	133	$p = 0.092$
			algae	3	133	$p = 0.004$*
Sea Duck Rock	MPA	'96-'02	urchins	6	214	$p < 0.79$
			algae	6	214	$p < 0.0001$***
Little Drisko	Control	'98-'02	urchins	3	117	$p = 0.003$*
			algae	3	117	$p < 0.0001$***
Outer Ram Island	MPA	'96-'02	urchins	6	261	$p = 0.003$*
			algae	6	261	$p = 0.052$
Ram Island	Control	'98-'02	urchins	3	126	$p = 0.423$
			algae	3	126	$p = 0.1$

urchin biomass difference in the BACI t-test (df=5, p=0.178). The algae, however, did show differences before and after closure (df=5, p=0.014) because the control site came to have a slightly greater percent cover (Fig. 1.5B). These results may be misleading since the range is not very great and the difference appears to be converging on zero.

Seal Head Point, York

Like the East Point MPA, Seal Head Point MPA has been a macroalgal bed since 1994 (Fig. 1.6). Since 1996, sea urchin biomass has never been above a mean of 11 g m^{-2} and has been zero for the last two years. Macroalgal cover has changed over time and generally increased over the last couple of years (Table 1.2).

The control site by Stones Rock, also a macroalgal bed for eight years, exhibited the same sort of stability (Fig. 1.6). Sea urchin biomass remained below 5 g m^{-2}, and no urchins were found in four of the last five sampling years (1999 data were not available). Similar to Seal Head Point, macroalgal cover increased slightly in the last few years but has always been 90% or greater (Table 1.2).

Given the small fluctuations within the sites, there was little change in the differences between sites (Figs. 1.6B and D). Differences in sea urchin biomass between the sites are very close to zero and differences in macroalgal cover show no pattern. Neither show a BACI difference before and after closure (Student's t-test, df=5, p=.052 for biomass and 0.48 for macroalgal cover).

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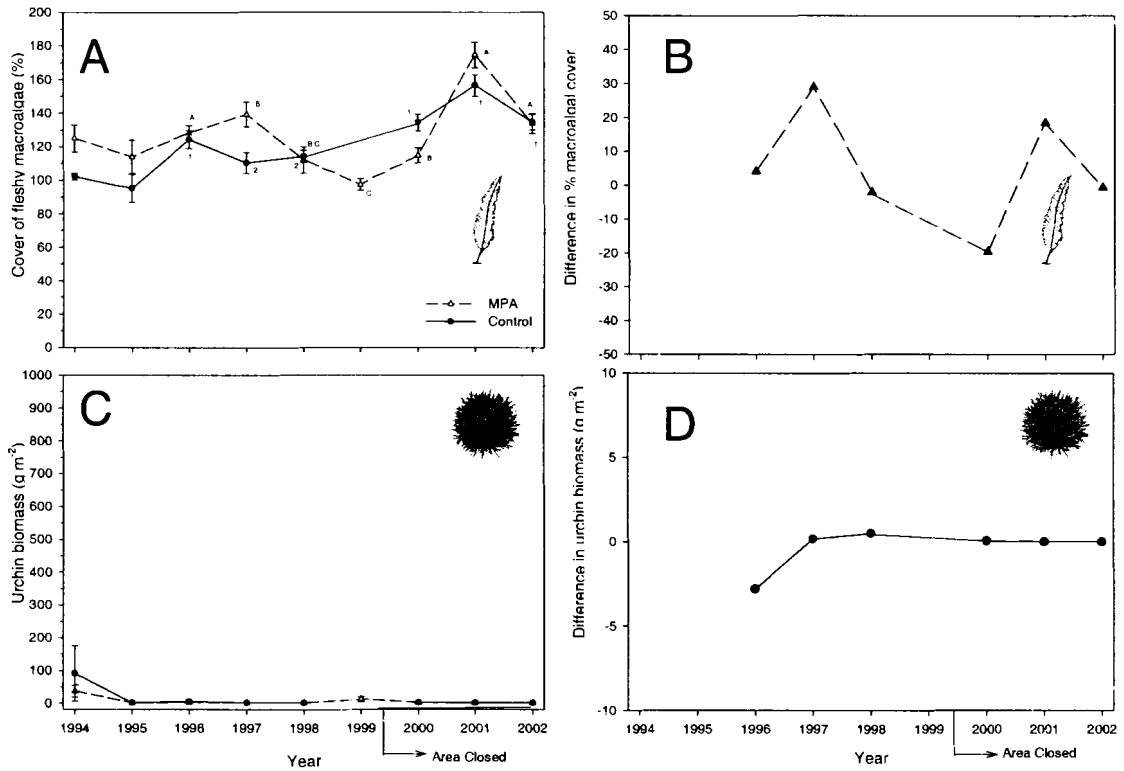
Figure 1.6. Data for the Seal Head Point MPA and Stone's Rock control site in York, Maine. Legend is the same as Fig. 1.5.

Pemaquid Point

Unlike the York sites, both the Pemaquid Point MPA and its control started as coralline communities. Biomass in the MPA remained relatively stable from 1996 through 2002 although there were some significant changes detected (Fig. 1.7, Table 1.2). A decrease in biomass did occur during the first year of MPA closure which we believe is due to a patchy, statewide sea urchin mortality event observed that year (see discussion) and not due to the effects of the closure. After the decrease in 2000, there was a small, but non-significant trend of increasing biomass (Fig. 1.7C). Percent cover of macroalgae showed very little change with almost no macroalgal cover over the duration of the study.
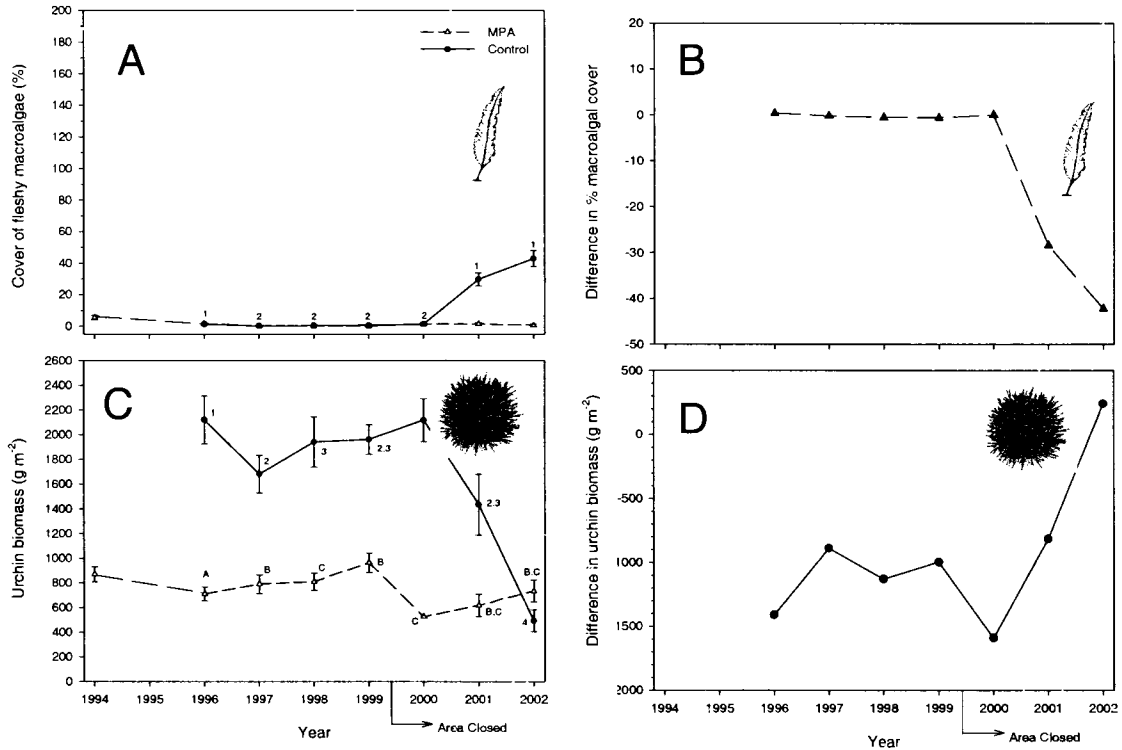
Figure 1.7. Data for the Pemaquid Point MPA and Thrumcap Island control site over time. Legend is the same as Fig. 1.5.

Results of a Kruskal-Wallis test were significant (Table 1.2), which appears to be due to slight differences in the first year (Fig. 1.7A) and not necessarily associated with MPA closure.

Thrumcap Island, the Pemaquid Point control site, exhibited a different response over the same time period (Fig. 1.7). Significant differences were seen in both the sea urchin biomass and macroalgal cover (Table 1.2). Sea urchin biomass varied before 1999 and decrease by 75% soon after Pemaquid Point was closed (mean of 2117.2 g m^{-2} in 2000 to 492.8 g m^{-2} in 2002) such that biomass 2002 was not equal to that in any other year (Fig. 1.7C). As sea urchin biomass decreased, macroalgal cover increased from a mean of 1.3% in 2000 to 29.8% in 2001 and 42.9% in 2002, indicating the beginning of a shift to a macroalgal bed.

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Comparing the differences in biomass and macroalgae between sites showed similar trends (Figs. 1.7B and 1.7D). While there were no significant effects before and after closure (Student's t-test, df=5, p=0.44), differences in sea urchin biomass were starting to lean in favor of the MPA in the last year (i.e. the difference in biomass between the control and MPA was becoming less). While not significant (t-test, df=5, p=0.07), the difference in macroalgal cover suggests increasing macroalgal cover in the control after virtually no changes for five years (Fig. 1.7D).

Schoodic Peninsula

The Schoodic Peninsula MPA started as a coralline community but, by the end of the study, showed signs of a phase shift to a macroalgal bed (Fig. 1.8). Sea urchin biomass remained relatively stable since 1997, with an anomalously high mean in 1999 accounting for all the significance differences (Table 1.2; also see Multiple Comparisons test results, Fig. 1.8C). Macroalgal cover, however, increased after closure (Table 1.2).

In contrast to the MPA, the control at Little Moose Island remained a sea urchin dominated coralline community (Fig. 1.8). Sea urchin biomass was lower in 2002 (954.6 g m^{-2} versus 1459.4 g m^{-2} in 1999) but the results were not significant (Table 1.2). The percent cover of macroalgae remained close to zero and the significant difference detected (Table 1.2) was probably an artifact of ranking such low values, especially since the Multiple Comparison of Mean Ranks test did not distinguish any differences between years.
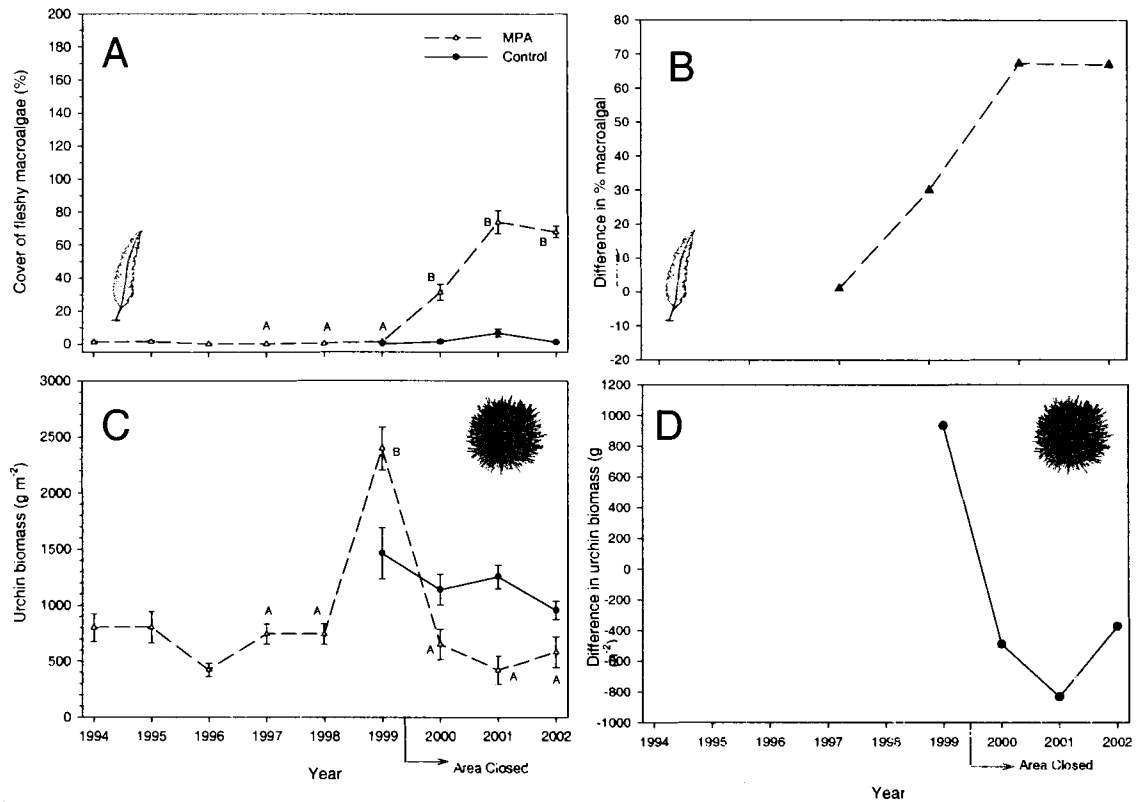
Figure 1.8. Data for the Schoodic Peninsula MPA and Little Moose Island control site. Legend is the same as Fig. 1.5.

The differences between the control and MPA (urchin biomass and algal cover) suggest the MPA was not benefiting from the closure (Figs. 1.8B and D). Again, the small sample size precluded any statistics. The initial large difference in the 1999 sea urchin biomass can probably be attributed to the unusually high sea urchin biomass seen in the MPA, but the changes in the algal community were noticed by the researchers.

Sea Duck Rock, Jonesport

Sea Duck Rock MPA was our eastern most macroalgal site, and like the others was relatively stable in sea urchin abundances (Fig. 1.9). Statistically there were no differences between years in sea urchin biomass (Table 1.2), although biomass did

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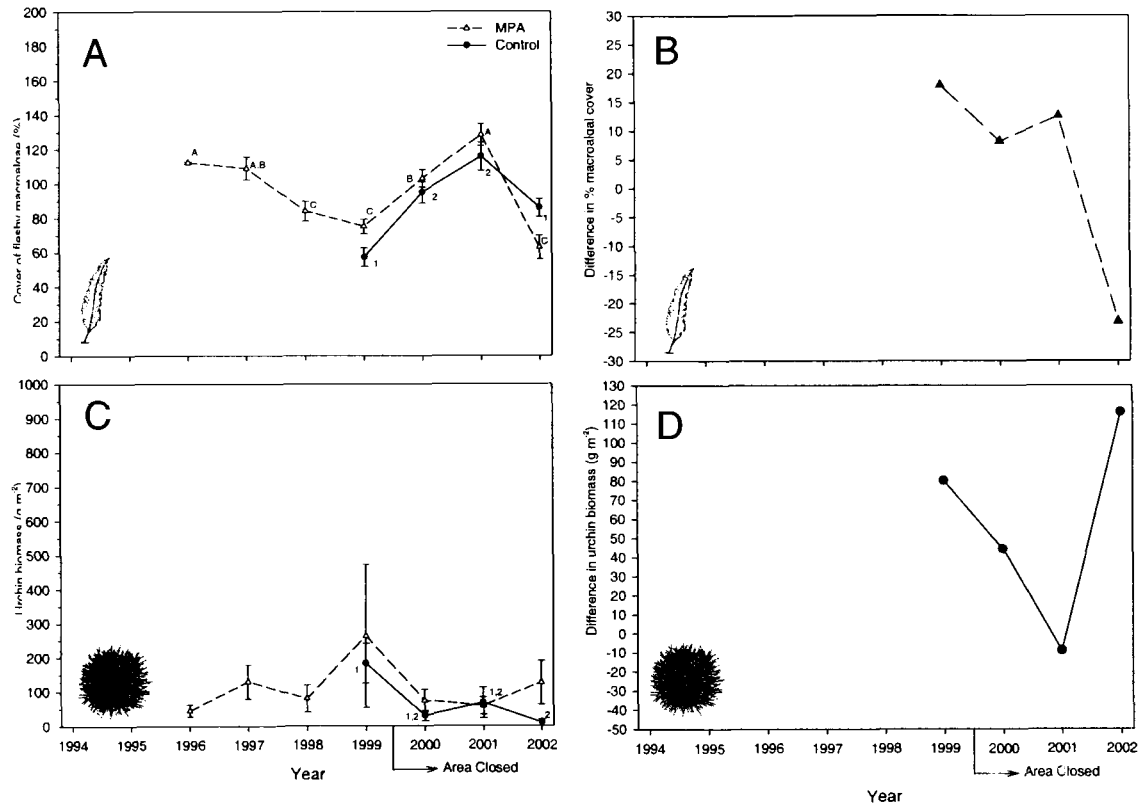
Figure 1.9. Data for the Sea Duck Rock MPA and Little Drisko Island control site in Jonesport. Legend is the same as Fig. 1.5.

fluctuate between 45 g m^{-2} in 1996 and 263 g m^{-2} in 1999. Macroalgal cover varied over time (Table 1.2) but was always above 60% cover and averaged around 100%.

The Little Drisko control site also maintained a macroalgal state (Fig. 1.9), but there were changes in sea urchin biomass over time (Table 1.2). Sea urchin biomass decreased slightly over time, but started with a mean of only 182 g m^{-2} in 1999. The macroalgal cover also fluctuated over time (Table 1.2, Fig. 1.9) but generally followed the same pattern as Sea Duck Rock. In fact, a 2-way ANOVA run on algal data (square root transformed) from 1999 – 2003 did not show a significant site effect (df=1, p=0.075), only significant year (df=3, p<0.0001) and interaction (df=3, p=0.018) effects. Differences between the MPA and control (Figs, 1.9B and D) indicate with no significant

BACI differences in sea urchin biomass or algal cover (Student's t-test, df=3, p=0.91 and p=0.42 respectively). While differences are small, however, the differences in macroalgal cover appear to be indicating more cover in the control.

Outer Ram Island, Jonesport

Outer Ram Island MPA showed very little change over the course of this study (Fig. 1.10) and remained a coralline community. Sea urchin biomass increased slightly over the duration of the study (Table 1.2) but was not significantly different one year before closure (1999) and in 2002 (Fig. 1.10B). Macroalgal cover was virtually nonexistent and showed no significant differences (Table 1.2).

The Ram Island control site coralline community also remained relatively constant. The sea urchin biomass did not have any significant differences over time (Table 1.2) but appeared to have decreased slightly since Outer Ram was closed (Fig. 1.10). The percent cover of macroalgae was also very low throughout the study and did not significantly differ over time (Table 1.2).

The BACI differences for both macroalgae and sea urchin biomass show very little change (Fig. 1.10). Student's t-tests could not be performed since there was only one "before" year, but the weak trends in the data suggest a slight improvement of the MPA in sea urchin biomass by the end of the study, although the changes are very small.
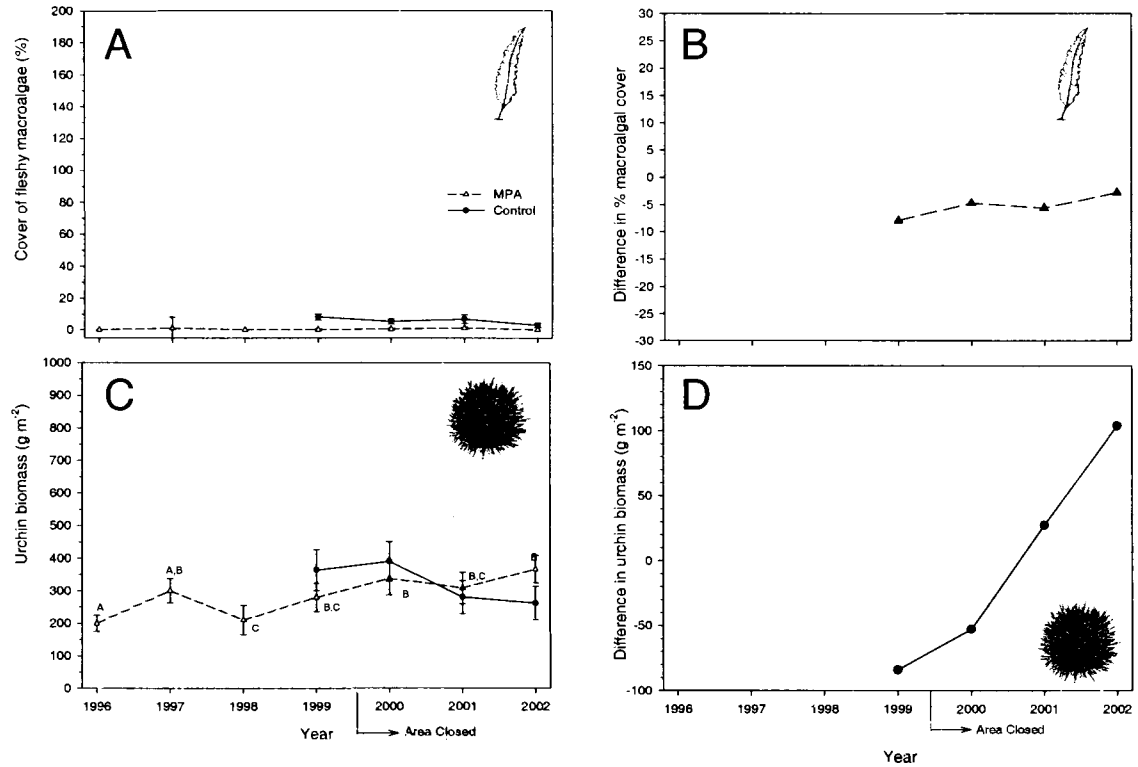
Figure 1.10. Data for the Outer Ram Island MPA and Ram Island control site in Jonesport. Legend is the same as Fig. 1.5.

Discussion

Effectiveness of the Marine Protected Areas

Evaluating the effectiveness of MPAs is very important for management (Allison et al. 1998). Ineffective reserves can harm a fishery if they provide a false sense of security that deters other management options (Carr and Reed 1992). Evaluation can be difficult, especially since low power of statistics and experimental design can often mask results (Allison et al. 1998). Here we look at the trends in the Maine sea urchin MPAs and try to determine their potential for sea urchin recovery.

The general trends along the coast would suggest that the highest recovery potential for sea urchins is in the western part of the state. Settlement is orders of

magnitude higher in York compared to Jonesport (Fig. 1.3). Sea urchin biomass appears

to be historically higher in the west (usually well over 1000 to 2000 g m^{-2}) than Jonesport

(with maximum biomass estimates around 400 g m^{-2}) (Figs. 1.5 – 1.10). Lastly, the more

nutrient rich waters of the EMCC should allow more primary productivity supporting an

alternate stable state (i.e. fleshy macroalgal beds).

The MPAs in Maine, however, did not respond as hypothesized above. The MPA

results can be broadly broken down into three groups: coralline communities (Pemaquid

Point and Outer Ram), Schoodic Peninsula, and fleshy macroalgal beds (Seal Head Point,

East Point, and Sea Duck Rock). We believe the potential utility of MPAs differs in

these groups.

The two MPAs that were initially sea urchin dominated coralline communities

and which remained so (Pemaquid Point and Outer Ram Island) may have been partially

successful in protecting sea urchin stocks. At least these areas protected the sea urchins

from further degradation. Sea urchin biomass remained relatively constant and fleshy

macroalgae was absent in these MPAs. One control (Thrumcap Island) lost 75% of its

sea urchin biomass and started to shift to a macroalgal bed (Fig. 1.7), while at the other

control (Ram Island) biomass may have also decreased in the last two years (Fig. 1.10).

Perhaps more important is the apparent (but not significant) trends in both of these MPAs

of increasing sea urchin biomass in the past year or two. This trend may have been

complicated at Pemaquid Point by a large scale sea urchin mortality that occurred in late

summer 1999. Patchy high sea urchin mortalities were reported throughout the state and

appeared to be associated with warm shallow waters (T. Creaser pers. comm.). Many

dead urchins were observed at Pemaquid Point in 1998, indicating that this unexplained

mortality may have affected the MPA, but none were noticed in the Thrumcap Island control site (J. Vavrinec pers. obs.). Without this unexpected mortality, the recent trend in increasing sea urchin biomass might have been more definitive. Perhaps in time these closed areas will show significant improvements in sea urchin stocks.

The Schoodic Peninsula MPA had results counter to our expectations. Sea urchin populations decreased the year after closure, although the year prior was an anomalously high biomass estimate and could have influenced the data (Fig. 1.8). Without the 1999 numbers, a case could be made that sea urchin biomass had been fluctuating about some mean level throughout the experiment. The algal data, however, do not support this since macroalgal abundances started to increase in the MPA after the closure but remained low in the control (Fig. 1.8). It would seem the Schoodic Peninsula MPA failed to protect both sea urchin stocks and community structure.

The remaining sites (East Point, Seal Head Point, and Sea Duck Rock) all started and ended as fleshy macroalgal beds (Figs. 1.5, 1.6, and 1.9). Overall, the macroalgal beds were fairly stable over time and no sea urchin recovery has occurred. All the York sites have been devoid of urchins for at least two years. The few urchins that persist at Sea Duck Rock are mostly large (>6cm) and widely spaced (J. Vavrinec pers. obs.). Macroalgal cover has remained over 100% and did not show any indication of decreasing.

Possible Reasons for MPA Failure

MPA failure has been blamed on a number of causes including inappropriate MPA placement, Allee effects, poor enforcement, the development of unexpected trophic

cascades (for reviews see Palumbi 2001, Gell and Roberts 2002, Palumbi 2002), and pollution (Allison et al. 1998, Jameson et al. 2002). We will address the possible threats to the Maine sea urchin MPAs and determine their likely impact on our study.

Poor site selection is commonly cited as a cause of MPA failure and can occur if the habitat is inappropriate for the species being protected (Gell and Roberts 2002). In this case, however, sites were specifically chosen because they represent areas where urchins used to be numerous. We do not therefore feel that the localities chosen for the MPAs would adversely affect the outcome of closure.

Another possible consequence of poor site selection is closing an area with little larval input (Tegner and Butler 1985, Allison et al. 1998, Botsford et al. 2001). Our data show poor settlement may factor into the recovery of some MPAs, notably Jonesport (Fig. 1.3). However, this is not true for other parts of the state (but see Harris et al. 2001 for hypotheses concerning recruitment overfishing in the whole Gulf of Maine). Schoodic Peninsula, the next lowest in settlement, averaged hundreds of settlers per m^2 and the highest level recorded for the York area showed over 16,000 urchins per m^2 settling in a given year (Fig. 1.3). With these numbers it is unlikely that low larval supply is causing the failure of MPAs in York.

Allee effects, or reduced reproductive potential at low population sizes, can also impact the recovery of populations (e.g. Ebert 1998). One manifestation is low fertilization success as populations become more widely and thinly distributed. The green sea urchin may to be susceptible to these effects (Wahle and Peckham 1999) but our settlement data do not indicate reproductive limitation in much of the state. Another Allee effect documented for sea urchins on the west coast is increased juvenile mortality

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when the spine canopy of adults is reduced (Tegner and Dayton 1977, Breen et al. 1985).

S. droebachiensis does not appear to have a similar spine canopy effect (see Chapt. 4)

and survival of juveniles is probably not directly related to the presence of adults.

Factors intrinsic to the urchins may also be responsible for delayed recovery.

Slow-growing species will probably respond slower to protection than short-lived, fast-

growing species (Russ and Alcala 1998, Halpern and Warner 2002). *S. droebachiensis* is

a relatively slow-growing species (Vadas et al. 1998, Russell 2001, Vavrinec et al. 2001)

that may only put on tens of grams per year. This slow growth combined with low

population densities may make differences associated with closed areas difficult to detect

and account for the ambiguous results of the coralline community MPAs.

Pollution can also cause the failure of MPAs (Allison et al. 1998, Jameson et al.

2002). Some coastal sections of Maine do have elevated levels of some pollutants

including trace metals, polycyclic aromatic hydrocarbons, and PCBs, but these levels are

generally low, particularly when compared to other areas along the Atlantic seaboard

(Larsen 1992). We do not think these pollutants are dramatically affecting the sea urchin

populations since the same areas have been experiencing record landings in another

benthic invertebrate, the American lobster *Homarus americanus* (DMR 2000).

Enforcement of MPA closures is an obvious concern of managers. Poaching can

easily negate any positive effects generated by closing an area (e.g. Russ and Alcala

1989). We think that poaching in our MPAs was minimal since we had industry support

for the closures from the beginning, areas initially had low sea urchin densities, and sites

were specifically chosen to be easily patrolled. We do know, however, that one site,

Schoodic Peninsula, was fished and probably quite intensively. Fishers admitted to us

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and DMR (R. Russell pers. comm.) that they had fished the area, at least during the 1999/2000 fishing season. This poaching probably explains the unexpected decreases seen in the MPA (Fig. 1.8) and the added attention placed on the MPA may have inadvertently reduced pressure on the control site.

Lastly, unexpected trophic cascades, where perturbations in one trophic level are transmitted down the food web, can create unanticipated results after the closure of MPAs (Pinnegar et al. 2000). Numerous studies around the world have seen an increase in higher order predators (e.g. fish and lobsters) within closed areas, which in turn prey on urchins (e.g. Cole et al. 1990, Sala and Zabala 1996, Cole and Keuskamp 1998, Babcock et al. 1999, McClanahan 2000, Shears and Babcock 2002). Therefore preventing fishing mortality may not protect species from unintended elevations in natural mortality. However, we do not think that trophic cascades resulting from closure are affecting our results for a number of reasons. First, the major predators of sea urchins in the Gulf of Maine including fish (Keats et al. 1986, 1987, Keats 1991, Vadas and Steneck 1995) and cancrid crabs (Scheibling 1996, Leland et al. in review) are not protected by the MPAs. Second, there is no evidence of predator based trophic cascades once the MPAs are closed. Lastly, we believe there are important lower order trophic cascades in this system that led to an alternate stable state (i.e. overfishing of sea urchins has created an increase in fleshy macroalgal beds), but they occurred *before* the macroalgal sites were closed, ensuring the stability of the community structure and failure of the MPAs to replenish sea urchin populations.

Ecosystem Changes and Stability of the Macroalgal State

Many changes in ecosystems are linear and gradual over time, but sometimes abrupt, dramatic changes occur that create an alternate state (May 1977, Knowlton 1992, Scheffer et al. 2001). These types of phase shifts between community states are well described for the Gulf of Maine (for reviews see Pinnegar et al. 2000, Steneck et al. in press). Historically large populations of predatory groundfish dominated the coastal Gulf of Maine (Steneck 1997) and probably controlled benthic invertebrate populations including crabs (Witman and Sebens 1992), lobsters and urchins (Vadas and Steneck 1995). Without a functional herbivorous trophic level, the benthos was probably dominated by large macroalgal beds (Vadas and Steneck 1988, Steneck 1997). In the early and mid 1900s, however, technological advances in the fishing industry allowed widespread depletions in groundfish stocks, releasing benthic invertebrates from predation pressure (Steneck 1997). Increases in sea urchin populations (and therefore herbivory) deforested much of the coast by the 1960s and shifted the hard benthos from fleshy macroalgal beds to coralline dominated sea urchin barrens (Steneck 1997). This state remained until the late 1980s when fishermen started harvesting the green sea urchin. Intense, targeted fishing of the sea urchins has led to localized depletions and allowed the reformation of macroalgal beds (Steneck 1997, McNaught 1999). Therefore, at least two phase shifts have occurred in the last century due to the serial removal of trophic levels (Steneck et al. in press).

This last phase, the fleshy macroalgal beds, exhibits the signs of being an alternate stable state. Multiple stable states describe numerous community assemblages that may be stable for a given environment, either at the same time or in the same place at

different times (Sutherland 1974). In theory, alternative states arise from different starting points (e.g. recruitment history) or as a result of perturbation pushing the system to a new equilibrium point (Lewontin 1969, May 1977, Bender et al. 1984, Knowlton 1992). Once this disturbance hits a threshold level, the changes in the community are usually quite fast and dramatic (May 1977, Knowlton 1992). After the change occurs, there needs to be some feedback in the community that prevents the re-establishment of the alternate dominant species (i.e. predation, low recruitment, etc.) (Sutherland 1990) and reversal usually requires a higher critical level or threshold (i.e. hysteresis sensu Scheffer et al. 2001). Lastly, stability is usually defined as persistence longer than the lifespan of the dominant organism (Connell and Sousa 1983).

Maine fleshy macroalgal beds demonstrate these characteristics. Coralline communities are stable until sea urchin biomass is reduced to a critical level (McNaught 1999, Chapt. 2) and then a rapid shift occurs forming a macroalgal bed (e.g. Fig. 1.5). It appears that much higher densities of urchins are needed (i.e. hysteresis) to convert the macroalgal beds back to a coralline community (Scheibling and Hatcher 2001, Leland et al. in review). The fleshy macroalgal beds in York have persisted for at least seven years in some cases (Figs. 1.5 and 1.6), much longer than the average lifespan of one to three years (Chapman 1986) of the dominant *Laminaria* kelp. Feedback mechanisms preventing the re-establishment of sea urchin populations are also being discovered McNaught (1999) found that post-settlement mortality can be as high as 99.9% by year one due to predation by small crabs and amphipods. Leland et al. (in review) demonstrated larger urchins are also susceptible to predation from large migratory Jonah crabs (*Cancer borealis*) and whole sea urchin populations introduced into macroalgal

beds were eliminated. The macroalgae itself may also deter sea urchin recolonization through whiplash (sensu Dayton 1975) effects (Kennelly 1989, Konar 2000, Konar and Estes 2003). Additionally, the macroalgal beds may be transitioning from the traditional kelp bed (Johnson and Mann 1988) to a complex dominated by understory (J. Vavrinec unpublished data) or invasive species (Levin et al. 2002) that is denser than the kelp, can occupy more substrate, and may further exclude urchins (Levin et al. 2002). Therefore we conclude that internal mechanisms and feedbacks, not artificial forces (Petraitis and Dudgeon 1999), are perpetuating this community state after the initial disturbance (i.e. fishing), creating a true alternate stable state for the region.

In Maine, the phenomenon is not just the stability of a few areas. Our data suggest that this phase shift is moving up the coast (Fig. 1.4). By 1996, all our study sites in York had changed to fleshy macroalgal beds but many had started shifting long before. In contrast, in 1996 nearly every site in the Pemaquid, MDI, and Schoodic regions were still coralline communities. Macroalgal cover started increasing in the Pemaquid region shortly thereafter and now it is difficult to find large intact sea urchin coralline communities in the area (J. Vavrinec pers. obs.). We are now also starting to see an increase in macroalgal cover in the central part of the state. This rolling community change is probably in response to shifting efforts by fishers as they deplete areas and move to more productive grounds (McNaught 1999). Consequently, Maine continues to lose productive sea urchin fishing grounds that will be difficult to reclaim for the fishery.

Implications

We believe this study reinforces the call for managers to understand the ecology of areas under their control (e.g. Allison et al. 1998). Realizing the presence, or even potential, of catastrophic shifts in the ecosystem (Scheffer et al. 2001) creating alternate stable states can mean the difference between success or failure of MPAs, and indeed whole management plans. This reason for failure is more natural but less obvious than traditional excuses (i.e. pollution, climate change, increased sedimentation, etc.) and could be easily overlooked in planning stages.

To make matters worse, current fishing practices may be predisposing ecosystems to these types of changes. Many studies are now showing that reducing species diversity, especially within trophic levels, can make communities more prone to trophic cascades (Tilman 1996, Naeem and Li 1997, Borrvall et al. 2000, McGrady-Steed and Morin 2000). Some systems like the Gulf of Maine start out with fairly low diversity (e.g. urchins are the primary functional herbivore in coastal habitats [Steneck and Dethier 1994]). However, most areas are being made simpler as industries continue to fish out populations and trophic levels (Pauly et al. 1998). Perhaps Scheffer et al. (2001) are correct in asserting that ecosystem resilience should be the focus of fisheries management because catastrophic shifts in the ecosystem may too big a problem to handle afterwards.

Finally, this study demonstrates the importance of reporting failures as well as successes in MPAs. The overwhelming evidence supporting MPAs in recent reviews (Palumbi 2001, Gell and Roberts 2002, Halpern and Warner 2002, Halpern 2003) could be partially due to the bias against publishing negative results, creating a lopsided argument (Gould 1993). However, these negative results, provided they are supported

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adequately by the experimental design and statistics (Allchin 1999), can help educate the

creators of MPAs and management plans and warn of potential problems. Informed

decisions, based on all the scientific facts, will allow more effective use of management

tools in protecting the ecosystems of the world.

Chapter 2. Ecologically effective population densities: quantifying breakpoints for alternate stable states.

Abstract

Population reductions in ecologically important species can degrade ecosystem function and drastically alter community structure. We calculated the point (ecologically effective biomass) at which green sea urchins *Strongylocentrotus droebachiensis* could no longer control the biomass of fleshy macroalgae in Maine leading to a community shift from urchin-dominated coralline communities to macroalgal beds. This ecologically effective biomass varied with depth and location along the coast, probably due to changes in macroalgal productivity and grazing abilities. These processes, in turn, are most likely dependent on abiotic (light, water motion, temperature) and biotic (metabolism, movement) factors. The data presented here are important for management of strongly interacting species because they demonstrate quantitatively ecologically effective population limits may vary greatly even over short distances and can generally only be determined after community structure has been altered. It is therefore recommended that managers be conservative in their estimates and allow for worst case scenarios to preserve healthy ecosystems.

Introduction

Many ecosystems do not respond gradually to environmental changes, but undergo rapid and dramatic transitions (for review see Scheffer et al. 2001). This is especially true when those changes affect strongly interacting species that control

community structure (Paine 1980). Reductions in important species may go unnoticed until a threshold, or point of no return, is reached, after which the system quickly shifts to an alternate state (May 1977, Knowlton 1992, Scheffer et al. 2001).

Therefore, in order to preserve ecosystem structure, important species must be kept above these threshold values. To this end, Soulé et al. (in press) recently called for the protection and restoration of "highly interactive species" above "ecologically effective population densities." These densities are not just the minimum viable population size but the level at which populations must be maintained for their impact to be felt on the ecosystem. Unfortunately these levels are usually unknown (Soule et al. in press).

We attempted to quantitatively determine the point at which the green sea urchin *Strongylocentrotus droebachiensis* became ecologically ineffective along the coast of Maine. Here, *S. droebachiensis*, like many sea urchins worldwide (Lawrence 1975, Harrold and Pearse 1987, Pinnegar et al. 2000, Steneck et al. 2003) can control the community structure of hard benthic substrates (Breen and Mann 1976, Lang and Mann 1976, Scheibling 1986). When sea urchin densities are high, the benthos is denuded of fleshy macroalgae and characterized by a pavement of crustose coralline algae (i.e. "urchin barrens"). That is, coralline communities dominate when the grazing (or disturbance – d) is greater than or equals the macroalgal productivity (p). When sea urchin densities fall below a certain level and herbivory is adequately reduced (p > d), however, the benthos undergoes a rapid and dramatic phase shift to expansive fleshy macroalgal beds. These macroalgal beds appear to be an alternate stable state and inhibit the repopulation of urchins (Johnson and Mann 1988, McNaught 1999, Chapt. 1).

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The green sea urchin populations in Maine have undergone dramatic changes in the last century. Historically, sea urchin populations were probably controlled by large predatory groundfish and existed in very low numbers (Vadas and Steneck 1995, Steneck 1997). Overfishing of the groundfish in the early 1900s removed this predatory control and by the 1960s sea urchin-dominated coralline communities were spreading throughout the state (Steneck 1997, Steneck et al. 2003). In 1986, an export fishery started to harvest the sea urchin and now urchins are becoming functionally absent in many parts of the state. Fleshy macroalgal beds are again becoming common (McNaught 1999, Chapt. 1).

As a result of these shifts in community structure, we have a natural laboratory to study the point at which sea urchin populations can no longer control fleshy algal populations. We present data quantifying this population level, and how that value changes with longitude and depth. We also attempt to explain these results as dependant on biotic and abiotic factors.

Materials and Methods

SCUBA divers performed benthic surveys to obtain the quantitative data used for these analyses. We conducted these surveys in July and August each year to allow full development of the algal community, to make logistics easier, and to avoid potential seasonal variations in the sea urchin populations (Konar 2001). Surveys were conducted at 5, 8, 10, 15, and 20 m depths from 1996 to 2002 (data prior to 1998 from McNaught 1999). Regional comparisons were conducted at sites (described in Chapt. 1) in four areas of the coast of Maine (York, Pemaquid, Mount Desert Island, and Jonesport; see

Fig. 2.1) and standardized for 10 m depth. We conducted all the multidepth surveys in the Pemaquid region (approximately N 43° 50', W 69° 31') at the sites marked in Fig. 2.1. Due to a number of circumstances we were not able to conduct surveys at all sites and all depths in all years. We haphazardly threw at least twenty 1 m^2 quadrats in each site on ledge substrate to standardize habitat characteristics.

Sea urchin surveys were conducted using a telescoping quadrat design (described in Chapt. 1). This design allows for adequate sampling of all size classes of sea urchins and placing them in 5mm bins based on test diameter (TD). With these data, we constructed size frequency distributions per m^2 for each quadrat. We then converted this distribution into a biomass estimate (g m^{-2}) since sea urchin biomass is a better predictor of herbivory (disturbance) than sea urchin density (Steneck and Dethier 1994). We multiplied the number of sea urchins in each size class by the mean wet weight for that size class (calculated from the regression log biomass = 2.84 (log TD in cm) - 0.23 [McNaught 1999]). Total biomass was then summed for the quadrat and all quadrats were averaged for a site average biomass.

We conducted algal surveys at the same time as the sea urchin surveys. We estimated the percent cover for each species within the same 1 m^2 used for the sea urchin surveys. Algae that could not be identified were quantified by functional group (Steneck and Dethier 1994). For the purposes of these analyses though we combined the species and functional groups into three tiers (crusts, understory, and canopy) for a potential total of 300% (100% for each tier) cover. Since crusts can be ubiquitous, found in both coralline communities and fleshy macroalgal beds (Harrold and Pearse 1987, Johnson and Mann 1988), they were not used in the analyses. We therefore plotted the sum of the
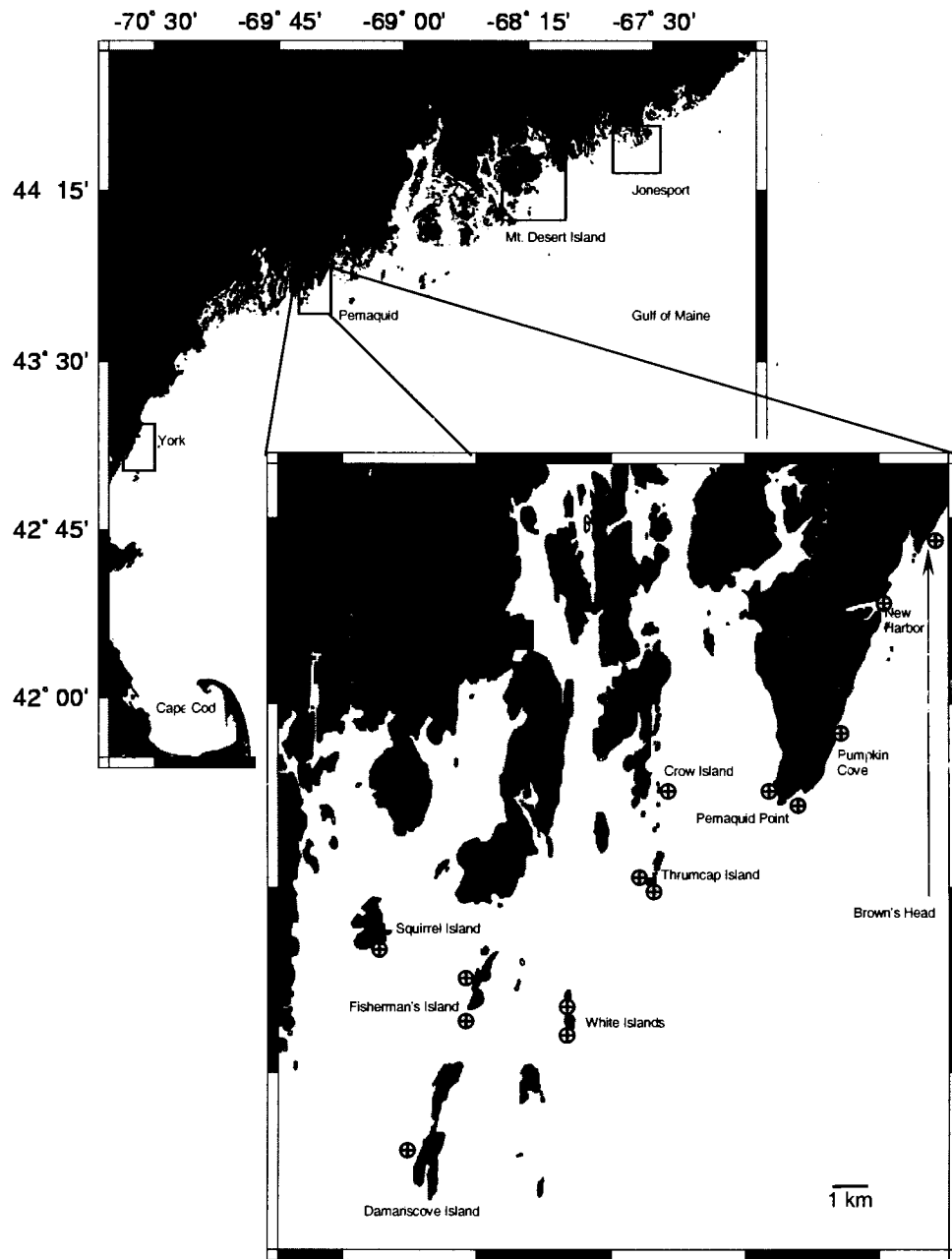
Figure 2.1. Map of the Gulf of Maine with our four study regions labeled. The enlargement of the Pemaquid Region indicates all the sites (⊕) used in the multidepth surveys.

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understory and canopy components for a possible 200% cover. In 2002, we saw a large

settlement of small blue mussels (*Mytilus edulis*) that completely covered the benthos and

all algae in places. Since sea urchins can feed on small mussels (Lawrence 1975, Briscoe

and Sebens 1988) and completely remove them from the benthos (J. Vavrinec pers. obs.),

we included mussels in the calculation of benthic cover. Lastly, a few areas had

extensive growth of the ascidian *Amaroucium lissiclum* in 2002 which could also

dominate the substrate. We rarely observed these colonies in well established urchin

dominated-coralline communities except in protected area (overhangs, vertical surfaces,

etc.), leading us to believe that urchins may well control these populations as well. While

we do not think that the urchins are feeding on intact colonies, they probably prevent the

establishment of new colonies in barrens (incidentally) as they move around the substrate

grazing (Harrold and Reed 1985). For these reasons, we added the percent cover of the

understory and canopy algae, the mussels, and the ascidian to determine the total benthic

cover for a quadrat. All the quadrats in a site were averaged to obtain a site average for

benthic cover.

To establish the point at which sea urchins could no longer control the community

structure, we plotted the benthic cover against sea urchin biomass for all sites in a

category (i.e. depth or region) and fitted a regression to the data. A three parameter

sigmoidal regression ($f = a / (1 + \exp(-(x - x0) / b))$) was then fitted to the data in

SigmaPlot (SPSS Inc., Chicago, IL). We chose a sigmoidal regression because it best

describes the rapid non-linear transition from coralline communities to fleshy macroalgal

beds (i.e. with high sea urchin biomass, macroalgal cover was consistently low; at low

sea urchin biomasses macroalgal cover was consistently high). We then calculated the

effective sea urchin biomass as the biomass in the regression where the macroalgal community gained dominance (i.e. where total cover equaled 50%).

Results

Effective sea urchin biomass estimates were calculated from sigmoidal regressions applied to data in each region and depth category. In all cases, the sigmoidal regression was a better fit) than a linear regression (using r^2 and p values for comaprison.

The depth specific effective urchin biomasses in the Pemaquid region were inversely related to depth (Figs. 2.2 and 2.3). The calculated effective biomass at 5m from McNaught (1999) was 1330 g m^{-2}. We calculated the effective biomass at 8, 10, and 15 m as 650, 292, and 48 g m^{-2}, respectively. Surveys conducted at 20 m could not find any established macroalgal beds with more than 20% cover (mostly small filamentous species), even though there were often no urchins present. The few 30 m surveys were all done at well developed crustose coralline communities with little sea urchin biomass, indicating there was probably no development of fleshy macroalgal beds even in the absence of urchins.

A compilation of the decreasing urchin biomass threshold is shown in Fig. 2.3A. For comparison, an average light attenuation curve from June and August 2002 (E. Annis unpub. Data) is also presented (Fig. 2.3B). To compare the sea urchin biomass threshold and light intensity curves, each value at depth was converted into a percent of the 5m value. While both curves are similar with an exponential reduction, the biomass threshold decreases faster than the light attenuates (e.g. 22% versus 47% of 5m values remain respectively at 10m).
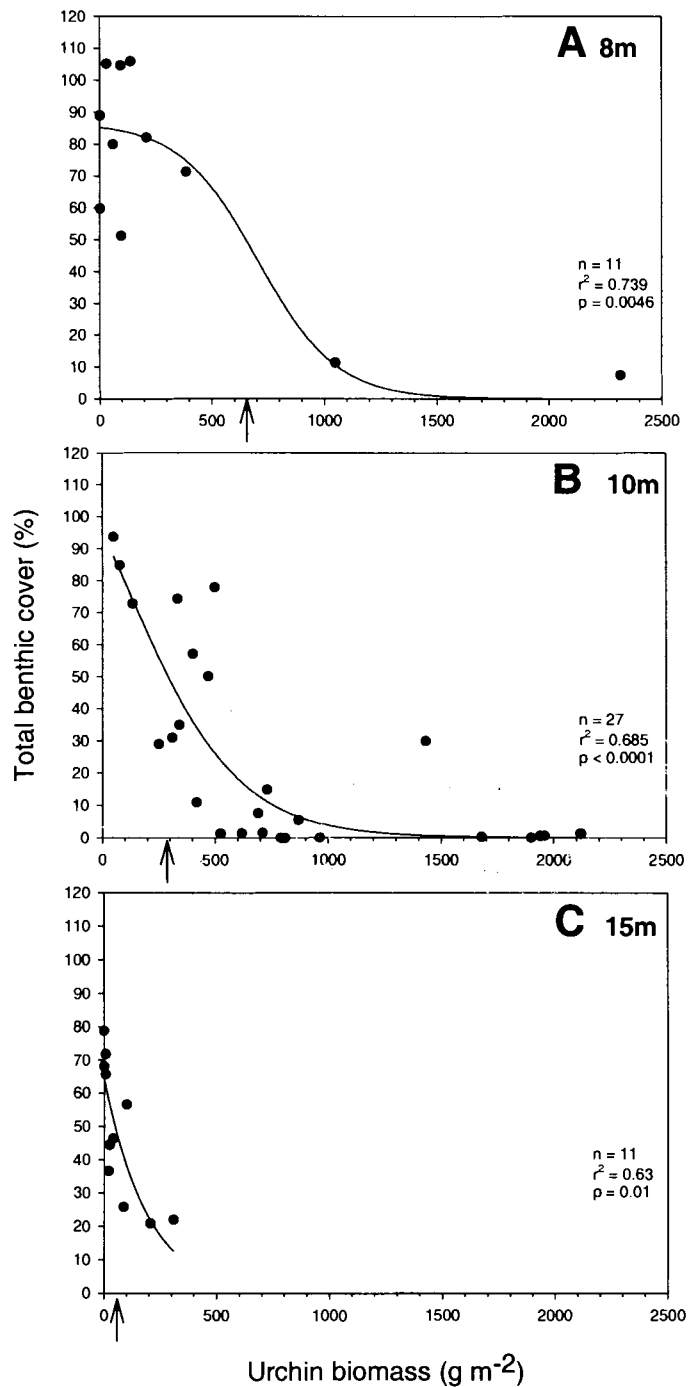
Figure 2.2. Plots of total benthic cover versus average urchin biomass for three different depths in the Pemaquid region. Each point represents the averages of one site for a given year. Curves are sigmoidal regressions fitted to the data. Percent benthic cover includes all fleshy macroalgae, newly settled *Mytilus edulis*, and the ascidian *Amaroucium lissiclum*. Effective sea urchin biomasses were defined as the biomass where the regression intersected 50% benthic cover. Effective biomass values from A to C are 650, 292, and 48 g m^{-2}, represented by arrows on the x-axis.

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Effective urchin biomass (g m^{-2})

Percent change from 5m
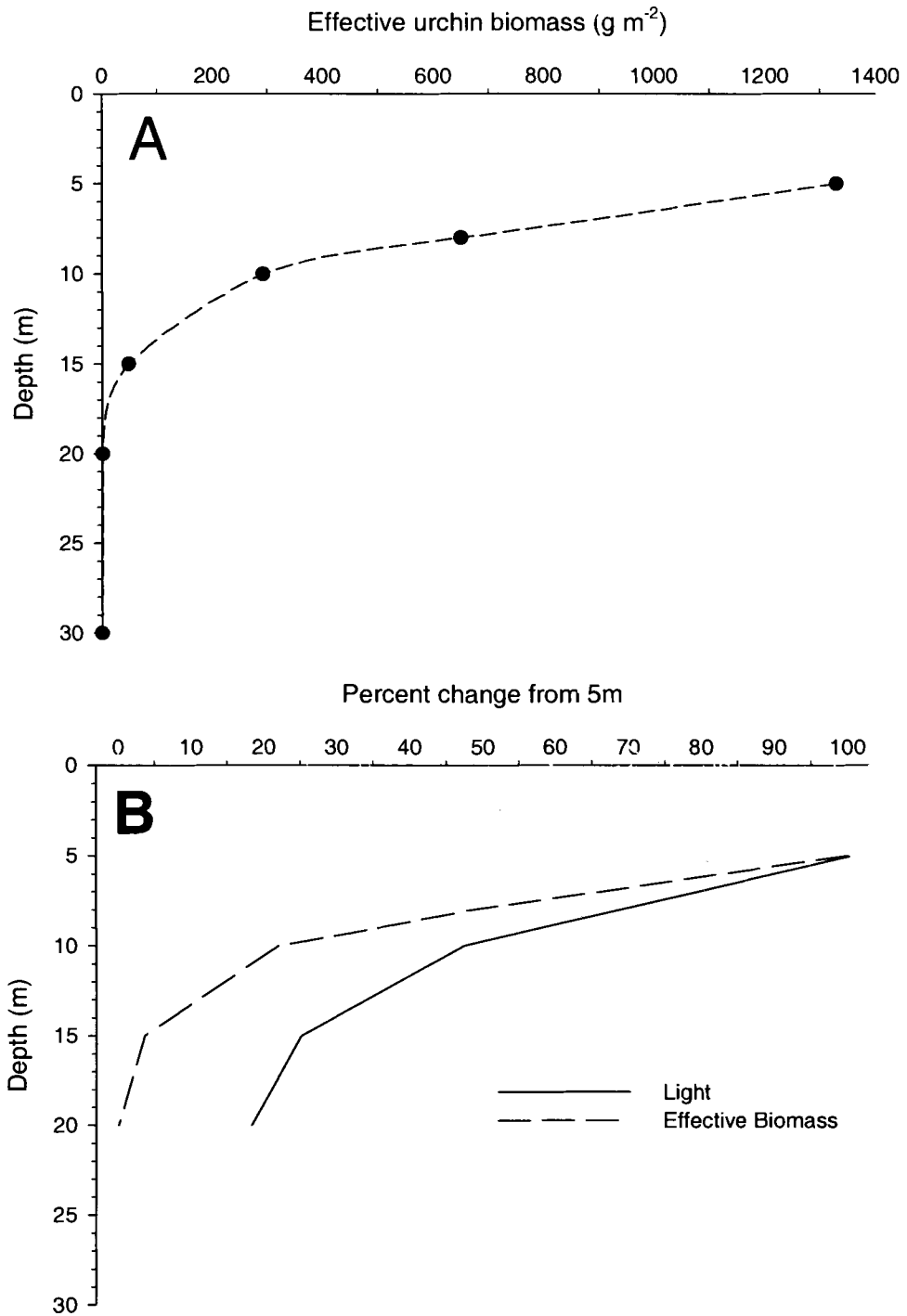
Figure 2.3. A. Calculated effective urchin biomass with depth from the Pemaquid region. The 5m value is from McNaught (1999) and the 20 and 30m values are estimates based on personal observations (see text). B. Comparison of changes in light intensity and effective urchin biomass with depth. Data are calculated as a percentage of the 5 m value (i.e. 5 m = 100%; 10 m = 10 m value / 5 m value).

Regional calculations of effective biomass along the coast were all within the same order of magnitude and exhibited some relationship with latitude (Figs. 2.4 and 2.5). The biomass of sea urchins needed to maintain a coralline at 10 m decreased from west to the east along the coast. In York, the effective biomass was calculated as 755 g m^{-2}. As already reported, the Pemaquid value was 292 g m^{-2}, which was very similar to the Mount Desert Island value of 280 g m^{-2}. The effective urchin biomass was lowest in the Jonesport region (186 g m^{-2}).

Discussion

Macroalgal development is a function of two processes: the ability of the urchins to remove the algae (disturbance potential) and the capacity of the algae itself for growth (productivity potential) (Steneck and Dethier 1994). If productivity increases, more urchins, or more efficient urchins, are needed to control algal populations. The opposite is true if productivity potential decreases. We believe that examining these two environmental characteristics can explain the trends seen in both the depth-related and regional effective urchin biomass values calculated as needed to control macroalgal growth.

Depth Related Differences

Fewer urchins were needed to maintain the coralline communities at deeper depths. Light is obviously an important contributor to this pattern, and can control algal communities even without herbivory (Vadas and Steneck 1988). Patterns of light attenuation and effective urchin biomass with depth are similar but do diverge (Fig. 2.
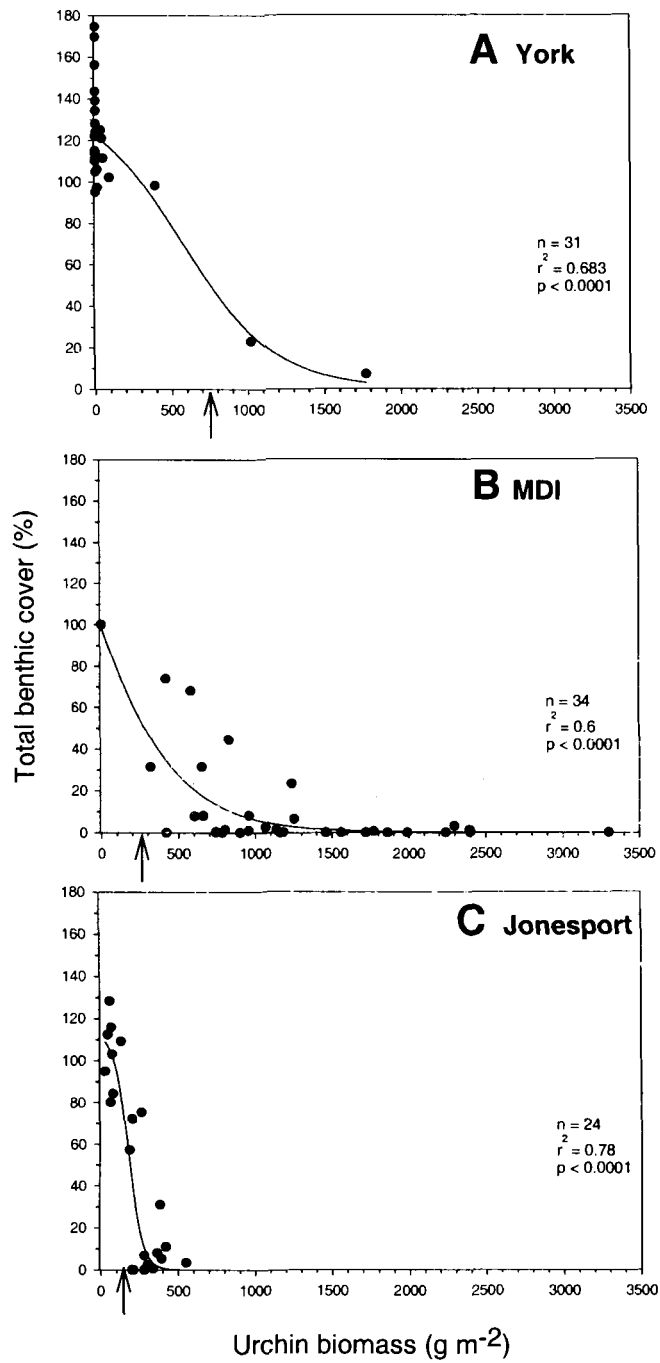
Figure 2.4. Plots of total benthic cover versus average urchin biomass for three remaining regions along the coast of Maine. MDI = Mount Desert Island. All sites were located at 10m depth. Effective urchin biomasses, from A to C, are 755, 280, and 186 g m^{-2}, represented by the arrows on the x-axis. The Pemaquid region (10m) curve is shown in Fig. 2.2 and the effective biomass was calculated as 292 g m^{-2}. Derivations of the data are the same as Fig. 2.2.
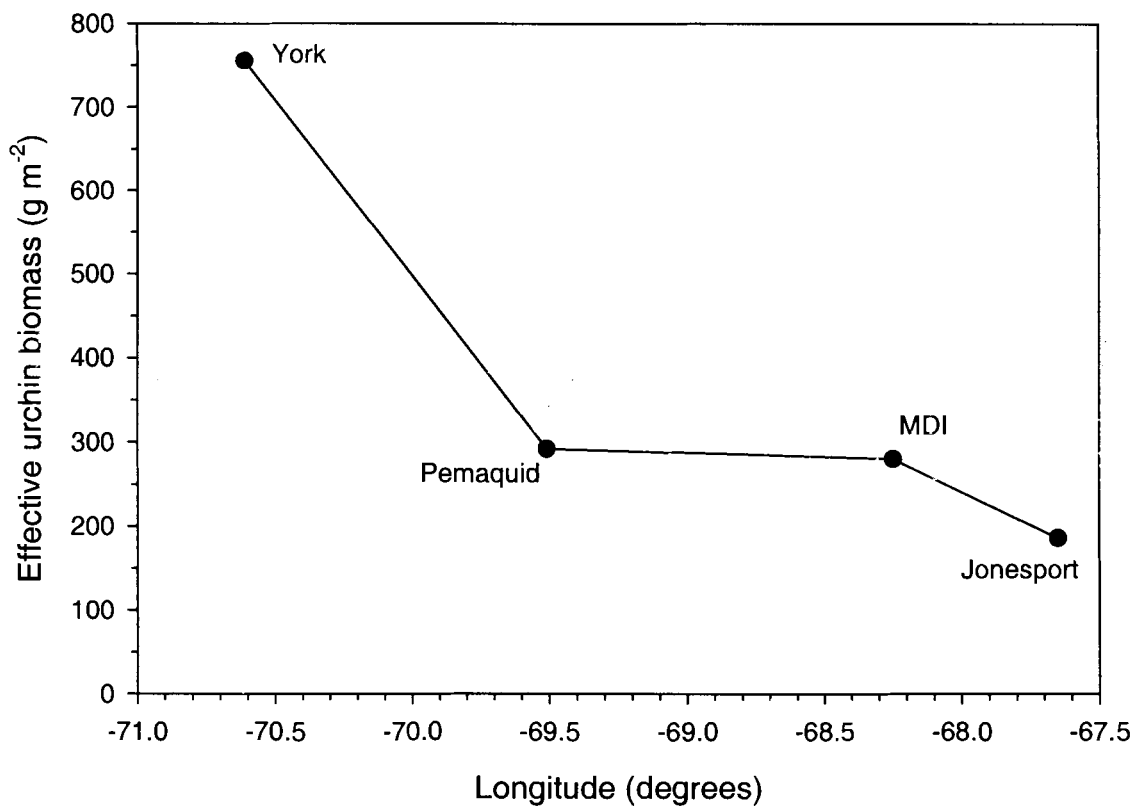
Figure 2.5. Calculated effective urchin biomass along the coast of Maine. Each region is labeled as indicated in Fig. 2.1.

3B), implying that deeper urchins are more efficient at controlling algal populations than shallow populations.

The difference in sea urchin impacts may be a due to urchin movement. All biomass estimates determined in this analysis were based on summer surveys. Unpublished data indicates that urchins may not stay shallow the whole year, but move up and down the ledge with changing conditions (Fig 2.6). The urchin population was greater at 4 m in April than January, and appeared to move slightly deeper as the year progressed. Sea urchins may move deeper in the winter (probably due to winter storms) and summer (probably due to increasing temperatures) (J. Vavrinec unpubl. data). The result is an average annual urchin biomass that may be different from the biomass we calculated in shallower waters.

Wave energy may also affect the impact of sea urchins in shallower waters. Water movement can keep the urchins from accessing the algae or cause whiplash effects from the shallow band of macroalgae that can damage the urchins (Himmelman and Steele 1971, Konar 2000, Konar and Estes 2003). All our sites were exposed coastal areas and subject to rough seas. Shallow sea urchins may have had to spend more time holding on or seeking refuge than sea urchins at deeper sites, affecting their ability to feed.

Temperature may be a third important factor in urchin grazing. It has been suggested that *S. droebachiensis* increases grazing rate with rising temperature (for review see Scheibling and Hatcher 2001) but, above 17°C Leland (2002) found a rapid decline in grazing rate. If the sea urchins are subjected to these high temperatures in the summer, then we could expect to see the type of curve depicted in Fig. 2.3B. The
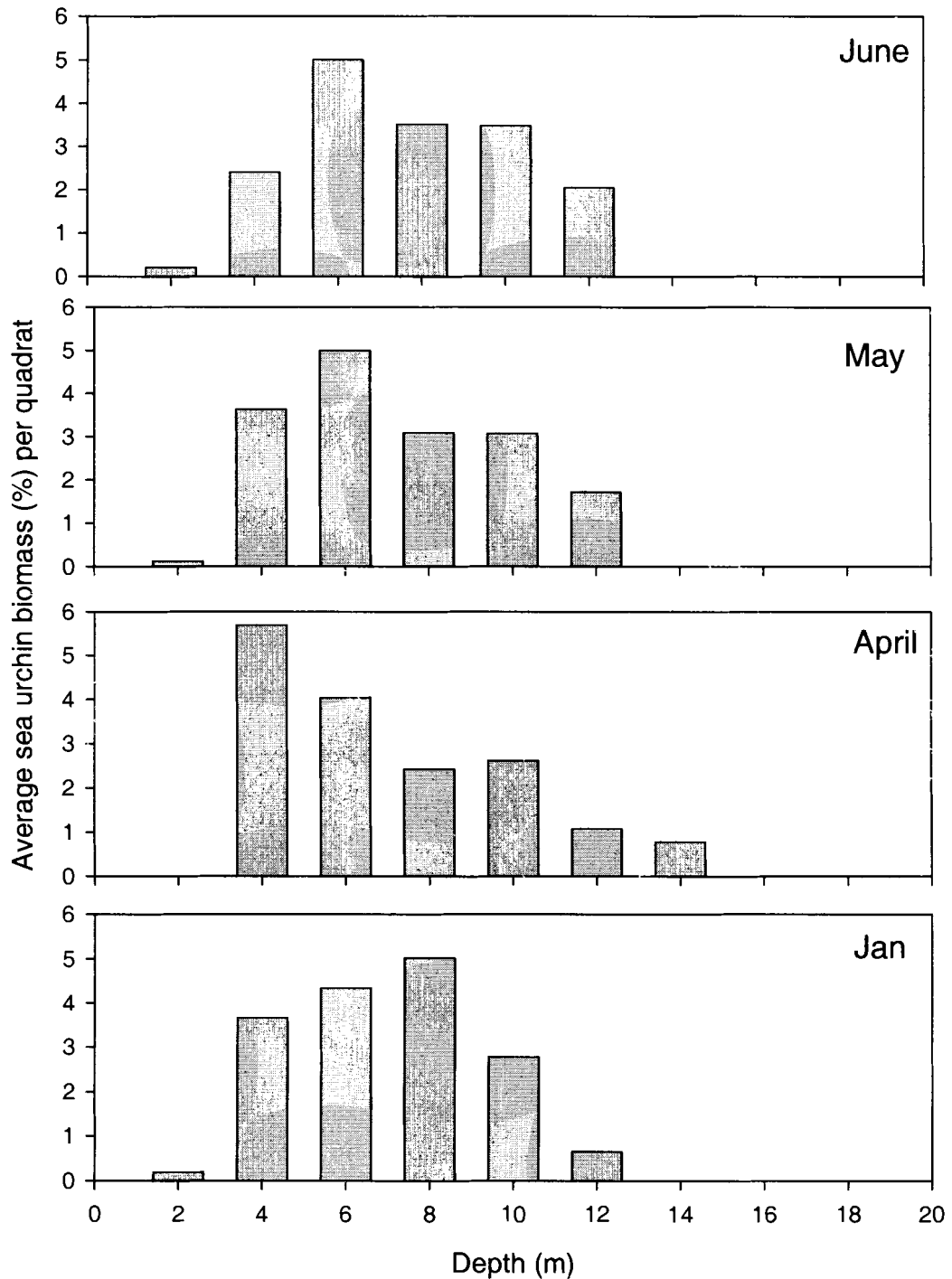
Figure 2.6. Average percent of the total urchin biomass per quadrat over four months in relation to depth. Samples were conducted at Pumpkin Cove (Fig. 2.1) in six permanent quadrats every 2m in depth from 2 to 20m. All surveys were conducted in the beginning of the respective month in 2002 as described in the text.

stratified surface waters at our study sites during the summer can easily experience

temperatures above 17°C (see Fig. 2.7 for a sample CTD cast) but the temperature

quickly drops as one goes deeper. Therefore, sea urchins found in very shallow waters

may be experiencing heat-related stress while other urchins a few meters deeper are still

within optimal temperature ranges for metabolism.

Regional Differences

Our data show that different effective biomasses are required along the coast of

Maine, the highest being in the southwestern part of the state. Many of these differences

are probably related to the differences in the complex currents associated with different

parts of the coast within the Gulf of Maine (see Fig. 2-8 for diagram and Beardsley et al.

1997 for a full description). The Eastern Maine Coastal Current (EMCC) in the

northwest is generally faster moving, less stratified, richer in nutrients, and colder than

the southern Western Maine Coastal Current (WMCC) (Townsend et al. 1987, Pettigrew

et al. 1998). These differences in the two coastal currents can cause some of the

differences observed in regional effective biomass estimates.

Summer sea surface temperatures in the well-stratified WMCC routinely exceed

the 17°C (satellite data from http://www.gomoos.com) temperature limit for effective

urchin foraging (Leland 2002), probably reducing the per capita impact of the sea urchins

as in the depth study. Water in Jonesport does not appear to get that warm, and our two

intermediate sites experience temperatures in between as mixing occurs between the

EMCC and WMCC. These patterns alone could help explain the differences seen in the

regional threshold estimates.
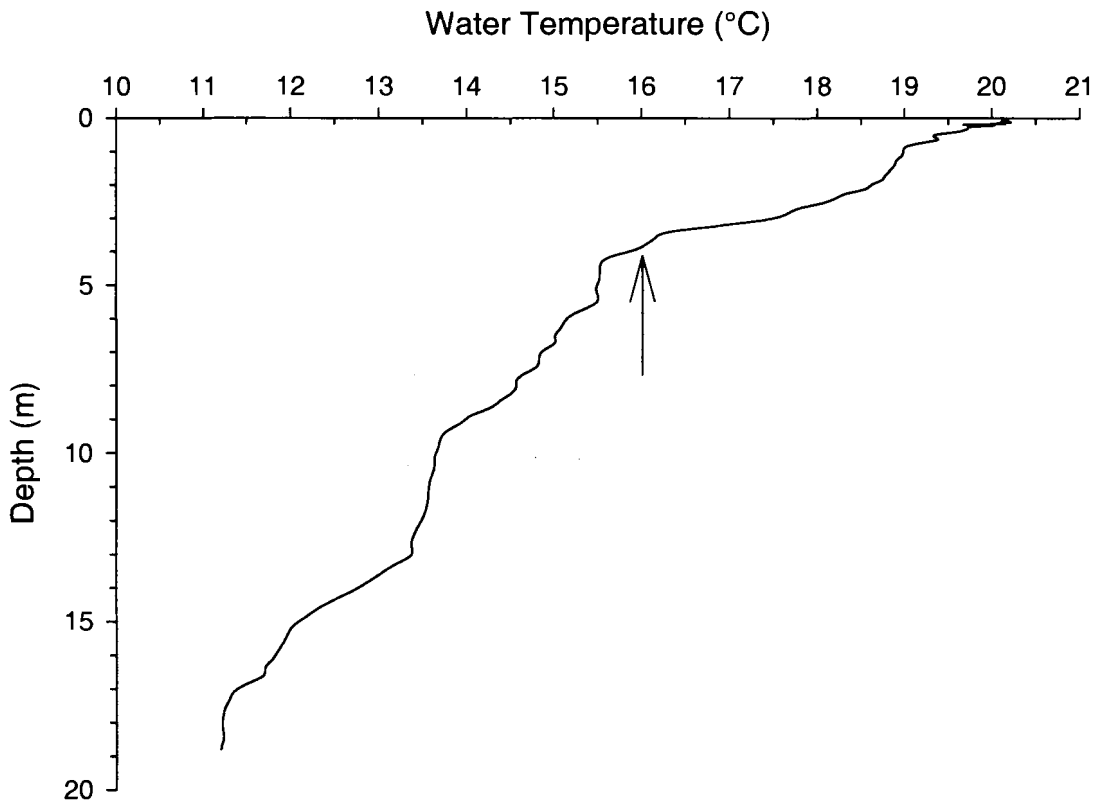
Figure 2.7. Representative temperature profile of a stratified summer water column. These data were collected off Damariscove Island, Pemaquid Region, on 15 August 2002 (data courtesy of E. Annis). The point where the temperature drops below 16°C is indicated by the arrow.
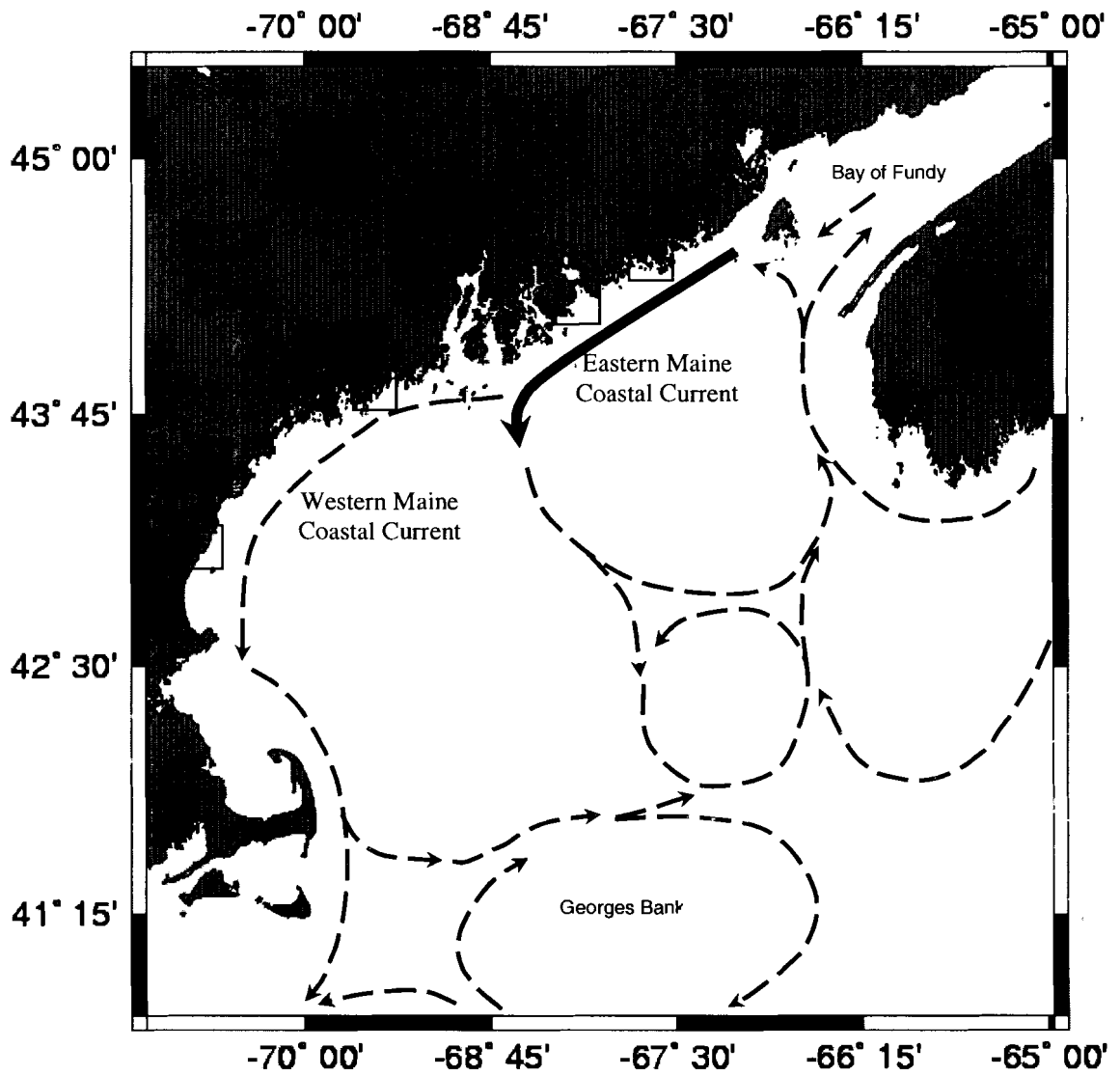
Figure 2.8. Map showing prevailing surface currents in the Gulf of Maine (adapted from Beardsley et al. 1997). Of interest are the strong, mixed Eastern Maine Coastal Current (indicated by the darker solid line) and the weaker Western Maine Coastal Current. Regional locations indicated are the same as in Fig. 2.1.

Potential productivity of the macroalgae can also be a factor in regional patterns. There is some indication that macroalgal growth in the WMCC experiences a seasonal nutrient limitation not seen in the EMCC (S. Zimsen pers. comm.). Despite this, there are limitations in light availability that may reduce productivity potential. First, the tides in the eastern part of the state are generally larger than the western (mean tidal range is 3.5m in Jonesport, 3.1m at MDI, and 2.6m at Pemaquid Point and York Harbor; http://co-ops.nos.noaa.gov/tides03/tpred2.html#MN). Since our sites are standardized for ~ 10 m mean low water, the difference in tidal range makes our sites in eastern Maine deeper on average (see previous section for implications). Additionally, light attenuation in the water column appears to be greater in the EMCC (from depth of 1% light penetration graphs at http://grre.umeoce.maine.edu/ecohab.html; S. Zimsen pers. comm..), probably due to resuspension in the larger tidal flows. Lastly, the colder water of the EMCC tends to produce more fog than the WMCC, further limiting light reaching the benthos. All of these factors could drive the effective urchin biomass estimate further down the depth curve from 10 m. The result of this is that a lower urchin biomass would be needed to maintain the coralline state.

Lastly, differences in the regional effective biomass estimates may be partially due to demographic differences in the urchin populations themselves. In general, urchins are much larger in the eastern than the western parts of the state. For example, if we pool all our regional data in 1998, we see that York possessed almost no sea urchins larger than 20 mm TD whereas Jonesport urchins reached almost 90 mm (Fig. 9). This could be due to the fact that areas in the western part of the state were being fished more heavily than the eastern parts at the start of this study (McNaught 1999), but there is also urchin

growth curve evidence to suggest that sea urchins do not attain as large a size in Pemaquid as they do in Jonesport (Vavrinec et al. 2001). For whatever reason, the York biomass estimate is based on smaller urchins than the other regions and could help explain the much higher biomass needed at the southern site (larger sea urchins can have a greater per capita impact).

Implications

Soulé et al. (in press) suggest that estimating ecologically effective population levels could be problematic and results could vary with the locale. Our estimates were calculated only after sea urchin populations in many areas had probably been reduced below ecologically effective levels. Additionally, these levels varied greatly not only between but within regions in response to intrinsic and extrinsic variables such as temperature, productivity potential, and growth characteristics. Therefore any management plan, especially without specific knowledge of the local ecosystem, should account for the highest levels needed to maintain ecologically effective populations. For example, coast-wide management measures based on effective urchin biomass estimates for Jonesport would allow the western part of the state of Maine to become overharvested, creating large-scale shifts in community structure from coralline communities to macroalgal beds. It is recommended that managers be conservative in calculating their ecologically effective biomass estimates and account for the ecology of the entire community as well abiotic characteristics of their ecosystems.

We also suggest that macroalgal biomass is a function of productivity minus the disturbance ($b = p - d$). This dynamic can be seen in other related alternate stable states.

For example, African woodlands have been decreasing as a result of increasing disturbance (due to elephant foraging and anthropogenic fires) while productivity remained constant (Dublin et al. 1990). Elevated white-tail deer populations (increased disturbance) may have lead to alternate woody plant communities in the eastern US (Stromayer and Warren 1997). Herbivory (increased disturbance) may affect community structure in semi-arid grazing systems, but changes in soil nutrient availability (decreased productivity) probably perpetuate the alternate state (Rietkerk and van de Koppel 1997). Lake eutrophication and changing water levels (changing productivity) probably cause communities to move to alternate stable states in many lake environments (Blindlow et al. 1993). Sea otter populations determine community organization in the Pacific Northwest based on changing disturbances from hunting or killer whale predation (Estes and Palmisano 1974, Estes and Duggins 1995). Macroalgal growth on coral reefs is largely due to reductions in herbivory (for review see Knowlton 1992) and may be exacerbated by increases in nutrient (increased productivity) availability (e.g. Hughes et al. 1999).

Our results show the significance of effective populations in controlling the stability of community types. Thresholds have been dealt with conceptually (May 1977, Knowlton 1992, Scheffer et al. 2001), but our results quantify actual biomass levels needed to preserve the community composition. Once this level is reached, dramatic and severe consequences occur. Understanding these values and planning for them in conservation goals is a difficult but necessary component of any management strategy seeking to preserve the ecological structure of ecosystems.

Chapter 3. Transport of a benthic invertebrate to shallow settlement grounds: downwelling in the North Atlantic.

Abstract

Settlement of the green sea urchin *Strongylocentrotus droebachiensis* was monitored for five years on the coast of Maine. In most years settlement was associated with strong northwest wind events that would advect warmer surface waters onshore, creating "downwelling" conditions. We present data that show the influx of warmer stratified surface waters into coastal regions during these events and show how larval placement high in the water column contributes to the success of the system. Times when settlement did not correspond to this pattern were also explored. They were probably due to decreases in water column stratification or the effects of direct wind forcing. We also document for the first time the apparent presence of newly metamorphosed *S. droebachiensis* sea urchins in the water column.

Introduction

The majority of marine invertebrate life cycles have planktonic larvae with benthic juveniles and adults phases (Thorson 1950). This larval phase facilitates dispersal both away from and to appropriate benthic settlement substrates (Thorson 1946). Since dispersal and settlement often drive the structure of populations and communities (e.g. Underwood and Denley 1984, Gaines and Roughgarden 1985), many scientists have called for a marriage of the fields of benthic and larval ecology to better study marine ecosystems (e.g. Eckman 1996).

Many studies have been done attempting to link physical oceanographic processes with larval delivery, since most larvae cannot swim well against prevailing water movement and often have to rely on placement in wind- or tidally-driven currents (Shanks 1995). This research has included work on local currents (e.g. Sammarco and Andrews 1988, 1989, Phillips et al. 1991, Gabric and Parslow 1994, Pattiaratchi 1994, Sammarco 1994, Cowen et al. 2000), internal waves (Pineda 1999), pycnoclines (e.g. Metaxas and Young 1998a, Pearce et al. 1998), frontal zones (Franks 1992, Shanks et al. 2000), and wind-driven movement (e.g. Bertness et al. 1996).

The transport of invertebrate larvae onshore by relaxations in upwelling events is a well known wind-driven dynamic on the west coast of North America where upwelling is very strong and dominates the ecosystem (e.g. Wing et al. 1995a, Wing et al. 1995b, Miller and Emlet 1997, Botsford 2001). With the exception of Shanks (2000) in North Carolina, little has been done on the east coast, however, probably because upwelling is not as obvious and dramatic. Yet we think that the wind-driven advection of surface waters onshore (i.e. "downwelling") can have important impacts on in the North Atlantic and may be responsible for delivering larvae to preferred settlement grounds along the coast. To determine the effects of wind direction on settlement of the green sea urchin (*Strongylocentrotus droebachiensis*) we studied larval distributions in the water column, settlement, wind stress, and hydrographic conditions along the midcoast of Maine for five years. These data suggest that the position of competent sea urchin larvae in the water column allows them to be advected inshore to shallow water settlement sites during periods of "downwelling".

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Materials and Methods

Study Organism

The green sea urchin (*S. droebachiensis*) is an important component of the Gulf of Maine benthos. Functionally, the green sea urchin is the primary coastal herbivore (Steneck and Dethier 1994) and like many urchins worldwide (Lawrence 1975, Harrold and Pearse 1987, Pinnegar et al. 2000, Steneck et al. 2003) its population dynamics can control benthic community structure on hard substrates (Breen and Mann 1976, Lang and Mann 1976, Scheibling 1986). In the last 15 years, the sea urchin has become an extremely valuable fishery in the state of Maine and populations in many areas have been severely depleted resulting in the spread of high-biomass fleshy, macroalgal beds (Steneck 1997, McNaught 1999, Chap. 1).

The green sea urchin is a broadcast spawner with a pelagic larval phase. Gametes are released late winter, early spring, with sea urchins at the southwestern end of the Gulf of Maine coastline spawning approximately six weeks before those at the northeastern border (Vadas et al. 1997). The sea urchin larvae (or echinoplutei) then develop through four-, six-, and eight-armed stages (Strathmann 1987). Echinoplutei can swim (and feed) using ciliary action once the larval arms develop (Strathmann 1971). Development of the larvae to metamorphosis can take between 5 and 21 weeks in *S. droebachiensis* depending on temperature (Strathmann 1978, Strathmann 1987, Hart and Scheibling 1988), but probably average around eight weeks in Maine (Towers 1976).

Sea urchin settlement varies along the Maine coast. Settlement usually occurs in late May and June, probably starting earlier in the south and later in the north (Harris et al. 1994, McNaught 1999). The level of settlement also differs, often by orders of

magnitude, with the highest densities of new urchins occurring in the southern parts of the state (Harris and Chester 1996, Balch et al. 1998, McNaught 1999, Chapt. 1). Harris et al. (1994) determined sea urchins preferentially settle in shallower waters (maxima around 6 to 9 m).

Sea Urchin Settlement

Two separate settlement experiments were performed to examine the settlement in this sea urchin. Both used the artificial turf (Astroturf™, Monsanto Corp., St. Louis, MO) collectors described in Chapt. 1 and McNaught (1999). These collectors were 9 x 20 cm, attached to flat PVC plates for rigidity, and fastened to bolts cemented into the ledge. Collectors were carefully collected by SCUBA divers, washed, and sorted (see McNaught 1999, Chapt. 1).

To examine possible effects of wind direction on settlement, we placed collectors on the east and west sides of Pemaquid Point, Maine (N 43° 50' W 69° 31', Fig. 3.1). Sites were granitic ledge in 10m of water scraped of all fleshy macroalgae. We placed four settlement collectors at each site for short durations during the month of June, after which we retrieved the collectors and replaced them with fresh ones. We tried to exchange the collectors every day in 1998, 1999, and 2000, and averaged every three or four days in 2001. The contents of the collectors were sorted and the number of sea urchin settlers was determined. When the collectors were out for more than one day, the total number of urchins was divided by the number of days in the water for an average settlement per day.
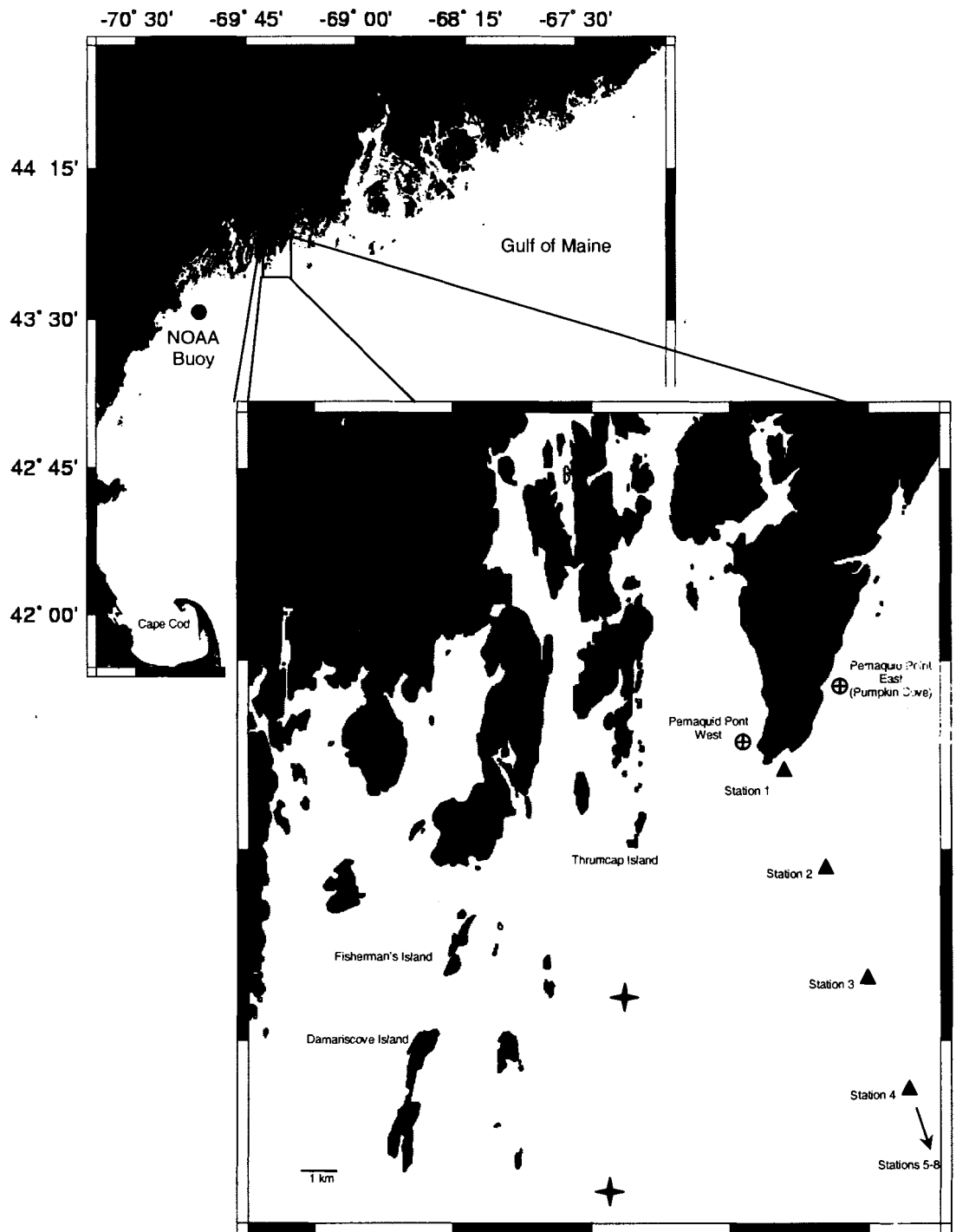
Figure 3.1. Location of study sites in the Gulf of Maine. Settlement sites are denoted by a crossed circle (⊕), larval sampling sites are marked with a cross (✦), and stations where CTD casts were conducted are shown with a triangle (▲). The filled circle (●) indicates the location of NOAA Buoy #44007.

We conducted a second experiment in 2002 to determine the effect of depth and wind on settlement and coastal water temperature. These trials were conducted on the east side of Pemaquid Point (Pumpkin Cove, Fig. 3.1) from 1 June to 28 June. Four turf collectors were placed at 6, 8, 10, 12, and 14 m depths and exchanged every four to five days. Again, the number of settlers on a settlement collector was divided evenly by the number of days in the water. Each depth station also had a Hobotemp (Onset Corp., Pocassett, MA) temperature logger placed by the collectors for the duration of the experiment.

Wind Estimates

In each year, we calculated daily wind stress using wind velocity and direction data from the NOAA Buoy #44007 located off Portland, Maine (Fig. 3.1). Since winds from 75° T are approximately parallel to the shore and most likely to affect settlement, we defined these east-northeast winds as a positive wind stress and west-southwest winds as negative. For each entry, we converted wind velocity into wind stress (τ) using the formula $\tau = \rho_a\, C_D\, W^2$ where ρ_a is the density of the air (1.3 kg m^{-3}), C_D is a drag constant (0.0013), and W is the longshore velocity of the wind (Pond and Pickard 1983). All values were then averaged for the whole day to characterize the wind for the time the settlement collectors were out (i.e. starting and ending ~0900 hrs EST).

CTD Stations

In 2001, we conducted CTD (Conductivity, Temperature, Depth) casts to characterize the temperature profile of the coastal waters by our settlement sites. Eight

stations were set up in a line off Pemaquid Point perpendicular to the shore (165°, Fig. 3.1). The first station was close to land in 25m of water. The other stations were spaced approximately every 1.84 km (1 nmile) off shore, and all were deeper than 50m. Temperature casts were performed using a SEACAT19 CTD (Sea-Bird Electronics Co., Bellevue, WA) and temperatures were averaged into 0.5 m depth categories. Four sets of CTD casts were made on June 18, 22, 27, and 28 (Julian Day 169, 173, 178, and 179). The first three dates we were able to sample all eight stations, but we could only sample the first five stations on JD 179.

Larval Distribution

We attempted to determine the vertical distribution of echinoplutei in the waters off Pemaquid Point. We sampled two sites (~ 5 and 9 km south of Thrumcap Island) where shallow water turbulence was less (Fig. 3.1). We used a homemade pump plankton sampler. Water was drawn through a garden hose (~ 16 mm dia.) at depth by an impeller driven sprinkler pump. The water then passed through a modified home water filter (similar in design to the system of Berman and Kimor 1983) using a Nytex mesh filter. The filtered water was metered to quantify the volume sampled. In 1998, water was passed through an in-line 300 µm mesh filter. To insure that smaller echinoplutei were captured during sampling and not passing through the filter, we reduced the mesh size to 156 µm in subsequent years. In 2000, the filter was removed from the sampler, and water was passed through a plankton net to reduce pressure on the mesh. In both cases, the in-line filter or cod end of the net were modified to create a sample container that could be easily switched in the field and capped to allow multiple samples in a given

day. We also recorded the temperature and salinity of the water at each depth with a YSI 30 Salinity / Conductivity/ Temperature meter (YSI Inc., Yellow Springs, OH). This method was later validated with concurrent casts with the CTD.

Water samples were taken from discrete depths to quantify vertical distribution of the larvae. We sampled the entire water column from the surface to the sea floor (usually 27 to 33 m depending on the tide) in 3m intervals. A sampling head was placed at the end of the collection hose to increase the precision of sampling. It was constructed of two 40.6 by 40.6 cm pieces of sheet metal spaced 5cm apart, with the hose protruding through the top piece of metal so that water was drawn laterally from the sides. The sampling head could also be detected via a depth sounder to confirm the depth of sampling.

The filtered samples returned to the laboratory for sorting. In 1998, the samples were placed in a cold cooler and kept alive. In later years we placed all the samples in alcohol to prevent further development of the echinoplutei in the sample. Samples were rinsed in the laboratory with 10 μm filtered water and carefully sorted under a dissecting scope. Larvae from all echinoderms and decapod crustacean larvae were counted. The stages of development were noted for all echinoplutei.

Results

Effects of Wind on Daily Settlement

In 1998 and 1999, peaks in settlement did not differ between sites on either side of the peninsula and both sites in both years had a significant correlation between settlement and the longshore wind stress with 24 hr time lag (Figs. 3.2 and 3.3). In 2000,
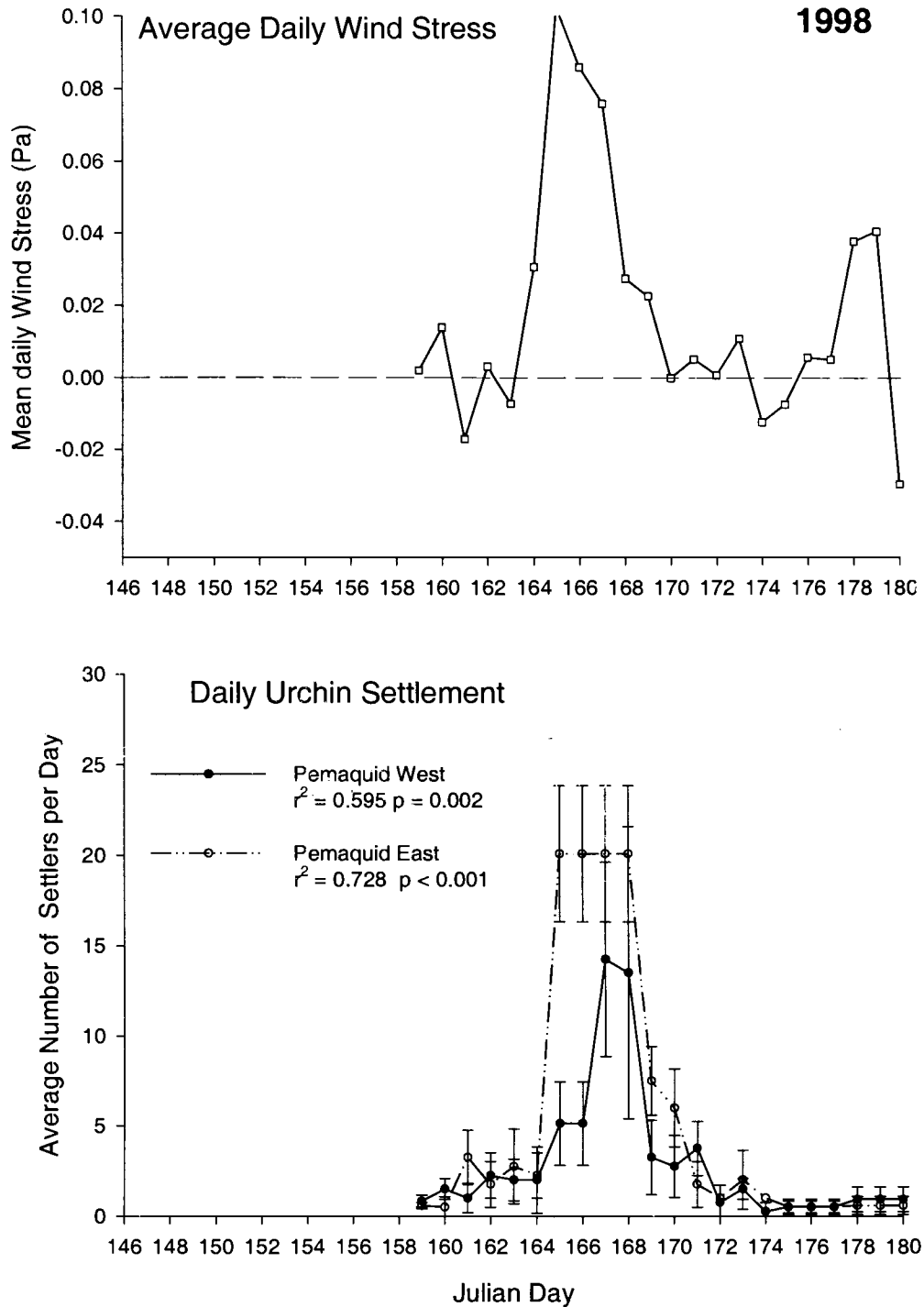
Figure 3.2. Average daily longshore wind stress and average daily settlement per settlement collector in 1998. Alongshore wind stress has been defined so winds from 75° is positive and 255° is negative. Error bars on daily settlement show ± 1 SE. Values given in the legend are for correlations between settlement and wind stress (with a 24 hr time lag) for each site.
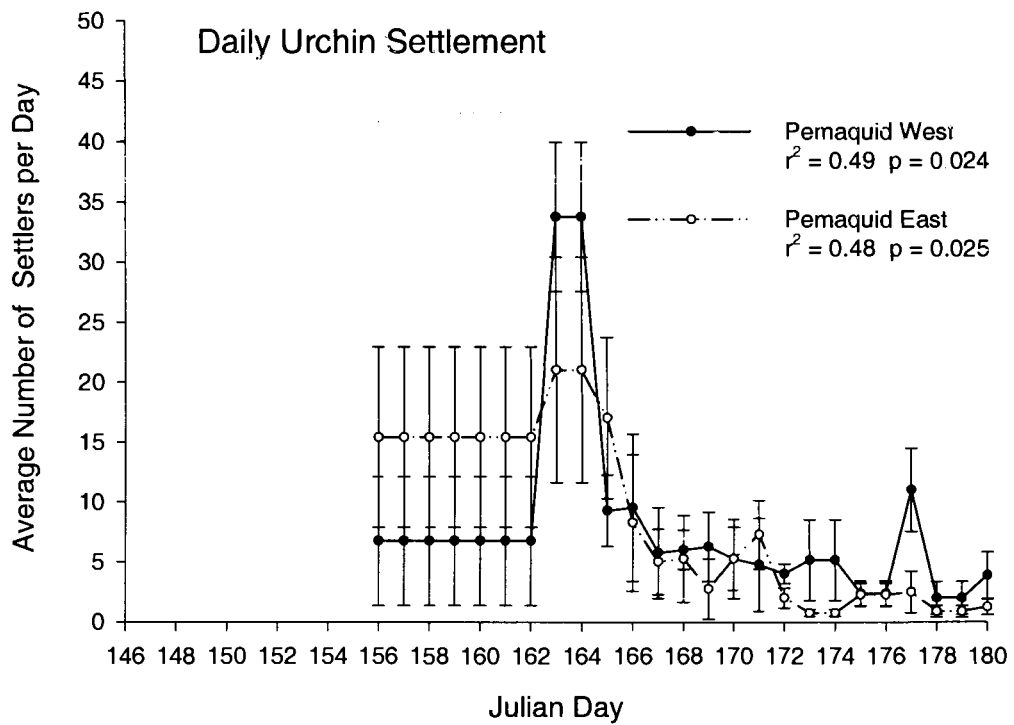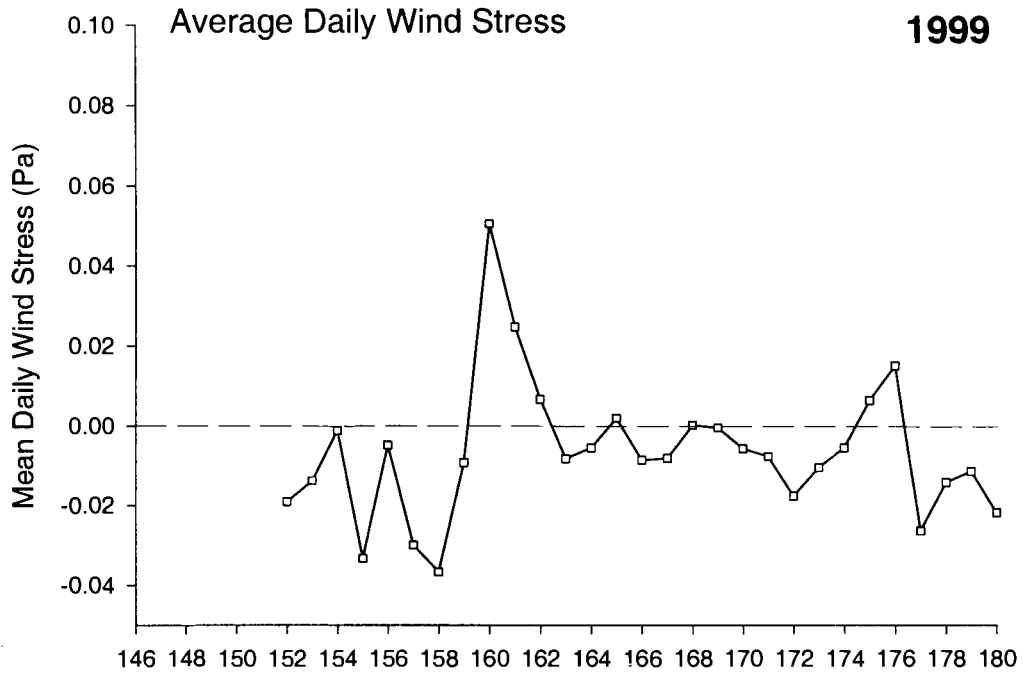
Figure 3.3. Average daily longshore wind stress and average daily settlement in 1999. See Fig. 3.2. for additional details on notation.

however, wind was not correlated with settlement, and average settlement was generally

less than half that seen in previous years (Fig. 3.4). Settlement in 2001 rose to levels

similar to those observed in 1998 and 1999. The two sites did not always track together

(Fig. 3.5); thus, the sites exhibited different trends in relation to wind stress. The

Pemaquid East site had a significant but weak correlation with the wind stress. Pemaquid

West settlement did not show any correlation with wind stress, and definitely lacked the

peak in settlement on JD 164 and 165 that the east side showed after an easterly wind.

Effects of Wind on Depth Settlement and Temperature

Depth specific temperature data in 2002 from the Hobotemp dataloggers were

compiled in a contour graph and indicated a general association between the increasing

temperature at depth and wind stress with a 24 to 48 hr. time lag (Fig. 3.6). Early in June

the water was relatively cold and only stratified at the surface, but a small positive (i.e.

northeast) wind stress event on JD 155 and 156 caused an increase in water temperature

to 10 m depth in the following two days. A shift in the wind direction to the southwest

quickly caused a cooling surface temperature during the next two days. This would be

expected if a positive wind stress had led to advection of warmer surface water onshore

("downwelling") and the opposite wind stress forced the warmer waters offshore. This

trend was repeated after the positive wind events on JD 158 and 159 and on JD 164. A

large northeaster on JD 167 resulted in a pulse of warm water that reached our deepest

stations. As the winds relaxed in the following days the depth of warmer water grew

shallower.

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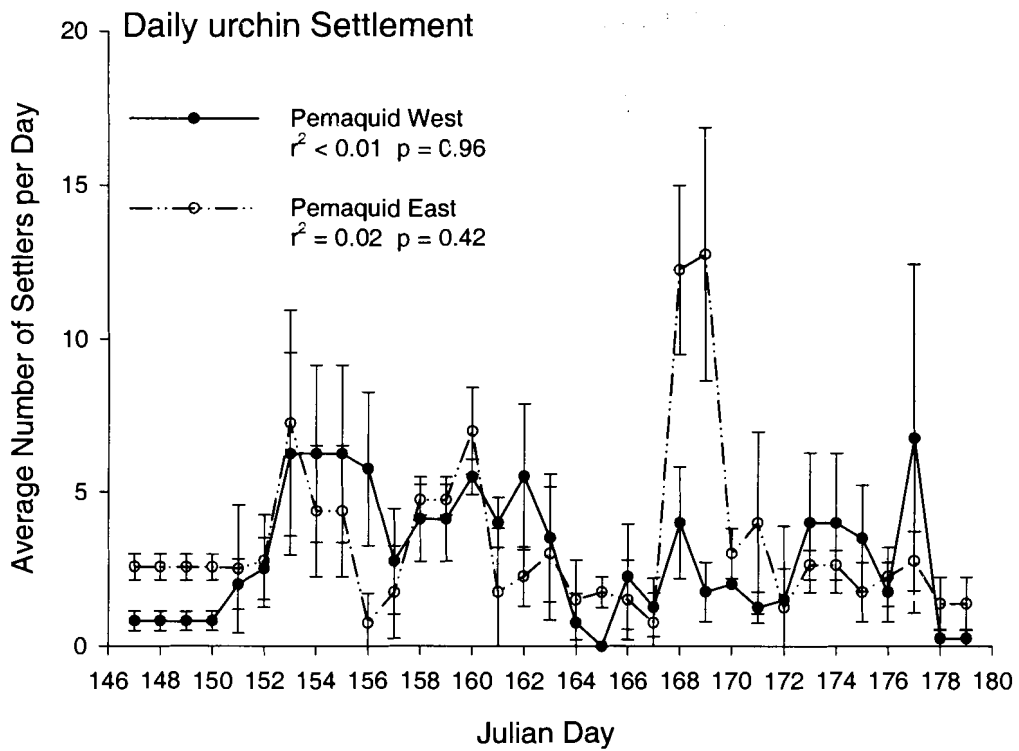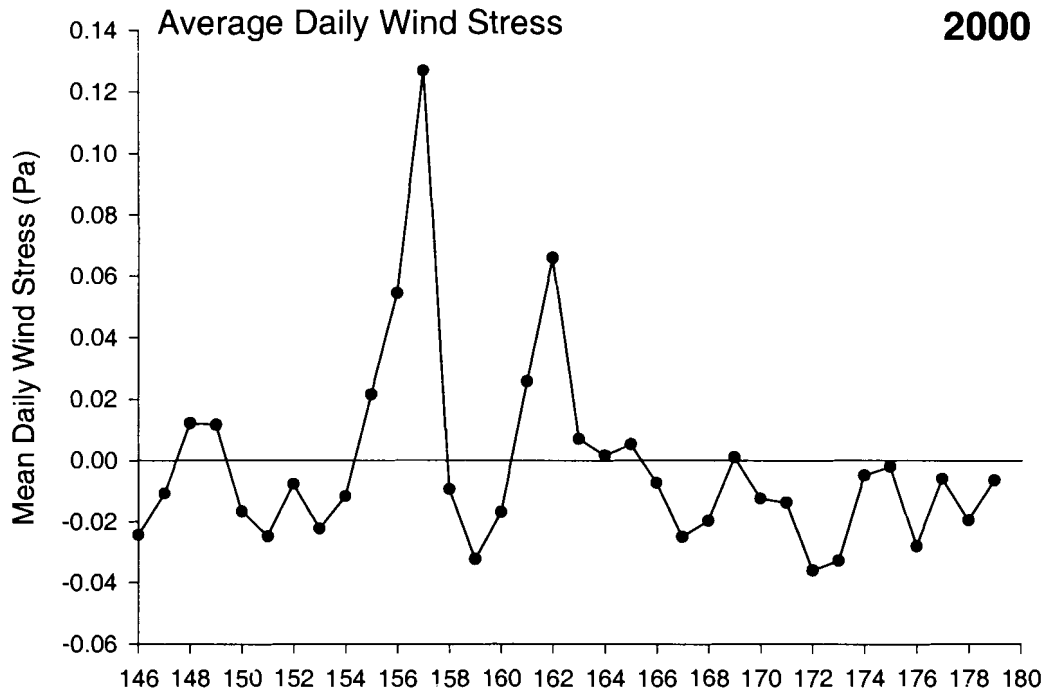
Figure 3.4. Average daily longshore wind stress and average daily settlement in 2000. See Fig. 3.2. for additional details on notation.
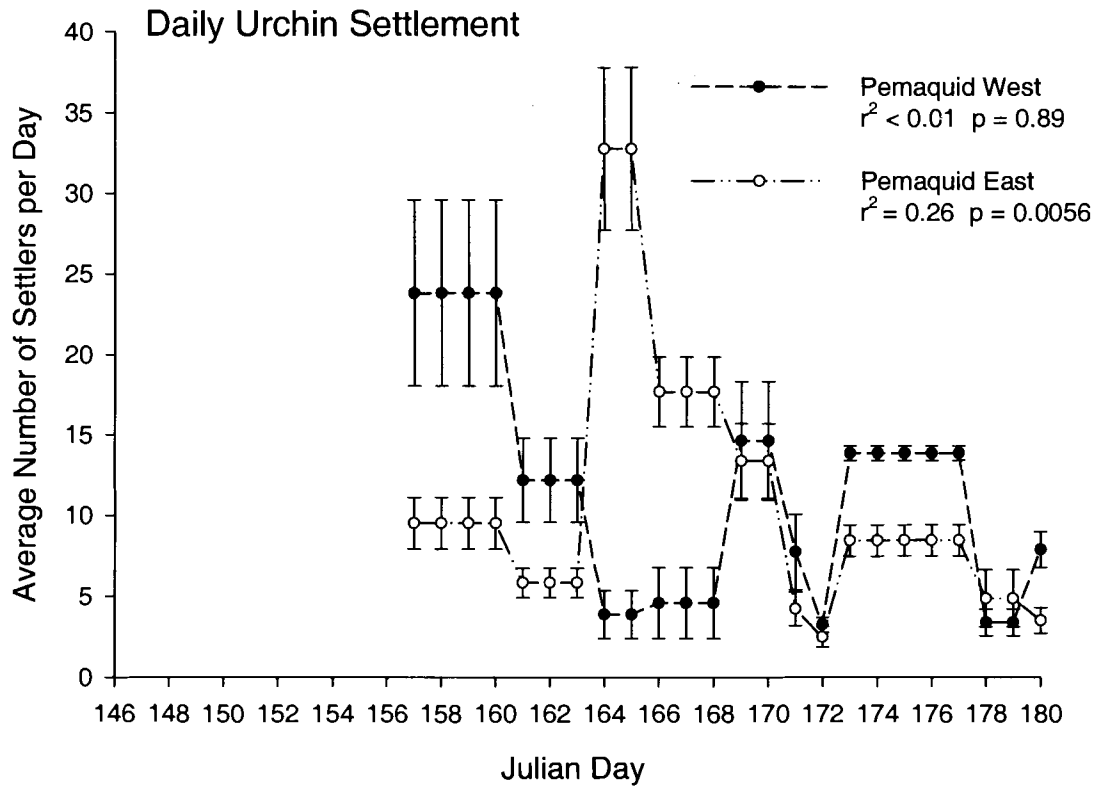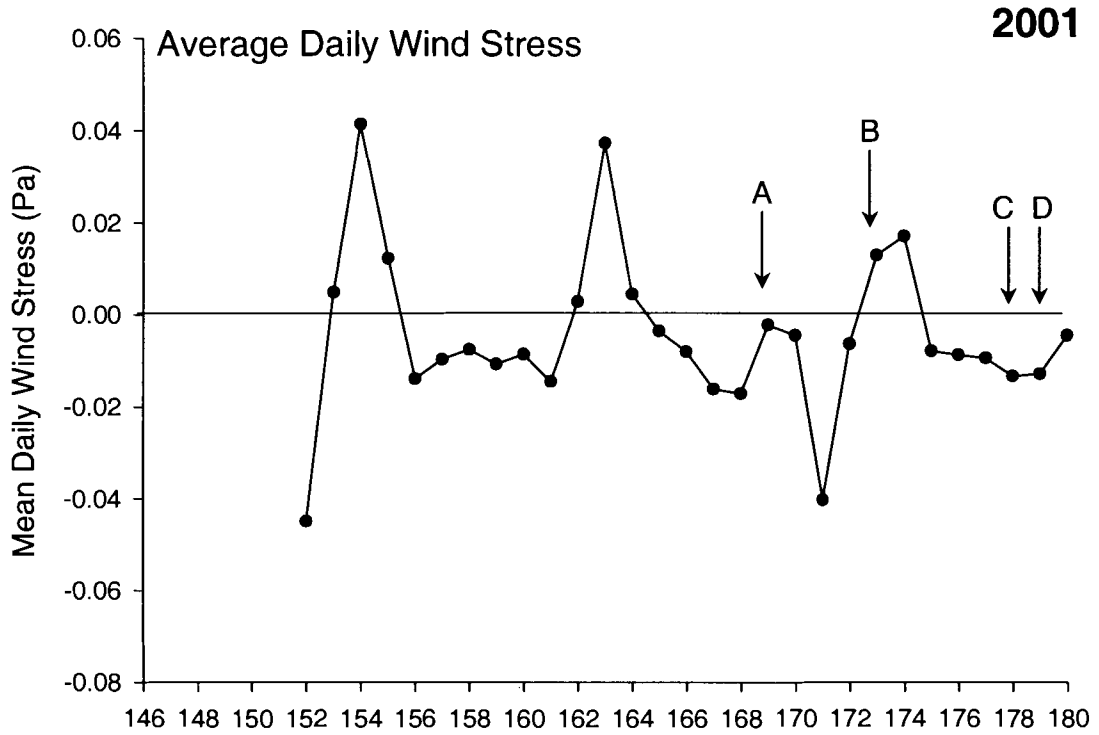
Figure 3.5. Average daily longshore wind stress and average daily settlement in 2001. Arrows and letters correspond with CTD profiles show in Fig. 3.9. See Fig. 3.2. for additional details on notation.
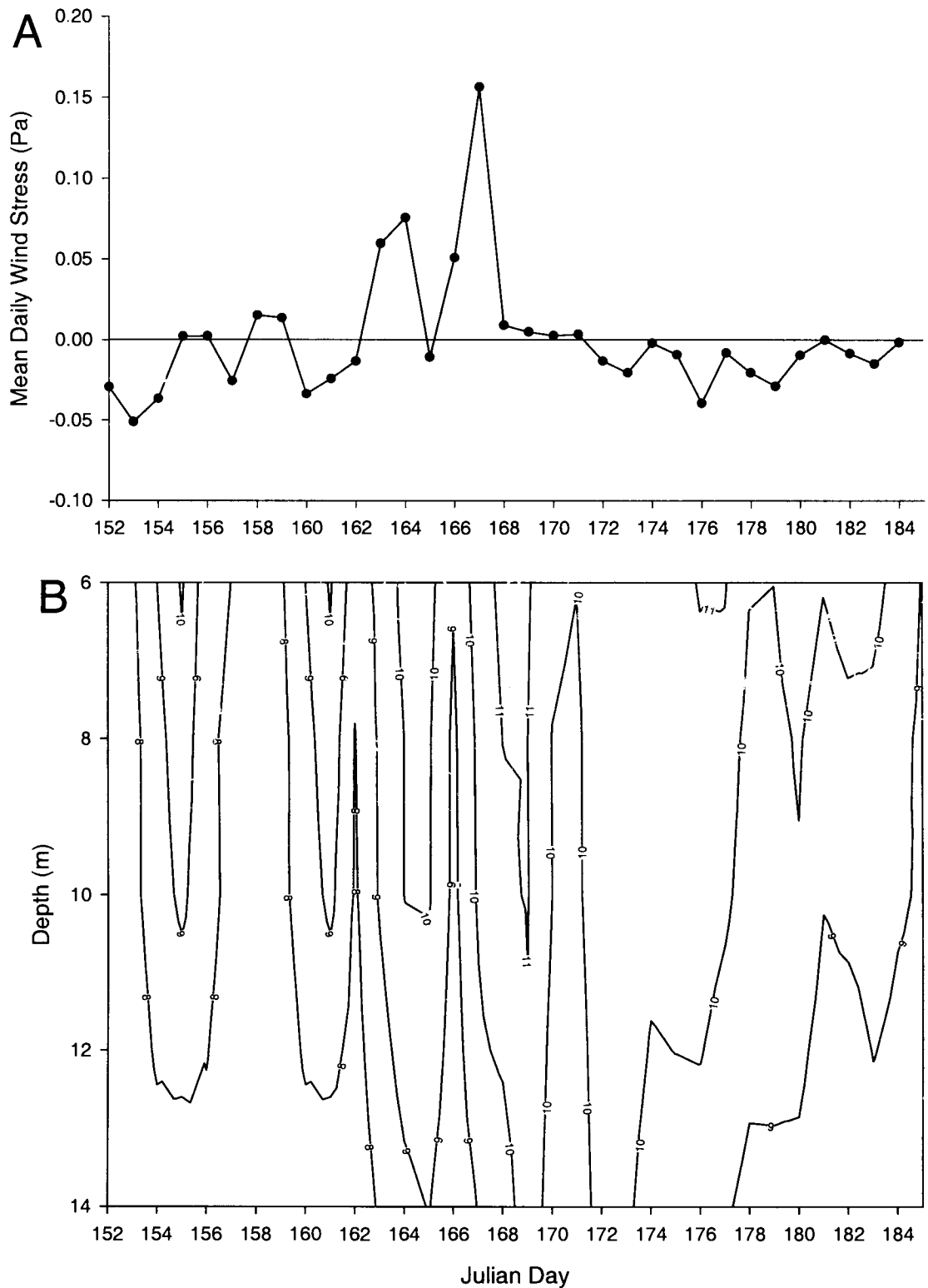
Figure 3.6. Average daily longshore wind stress and average daily water temperature with depth in 2002. A) Mean alongshore wind stress similar to that in Fig. 3.2; B) Mean water temperature (°C) over time between the depths of 6 and 14m. Solid contours are shown for every degree.

The urchin settlement appears to be related to this wind stress and temperature dynamic with highly significant correlations between settlement and depth and settlement and temperature at depth (Fig. 3.7). Graphs of percent settlement at depth and water temperature (time-averaged; see Table 3.1 for statistical analysis) for the individual dates exhibited similar trends (Fig. 3.8). Specifically, the first three dates (JD 155, 161, and 165) indicated that settlement was lower in the coldest waters with these decreases often at or below the thermoclines. Settlement on JD 170 exhibited no significant differences in depth settlement, and was associated with a warm water mass over the whole depth range (also see Fig. 3.6). On JD 175, high deviations were observed in settlement at each depth, resulting in no significant differences between depths. A general trend in the data, however, suggested that the higher densities of settlers were present at the warmest shallow depth. Lastly, on JD 179, with the exception of the 12 m depth, settlement was observed to decline with decreasing temperatures.

Water Mass Temperature Profile

In 2001, we compared changes in the temperature structure for each of the four days with CTD casts (Fig. 3.9) against the longshore wind stress (Fig. 3.5) found a trend similar to that observed earlier. That is, on JD 169, after a small negative wind stress (promoting "upwelling") the entire water column was relatively cool, with only the near-coastal surface waters being above 15°C. On JD 173, after the occurrence of a stronger wind causing local upwelling, temperatures appear even colder at the surface (after station 5). Along the shore, the deeper waters were also colder (the 9°C isotherm was at 12 m vs. 18 m four days earlier). The thermocline appeared to be stronger and deeper

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Table 3.1. One-way ANOVA results comparing average number of urchins per settlement plate per depth on each date of study. Asterisk (*) indicates a significant difference in the average settlement (at $\alpha = 0.05$)

Julian Day	Effect	SS	df	MS	F	p
153	Depth	42.672	4	10.668	3.563	0.031*
	Error	44.909	15	2.994		
161	Depth	89.342	4	22.335	3.211	0.043*
	Error	104.329	15	6.955		
165	Depth	137.729	4	34.432	4.850	0.010*
	Error	106.487	15	7.099		
170	Depth	8.559	4	2.139	0.758	0.567
	Error	42.294	15	2.819		
175	Depth	119.797	4	29.949	1.460	0.263
	Error	307.669	15	20.511		
179	Depth	181.202	4	45.300	5.939	0.004*
	Error	114.397	15	7.626		

and was associated with the increasing positive wind stress on that day. In contrast, five days later on JD 178 (a few days after a positive wind stress), warm surface waters over 17°C extended fully to the shore. This pattern may have been more pronounced a couple of days earlier since there had been weak negative wind stress acting on this water mass. The subsurface waters along the coast appear to be bulging up towards the surface, suggesting the beginning of upwelling. This pattern is more apparent the next day (JD179) as cooler waters pushed up along the coast making the coastal thermocline shallower and pushing the warmer surface waters several kilometers offshore.
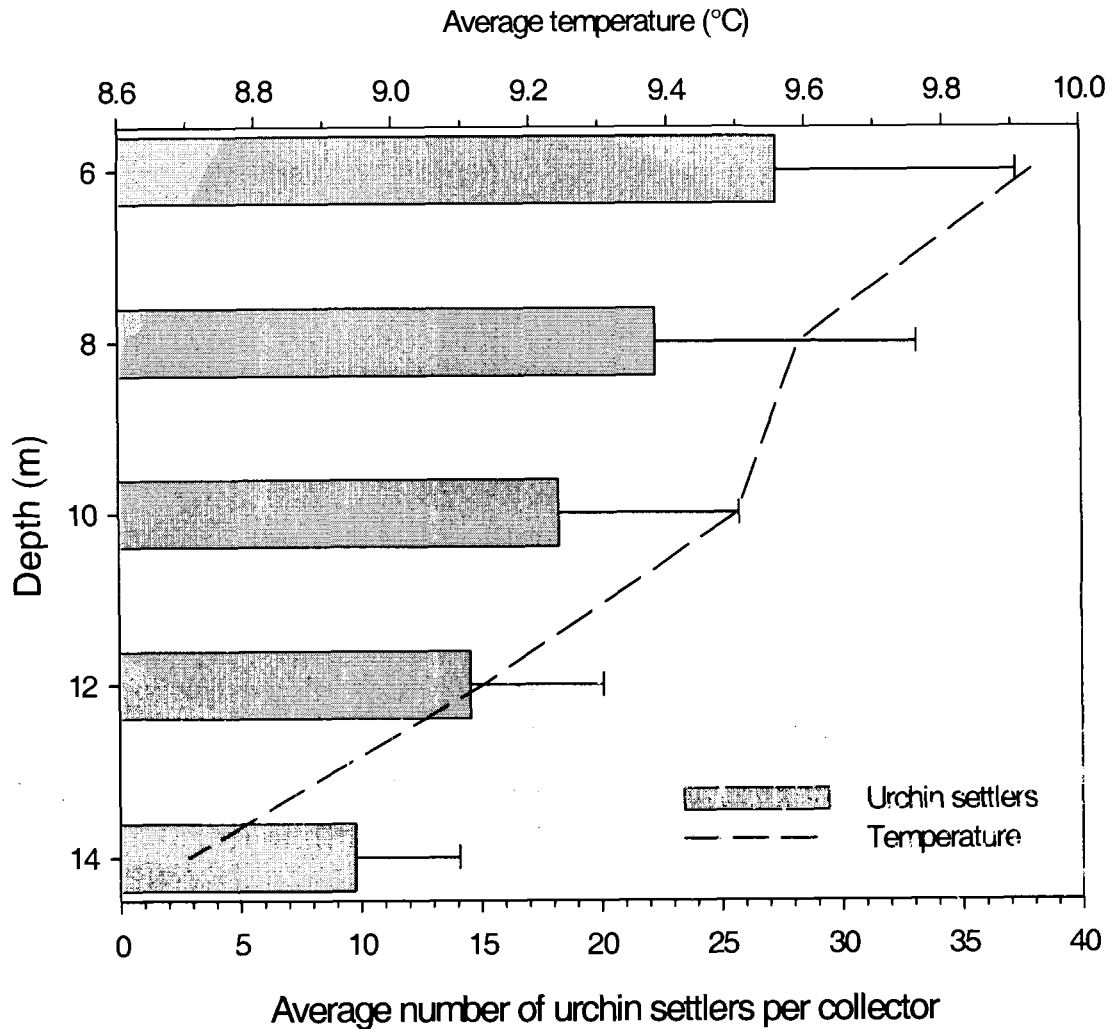
Figure 3.7. Average of total sea urchin settlement per collector and average temperature for each depth in June 2002. Correlation statistics describe linear correlation between the number of settlers, depth, and temperature.
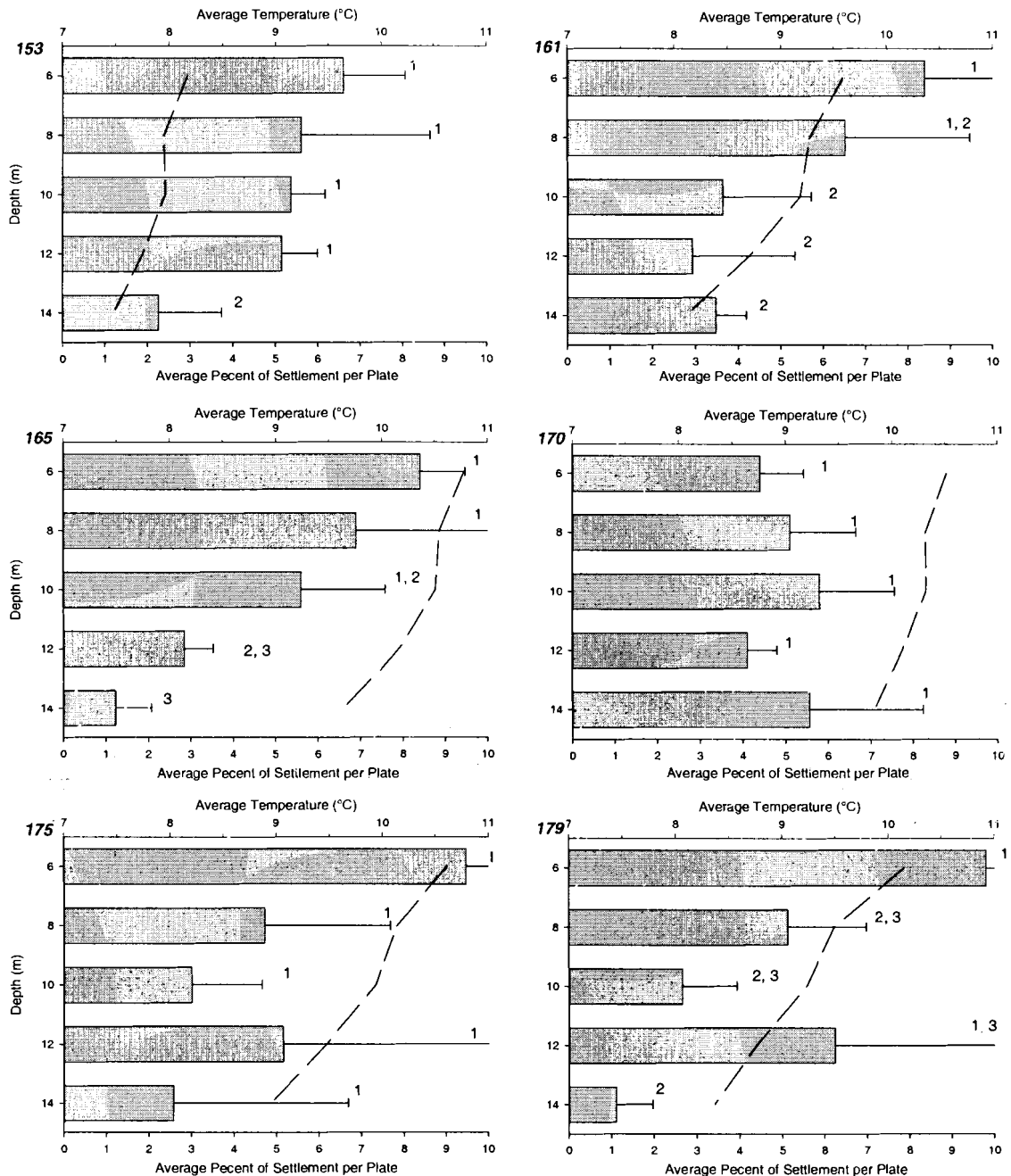
Figure 3.8. Average percent of the total settlement by depth for each collection date (solid bars) and average temperature at each depth (dashed line) during the time the collectors were in the water. The Julian day the collectors were retrieved is in bold italics by each graph. Identical numbers by standard deviation bars indicated no statistical difference (using Fisher LSD *post-hoc* test). For ANOVA results on each date, see Table 3.1.
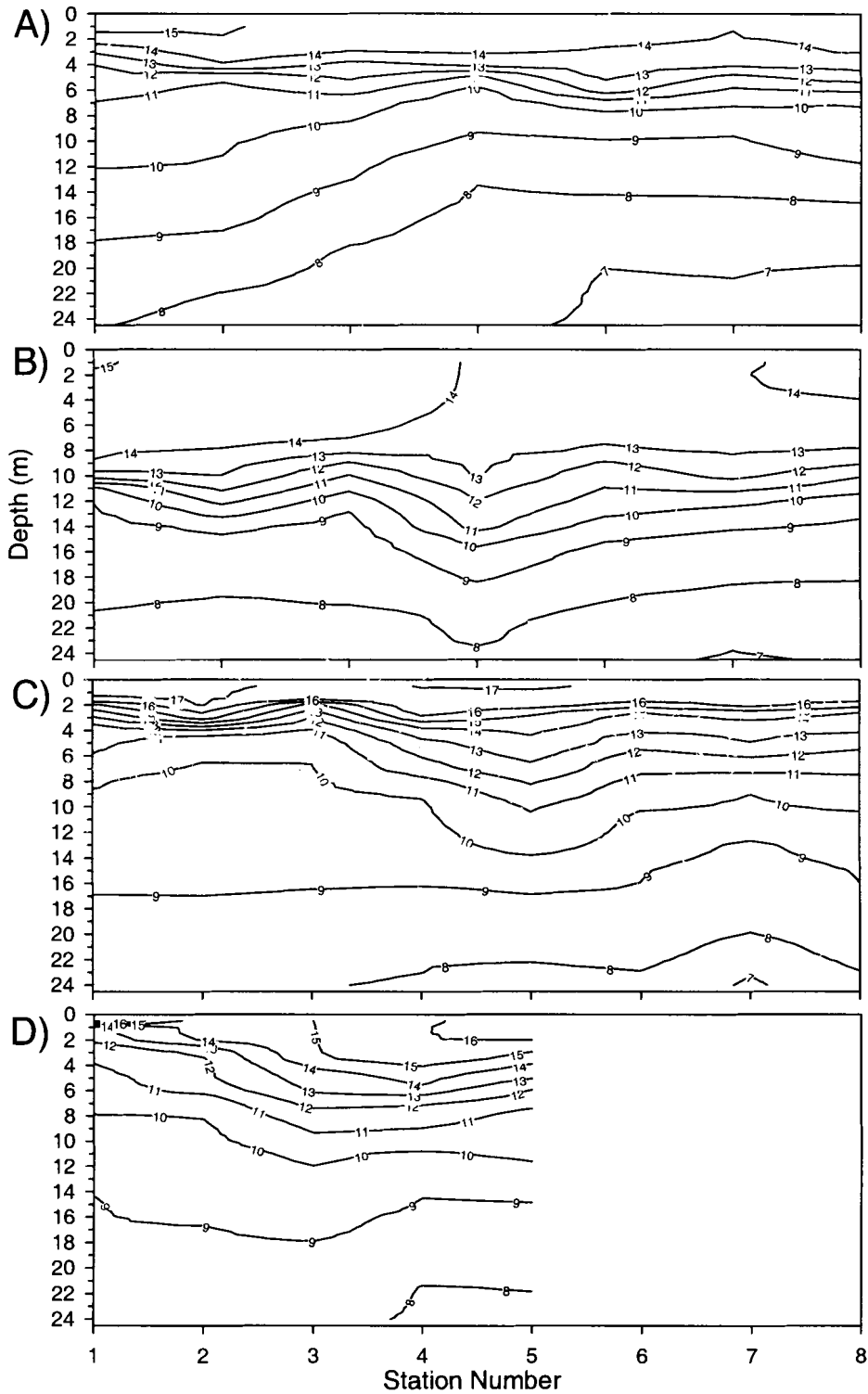
Figure 3.9. Temperature profiles of the water mass off Pemaquid Point perpendicular to the coastline. Station numbers correspond to those shown in Fig. 1. Plots are for four different days in 2001 as seen in Fig. 5: a) Julian Day 169; B) JD 173, C) JD 178; D) JD 179. Solid contour lines are labeled for each degree C.

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Larval Vertical Distribution

A total of 153 echinoplutei were found during the study (1998 – 2002). Their distribution was patchy and they were not dense. Larvae were found between May 8 and July 10 (both in 1998), but always in densities < 0.1 echinoplutei l^{-1} of seawater. They were found at all depths to 27 m but never at the bottom. Larvae were also found in waters ranging in temperature from 6.6 to 13.9°C. Not all developmental stages of echinoplutei were found in the samples. Eight 4- to 6-arm stage plutei (hereafter referred to as early stage) were captured in 1998, and the rest of the samples were all late stage 8-arm plutei (few) or newly metamorphosed individuals (majority). These newly metamorphosed sea urchins were found high in the water column, and usually retained the skeletal arm segments of the plutei stage (Fig. 3.10). We do not believe the metamorphosis occurred on our filters (see discussion).

The depth distributions of the early and late stage echinoplutei were not statistically different (Kolmogorov-Smirnov Test, p > 0.10; Fig. 3.11). This could be an artifact of the low sample size in the early stage. The two stages were associated with different water temperatures (Fig. 3.11c), with the earlier stage in water averaging 7.8°C and later stages in 11.6°C water. This could be due solely to temporal variations since there was not much overlap in the samples and the early stage was found in May when the water column was not strongly stratified. Late stage echinoplutei, both competent and newly metamorphosed, were more numerous at depths < 12 m (Fig. 3.11b) most occurring at or above the thermocline (i.e. in the warmer surface waters).
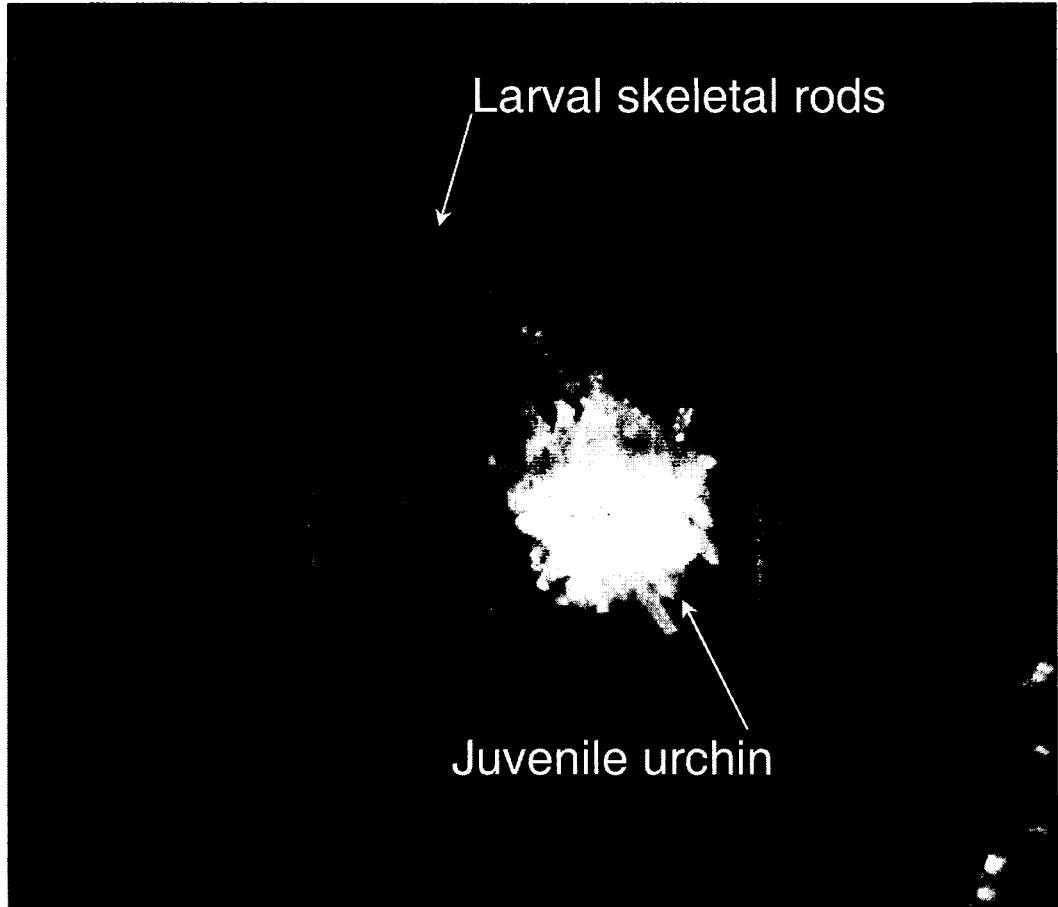
Figure 3.10. Photograph of newly metamorphosed sea urchin found in the larval samples. Notice larval skeletal rods still attached to the newly formed juvenile. This individual was collected from the water column.
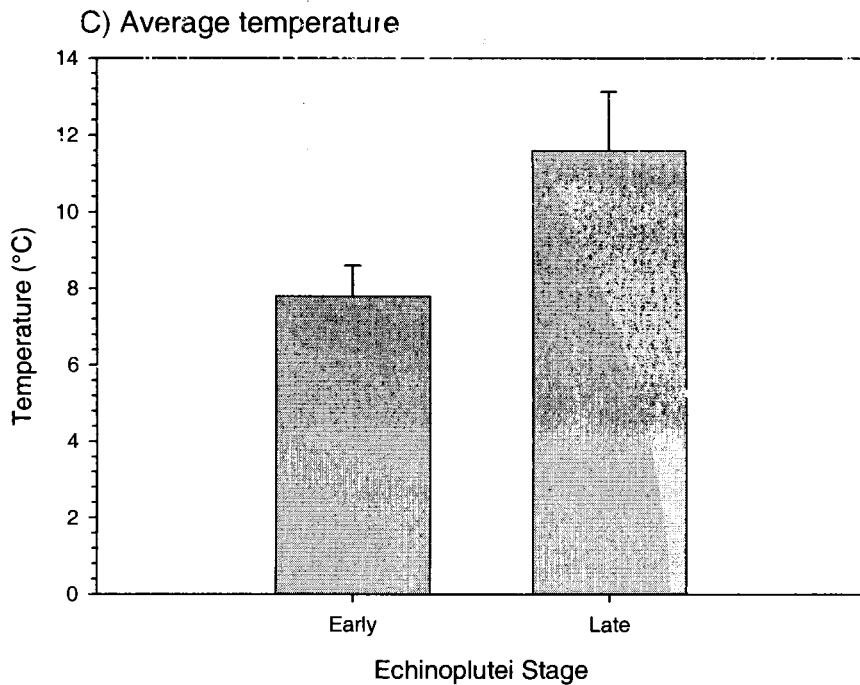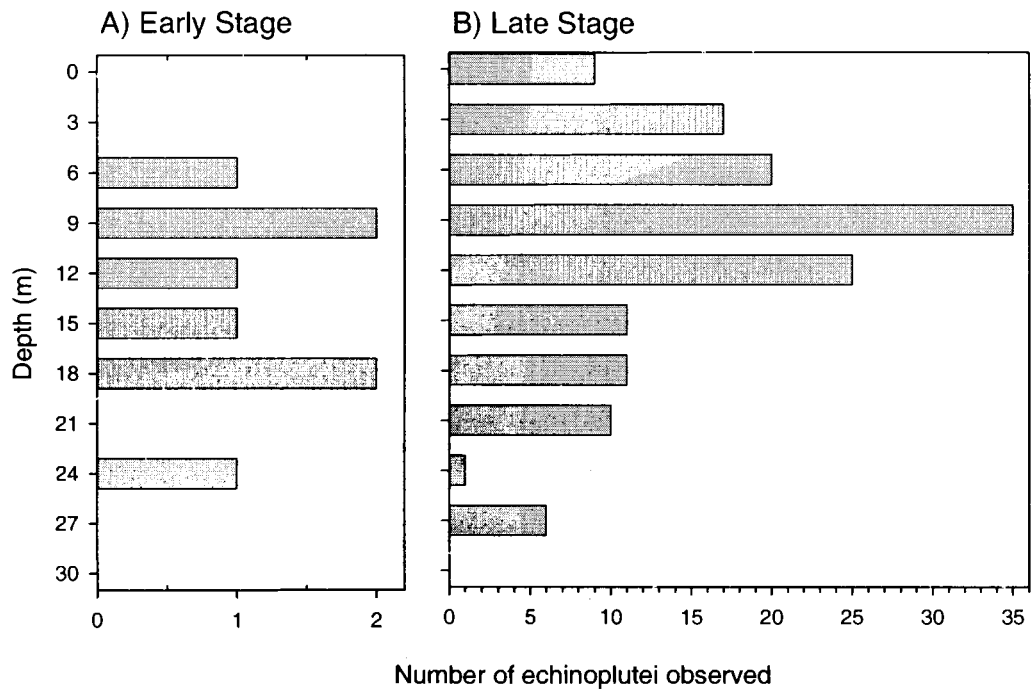
Figure 3.11. Locations and temperatures where echinoplutei of different stages were found. A) Bar diagram indicating the depths where early stage (4- to 6-arm) larvae were captured. B) Bar diagram indicating the depths where late stage (8-arm or newly metamorphosed) larvae were captured. C) Average water temperature (± SD) each stage was collected from.

Discussion

Echinoplutei Stages

While we did not expect to find or be able to identify blastula or gastrula stages in the samples, we did hope to find all the armed stages of echinoplutei. We found only eight early 6-arm plutei in 1998, however, and nothing other than competent late stage larvae at any other time. We do not know why we did not find earlier stages. It is possible there were problems with pressure buildup in the filter system or use of a mesh size which was too large for the fragile larvae. To counter this, we gently spilled the water through a 156 μm plankton net. The fact that we found the eight 6-arm plutei in good condition under the roughest sampling procedures the first year suggests that we were not destroying or passing the larvae. Concentrations of sea urchins were low, but similar to those found by Towers (1976). It is possible that the earlier stages simply were not present in the area we were sampling, since larvae are often transported large distances and life stages can be segregated in time and space (Shanks 1995).

We also found sea urchin larvae in the water column that had just undergone metamorphosis, but we do not believe that the echinoplutei were undergoing metamorphosis in our filter system. Firstly, we started preserving the samples in alcohol as soon as the collection was complete. Secondly, we ran the pump for less than 10 minutes on some of the trials but never found a range of metamorphosis stages in the samples. Thirdly, we never found any larvae in the bottom sample, and the majority of the sea urchins at a depth < 12 m, indicating sea urchins were not being stirred up

Encountering newly metamorphosed sea urchins in the water column was not predicted based on the literature. Burke (1980) described sea urchin tube feet penetrating

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the larval body presumably to sample the substrate. Other studies have suggested a number of algal and bacterial benthic species that induced metamorphosis in *S. droebachiensis* (Towers 1976, Pearce and Scheibling 1990, 1991). All this would imply that the echinoplutei would be searching for suitable habitat before undergoing metamorphosis. Thus we did not expect to encounter newly metamorphosed sea urchins in the water column. Metamorphosis in the water column is not unheard of though. Thorson (1946) encountered a number of species that had apparently undergone mid-water metamorphosis and states that "within the echinoderms this phenomenon seems to be rather common." More recently Fenaux and Pedrotti (1988) documented post-larvae of five different echinoids, some offshore in the top 30 m of a 2000 m water column. How these post-larvae are able to maintain their position in the water column is unknown, as is their fate. Their abundance in the upper part of the water column (perhaps riding pycnoclines), though, suggests that they can be carried into the coastal settlement grounds and still enter the population.

Relationship Between Advection of Surface Waters and Settlement

Downwelling events in upwelling areas may be the only way for invertebrate larvae to reach the coast for successful settlement (e.g. Wing et al. 1995a, Wing et al. 1995b, Miller and Emlet 1997, Botsford 2001). We believe that the wind-driven advection of surface waters onshore (i.e. "downwelling") is critical in facilitating the recruitment of the green sea urchin in Maine. Indeed, in three out of four years a positive wind stress from the northeast was correlated with pulses in settlement.

In order for this mechanism to work, the water column must be stratified and the larvae must be in the upper stratum. Our temperature data suggest that during the time of sea urchin settlement, surface waters are generally warm (> 16°C) and can be advected onshore by northeast wind events, which is typical of downwelling events (Wing et al. 1995a, Wing et al. 1995b, Miller and Emlet 1997). These wind events only happen an average of two or three times during June when sea urchin settlement is at its peak (Lambert and Harris 2000). Thus timing can be crucial to successful settlement. For example, the second peak in wind stress on JD 179 1998 (Fig. 3.2) was not effective in increasing settlement, probably because there were few larvae left in the water by that time. When conditions are optimum, these wind events can lead to major peaks in settlement, similar to those observed for ophioroids in Nova Scotia (Balch et al. 1999).

In 2000, wind events were not correlated with settlement as in other years. This could have been caused by a lack of water stratification. Temperatures in 2000 were colder than in 1999, and the water column did not stratify as dramatically. The Portland Buoy recorded an average surface temperature of 14.19 (± 0.79) °C for the month June in 1999, but a temperature of only 12.28 (± 1 51) °C in 2000. Our average June temperature profiles indicate the same trend. Average surface temperatures were 3°C colder in 2000 (Fig. 3.12). More importantly, the average difference between the surface and bottom temperatures was only 4.1 (± 0.28) °C in 2000 compared to 6.48 (± 1.38) °C in 1999. In that year there was less chance for thermocline development and a greater chance for mixing of larvae in the water column. It is possible that positive wind stresses in 2000 did advect surface waters inshore, but the larval densities were not any higher in those waters than in the resident water mass.
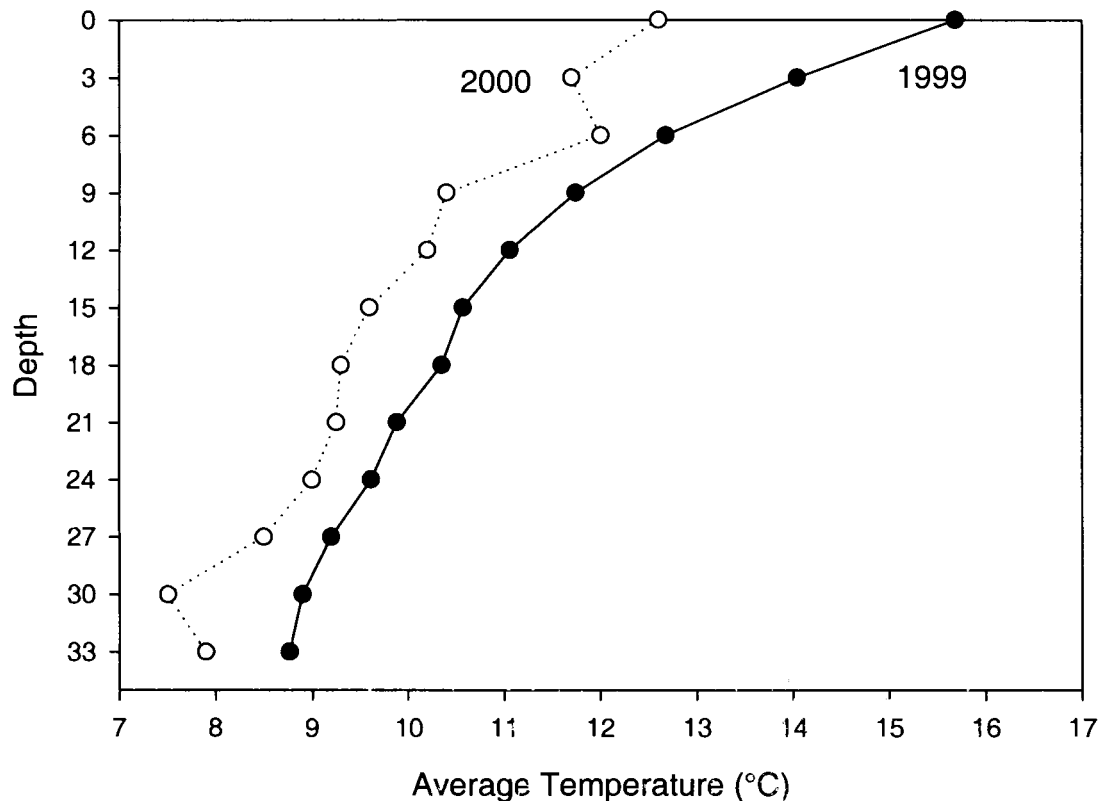
Figure 3.12. Average water temperature with depth in June of 1999 and 2000, compiled from June larval samples in each year.

The Pemaquid West site did not correlate wind stress with settlement in 2001. This could be due in part to the infrequent sampling obscuring the relationship, but there was no peak in settlement on JD 164 and 165. More likely this was caused by direct wind forcing rather than Eckman transport. The wind during the JD 162 positive wind event (Fig. 3.5) was often more from the north northeast and very strong. This would force the wind to travel over Muscongus Bay which is shallower than the waters offshore of Pemaquid Point. The entire water column of shallow waters tends to be pushed before the wind instead of initiating a traditional Eckman spiral (Shanks 1995). It is therefore

possible that winds advected offshore surface waters onshore, but locally pushed the larvae onto the east side of the peninsula and away from the west side. Lambert and Harris (2000) suggested that sea urchin settlement in York, ME was associated more with onshore winds than longshore winds. Direct wind transport has been seen for other invertebrate larvae in the region, namely barnacles (Bertness et al. 1996) and lobsters (Incze and Wahle 1991). Perhaps the system studied here is more complex and large-scale advection is coupled with local direct wind transport, delivering larvae to the shallow nursery grounds.

Larvae must be present in the stratified surface water if downwelling is to increase settlement. Late stage, competent larvae were observed at depths < 12m deep in the water column. This depth distribution curve matched the settlement depth curve of Harris et al. (1994), which showed a general increase in settlers to 6 – 9 m with a drop in settlement > 13 m Our average temperature curve for 1999 shows greater stratification above 12 – 15 m (Fig. 12). Lastly, the fact that the settlement collectors at different depths were strongly correlated with average temperature implies that the more time the collectors were above the thermocline, the better the supply of larvae.

We therefore conclude that the longshore winds can affect sea urchin settlement. Competent echinoplutei were certainly present in the warmer surface waters. Echinoplutei are known to be able to control their vertical distribution in relation to food concentration and pycnoclines in laboratory experiments (Metaxas and Young 1998c, b, a), but how much control they have in the turbulent ocean remains to be seen. Either way, the larvae were in position to be advected onshore to shallow settlement sites once a northeast wind created a downwelling event.

Chapter 4. Habitat complexity and recruitment of the green sea urchin *Strongylocentrotus droebachiensis* in the Gulf of Maine.

Abstract

Habitat complexity can impact species and community dynamics in benthic systems. We attempted to associate different scales of habitat complexity with the distribution and survival of recruiting green sea urchins (*Strongylocentrotus droebachiensis*) in the Gulf of Maine. We examined the importance of micro-complexity (smaller than adult sea urchins) created by ledge cracks and crustose coralline algae. We also studied the effects of macro-complexity (greater than or equal to adult size) provided by fleshy macroalgae and adult sea urchin spine canopies. We determined that juvenile *S. droebachiensis* are not preferentially found under adults. They are more often associated with increases in small scale spatial complexity (i.e. branching crustose corallines, cracks in the granite ledge, etc.), the utilization of which may change as the sea urchins grow. We found that habitat complexity also affected settlement of sea urchins in coralline dominated communities, but had no impact in fleshy macroalgal beds. Post-settlement mortality was not affected by substrate complexity in either community. Lastly, we show evidence that adult sea urchins may cannibalize newly settled juvenile sea urchins and be a source of mortality rather than refuge.

Introduction

Substrate complexity, or heterogeneity, can be important in structuring benthic communities, increasing both species abundances and richness (for reviews see Bell et al. 1991, Kolasa and Pickett 1991). Complexity can provide resources (e.g. space) for niche diversification (Schoener 1974), affect circulation which in turn affects supply of food and propagules (e.g. Eckman 1983), initiate settlement (e.g. Keough and Downes 1982), and protect recruits against disturbance (Woodin 1978). Many recent studies have quantified the impacts of habitat structure on benthic organisms, particularly the potential refuge afforded from predation (for reviews see Coull and Wells 1983, Nelson and Bonsdorff 1990, Bell et al. 1991, Kolasa and Pickett 1991). Studies are revealing that the impacts of habitat complexity are dependent on size and research must have a resolution appropriate to the organisms being studied (Bell et al. 1991).

Researchers have hypothesized that substrate complexity may be important in the western North Atlantic for the recruitment of the green sea urchin *Strongylocentrotus droebachiensis*. Keats et al. (1985) suggest that the bimodal size frequency seen in juvenile green sea urchins may be due to cunner (*Tautogolabrus adspersus*) predation once the urchins outgrow the refuge of the branching crustose coralline alga *Lithothamnion glaciale*, a theory reiterated Ojeda and Dearborn (1991). Himmelman (1986) and Scheibling and Hamm (1991) noticed higher juvenile densities (and possibly survival) in habitats with small interstices as refuge . Witman (1985) concluded that subtidal clumps of the horse mussel *Modiolus modiolus* are also an important refuge from predators for *S. droebachiensis*. Alternatively, McNaught (1999) determined that

increased complexity in macroalgal beds actually harbors sea urchin predators and decreases the survival of newly recruited sea urchins.

Here, we report on the effects of multiple scales of habitat complexity on newly settled and small juvenile sea urchins. We chose to test the hypothesis that small sea urchins utilize interstices of small habitats (Keats et al. 1985, Ojeda and Dearborn 1991), examining the micro-complexity structure formed by crustose coralline algae and small cracks in the rocky ledge and its effect on sea urchin distribution and survival. This micro-complexity is on a scale smaller then the adult *S. droebachiensis*, impacting the smallest of sea urchins.

We also examined larger components of habitat complexity. This macro-complexity scale was as large or larger than the adult sea urchins and included macroalgal beds, vertical walls, and the spine canopy of the adult sea urchins. Spine canopy effects were added because Tegner and Dayton (1977) observed that juvenile *Strongylocentrotus franciscanus* sea urchins in California were most often found under the spines of adult congeners. Breen et al. (1985) later confirmed this experimentally. This association is thought to afford protection from predators and/or enhance food resources for the juveniles (Tegner and Dayton 1977, Duggins 1981, Breen et al. 1985), both concepts of which have been recently confirmed experimentally (Nishizaki and Ackerman 2001).

Lastly, we investigated the possibility of incidental cannibalism by adult sea urchins, and explored the implications this might have on micro-habitat use. McNaught (1999) identified coralline communities as better settlement grounds for sea urchins, but still found up to 90% mortality in the first year in these habitats. The potential for

cannibalism as an agent of this mortality is great since coralline communities are usually

characterized by high densities of sea urchins.

Materials and Methods

Experiments on Juvenile Sea Urchins

Laboratory experiments were conducted at the Darling Marine Center, Walpole,

Maine in August 2001, to determine whether juvenile green sea urchins seek the spine

canopy of adults. Three tanks with four containment areas at the center were constructed

for the experiments (Fig. 4.1). Three treatments with different habitat options in the

containment were used: four adult sea urchins (~ 50 mm spine canopy width – SCW),

four similarly sized rocks, and two sea urchins with two rocks. Both the adult sea urchins

and rocks were held in place with four thin, clear Plexiglas "fingers" that bracketed the

aboral side of the adult sea urchins but did not reach the bottom of the tank. A random

sample of 20 juvenile sea urchins 3 – 30 mm in test diameter (TD) was released into the

middle of the tank. After 24 hours, we noted the number of juveniles in each of six

locations (Fig. 4.1): 1) under adult sea urchins, 2) under rocks, 3) in the center of the tank

between the containment areas, 4) in the corners of the tank (within one body length of

the corner formed by the wall), 5) along the edge of the tank (outside the containment

areas but outside of the corner zone), and 6) on the walls of the tank. Each juvenile was

only used once, each trial run comprised one replicate of each treatment, and the

treatments were rotated among tanks for each new trial. Six replicates of each treatment

were run over six days.
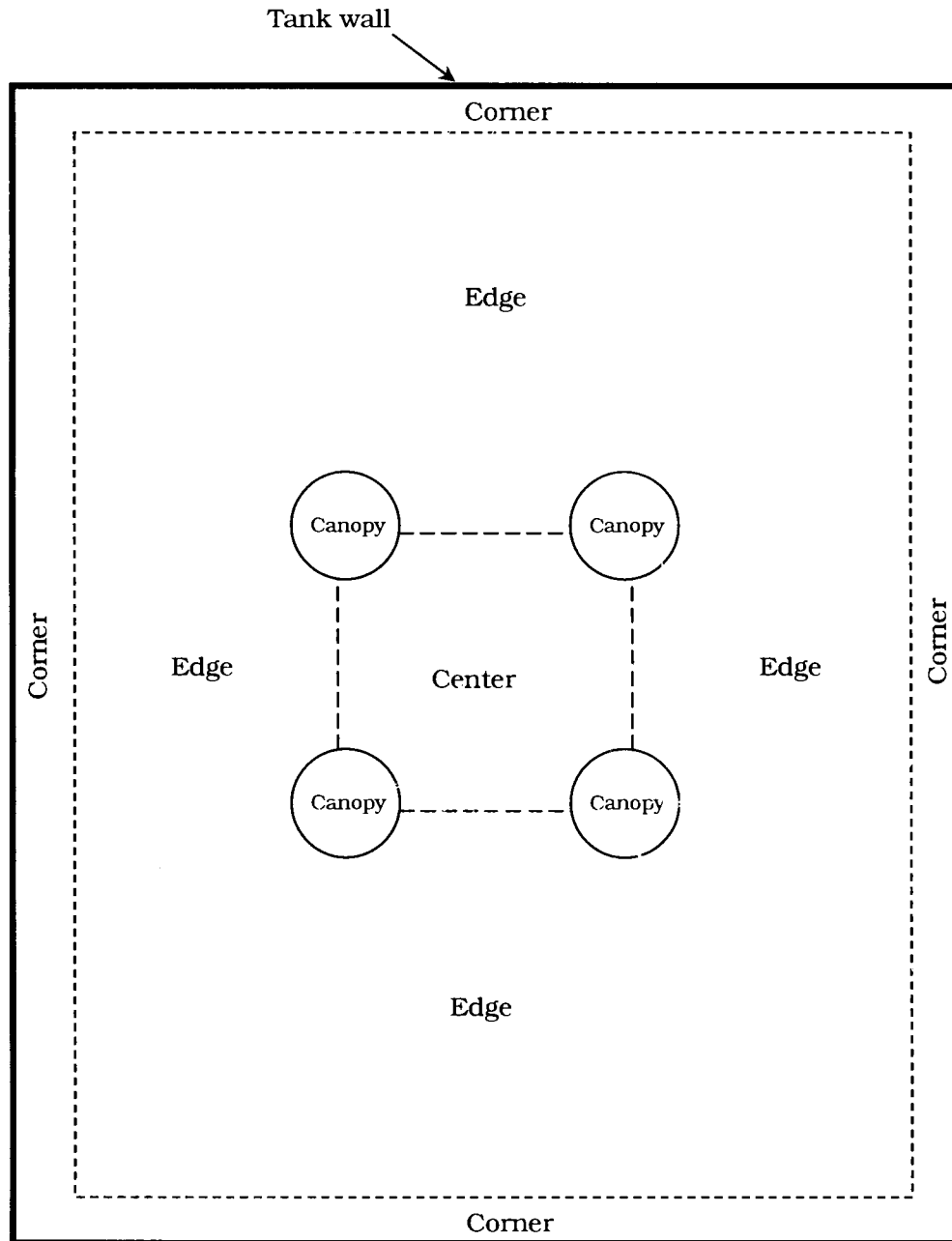
Figure 4.1. Diagram of the experimental aquaria used for testing the importance of the adult spine canopy in the green sea urchin. The dark line around the outside symbolizes the wall of the tank and the only hard boundary in the figure. The circles ("Canopy") indicate where the adult sea urchins or controls (rocks) were placed. The "Center" was the area of the aquarium bottom between the urchin/rock stations. The "Edge" is the area outside the urchin/rock stations but not within one body length (of the juvenile urchins) of the aquaria walls. The "Corner" was the perimeter of the tank one juvenile body width wide where the bottom of the aquarium met one or more of the sides.

We also conducted field surveys to determine if wild juvenile *S. droebachiensis* were more common under the spine canopy of adults than in the open. These surveys were conducted at Pumpkin Cove (N 43° 50', W 69° 31') on the east coast of Pemaquid Point, Maine. We performed these surveys in an urchin dominated crustose coralline community at ~ 10 m depth. To standardize the area quantified, we created a template with a 50 mm diameter circular cutout. This template was placed over a sea urchin with a 50 mm SCW to define the edge of the spine canopy. The adult sea urchin was carefully removed and inspected for juvenile sea urchins (< 30 mm) among the interstices of the adult spines. We then counted the juvenile sea urchins in the template (i.e. that were under the adult) and measured them into 5 mm size categories. We also quantified the substrate type where juveniles were found into three categories, based on habitat complexity. The most complex of these micro-habitats were the cracks in the ledge (crack). Cracks were generally "deep" with a height:width ratio of at least 5:1. Branching coralline crusts (*Lithothamnion* sp.) afforded the next highest level of physical complexity, with interstices averaging 2 x 2mm (1:1 ratio; R.S. Steneck, pers. comm.). The final category was flat substrate (either smooth rock or flat corallines such as *Phymatolithon laevigatum* and *Clathomorphum circumscriptum*) with a zero height:width ratio. We also quantified the available substrate in the quadrat (percent cover) using these same three categories. Finally, for each adult sea urchin sampled, we placed the template on adjacent substrate without an adult, counted and measured the juveniles, and quantified the habitat complexity.

Experiments with Newly Settled Young of the Year (YOY) Sea Urchins

The following experiments were all performed on newly settled sea urchins to

determine preferential use of different habitat complexities. These young of the year

(YOY) sea urchins were generally < 2mm TD. All of these urchins were collected from

the field using passive collectors (Astroturf[TM] panels) and kept in containers with

constant flowing seawater and an air source.

Ceramic plates were used to determine the effect of habitat complexity on

settlement and post-settlement recruitment *in situ*. These plates were 8.5 x 18 cm and

constructed with three different surface complexities: high, low, and none or flat (Fig.

4.2). We attempted to duplicate the interstices of branching *Lithothamnion* sp. coralline

crusts with the high-complexity plates, using branch interstices ~ 2 x 2 mm. These plates

had an average total surface area (including irregularities) to dimensional surface area

(simple length x width of the plate) ratio of 1.59:1. The flat plates (without micro-

complexity), mimicking the smoother *P. laevigatum* and *C. circumscriptum* coralline

crusts, had a surface area ratio of 1:1. The low-complexity plates represented an

intermediate complexity. These plates had a corrugated pattern of complexity with

interstices approximately 3mm by 16mm and had a surface area ratio of 1.03:1. We

placed 20 of each plate type in an urchin-dominated coralline community on 22 May

2002. Twenty high-complexity and twenty flat plates were also placed in an adjacent

fleshy macroalgal bed dominated by the kelp *Laminaria longicruris*. All the plates were

placed in 6m of water, attached to bolts epoxied to the substrate, and allowed to rest

directly on

A. High complexity plate
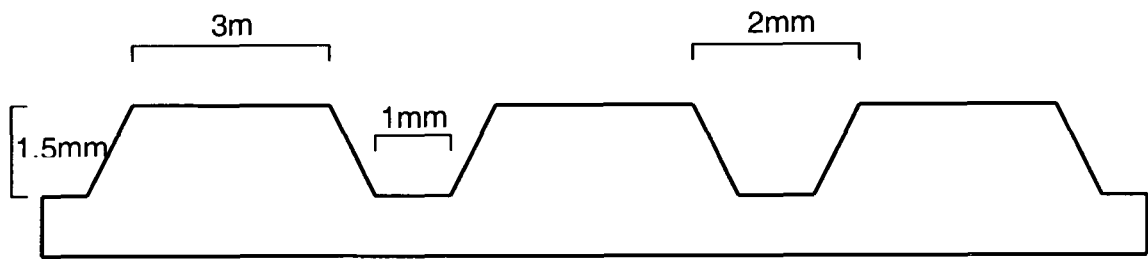
B. Low complexity plate
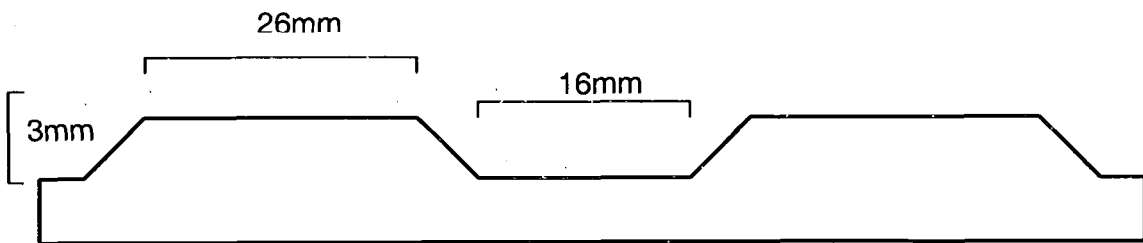
C. No complexity (flat)

Figure 4.2 Cross sections of the three different complexity plates. Note that the drawings are not to scale and only change in rugosity.

the bottom. Since settlement of *S. droebachiensis* occurs in late May and June (Harris et al. 1994, McNaught 1999, Chapt. 3), we picked up half the plates (ten from each treatment) five weeks later on 26 June 2002 (referred to as early postsettlement). The remaining plates were retrieved 12 weeks later on 12 August 2002 to determine the effects of differing complexity on post-settlement mortality (also referred to as recruitment plates). Plates were soaked in magnesium chloride to relax the urchins and washed with 10 μm filtered seawater. The water was passed through a 300μm sieve (McNaught 1999, Chapt. 3), and we then quantified the abundance and size distribution of YOY sea urchins under a dissecting microscope.

We conducted laboratory experiments using ceramic plates constructed using the same models of complexity. One experiment was designed to determine if YOY sea urchins would choose a particular habitat complexity type. Circular plates ~13 cm dia. were divided into three equal sections. Each section was one of the three complexities (flat, low, and high). Ten YOY sea urchins were placed in the center of the plate (where all three complexities joined) and left for three hours. At the end of the trial, the number of sea urchins on each complexity and on the vertical wall of the container was counted. We replicated this experiment ten times over two days (31 October and 1 November 2002).

A second experiment was conducted at the same time to determine the potential for predation on YOY sea urchins by adults. Larger (35 x 55cm) ceramic plates of high complexity (*Lithothamnion* mimic) and zero complexity (flat) were constructed and placed in aquaria. Ten measured YOY sea urchins were placed in the center of the tank with five adult sea urchins (at least 50 mm SCD.) and left for 24 hours. After 24 hours

all the remaining YOY urchins were collected, counted, and measured. Trials of the two

complexities were run concurrently and replicated ten times. Controls without adult sea

urchins were also run with each complexity type.

Results

Juvenile Sea Urchins

In laboratory tests juvenile sea urchins were rarely found under adult spine

canopies (Fig. 4.3). They preferred to be under rocks when available, on the walls of the

tank, or in the corners, rather than in out in the open or under adults (Table 4.1, Fig. 4.3).

The results were consistent between treatments (Table 4.1), and definitely did not support

the idea of a spine canopy effect in *S. droebachiensis*.

In the field surveys under the adult spine canopy and in the open, a total of 394

juvenile sea urchins were counted in 75 paired samples. These data show that

significantly more *S. droebachiensis* juveniles were found in the open (1.8 juveniles per

quadrat $\pm$ 0.21 SD) than under adult spine canopies (1.1 juv. $\pm$ 0.15; t-test: t = -2.87, df =

236, p = 0.0044). Additionally, there was no difference in juvenile size frequency

distributions from either location (Fig. 4.4).

Juvenile sea urchins, both under the spine canopy of adults and not, were more

likely to be found on cracks, even though cracks were the least represented habitat type in

our surveys (Fig. 4.5). Flat corallines, which were by far the most abundant substrate

available, were used the least when juveniles were not under the adult spine canopy (Fig.

4.5).

Average number of juvenile urchins

14 —

Adult urchins only
Rocks only
Urchins & rocks

12 —

10 —

8 —

6 —

4 —

2 —

0 —

Center Edge Spine canopy Rock Corner Wall

Location in aquaria
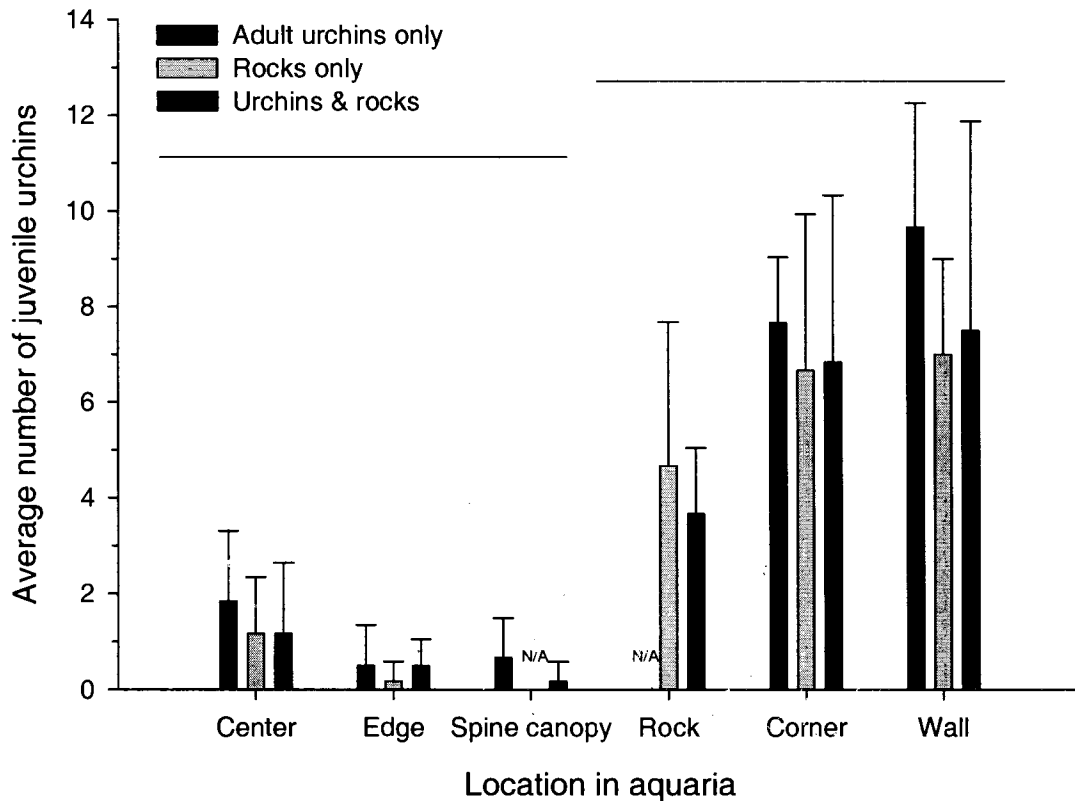
Figure 4.3. Locations of juvenile sea urchins when given a choice of habitats and cover. Data are presented as the average number ($\pm$ SD) of 20 juvenile seas urchins after 24 hours in the experimental aquaria. Experiment consisted of three treatments: 4 adult sea urchins, 4 rocks, and 2 sea urchins / 2 rocks. Lines indicate not significant difference between groups (based on LSD *post hoc* test). Locations are defined as follows and as in Fig. 1:

Center – juvenile sea urchins in the area between the containment areas (for rocks and adult sea urchins)

Edge – juvenile sea urchins in the area outside the containment areas but not in the corner

Spine canopy – juvenile sea urchins under the spines of the adult sea urchins

Rock – juvenile sea urchins under the rocks

Corner – juvenile sea urchin within one body length of where the aquaria floor met the side

Wall – juvenile sea urchins on the vertical surface of the aquaria
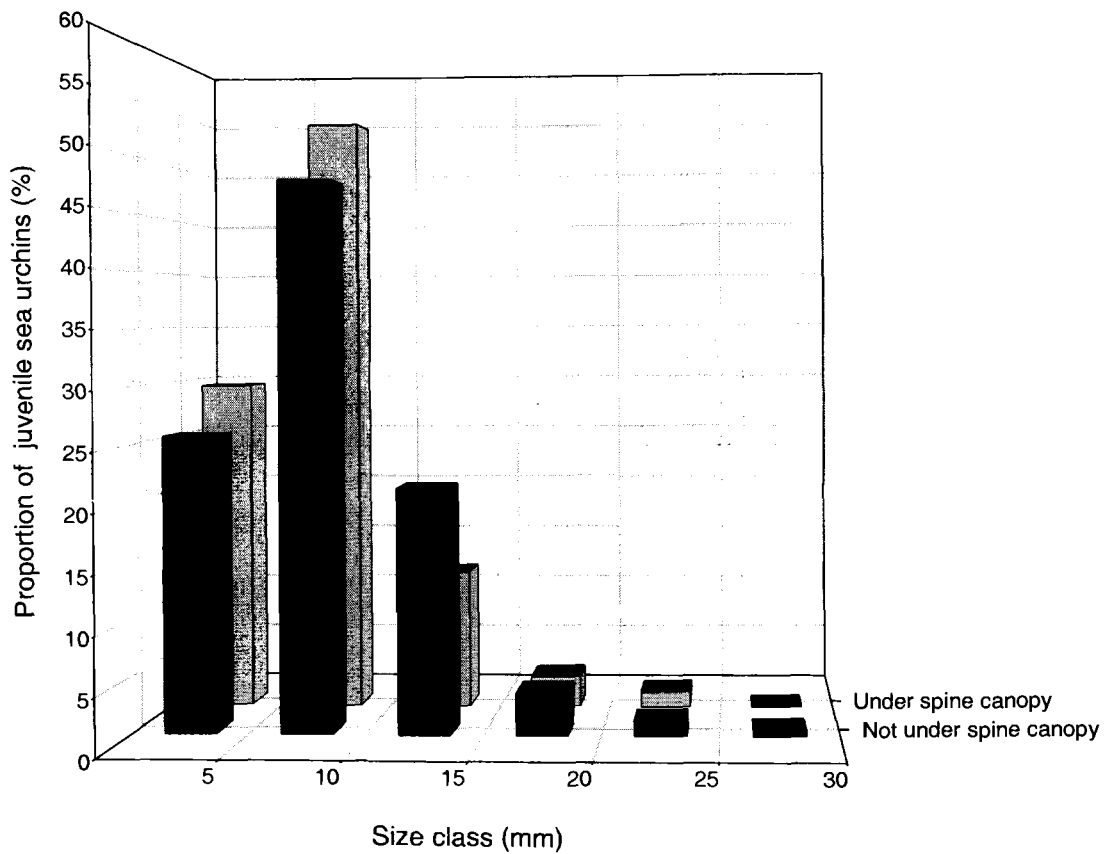
Figure 4.4. Size frequency of juvenile sea urchins found under the adult spine canopy in the wild vs. those exposed. The bars represent the 5mm size categories of sea urchin juveniles. The two curves are not statistically different based on a Kolmogorov-Smirnov Test (n=390, p > 0.10).
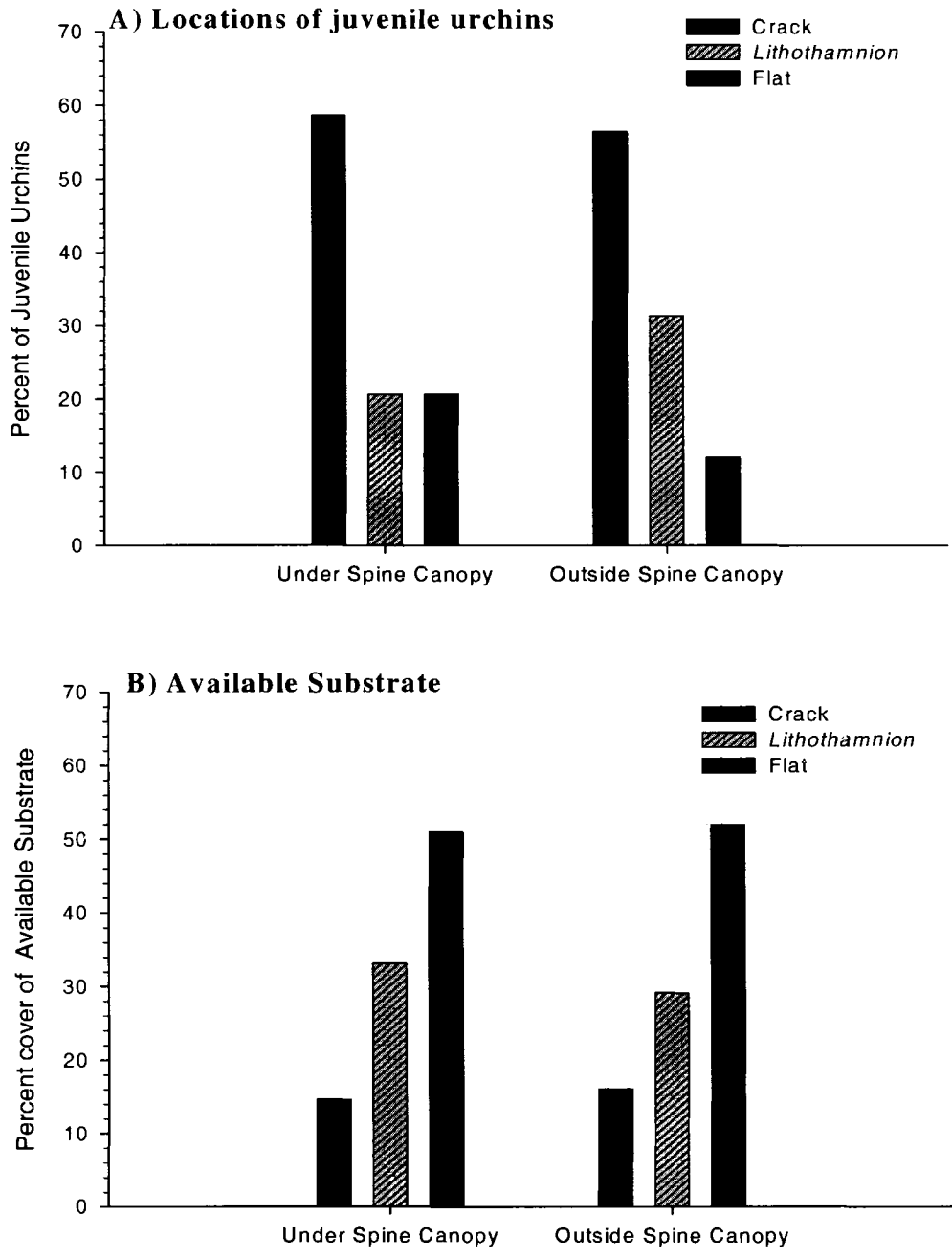
Figure 4.5. Comparison between substrate chosen by juvenile sea urchins and the available substrate in the quadrats. A) Proportion of the juvenile sea urchins found on each habitat type (see text for explanation). Juveniles are separated as those found under an adult urchin spine canopy and those found in the open. B) Percent cover of each habitat type from all quadrats.

Table 4.1. ANOVA results for laboratory experiments where juvenile sea urchins could choose location within the aquaria. Three habitat treatments were considered (four adult sea urchins, four rocks, two sea urchins and two rocks). Locations are described in the text and included the under the adult sea urchin spines, under the rocks, or the aquaria center, edge, corners, or walls. All data were square-root transformed and correspond with Fig. 4.3.

A. Effects of location for the combined treatment

	df	SS	MS	F	p
Location	5	29.74	5.94	15.01	< 0.0001***
Error	30	11.82	0.39		

B. Effects of treatment and location for all treatments

	df	SS	MS	F	p
Treatment	2	0.07	0.03	0.119	0.88
Location	5	94.56	18.91	63.52	< 0.0001***
Treatment*Location	10	14.73	1.47	4.947	< 0.0001***
Error	90	26.79	0.29		

The size of the juvenile sea urchins on each substrate type was related to the potential interstitial space of the habitat. Size frequency distributions for juveniles on each of the substrate types (Fig. 4.6) indicated smaller urchins were found in *Lithothamnion* (mode = 0 – 5 mm), 5 – 10 mm sea urchin were more common in cracks, and the largest juveniles (> 10mm) were often on flat coralline algae, although only the urchins on flat substrate exhibited a statistical difference in mean size (Table 4.2).

Young of the Year (YOY) Sea Urchins

In field experiments, macro-complexity in the habitat (i.e. macroalgal cover) had an effect on sea urchin YOY postsettlement success and altered the importance of the
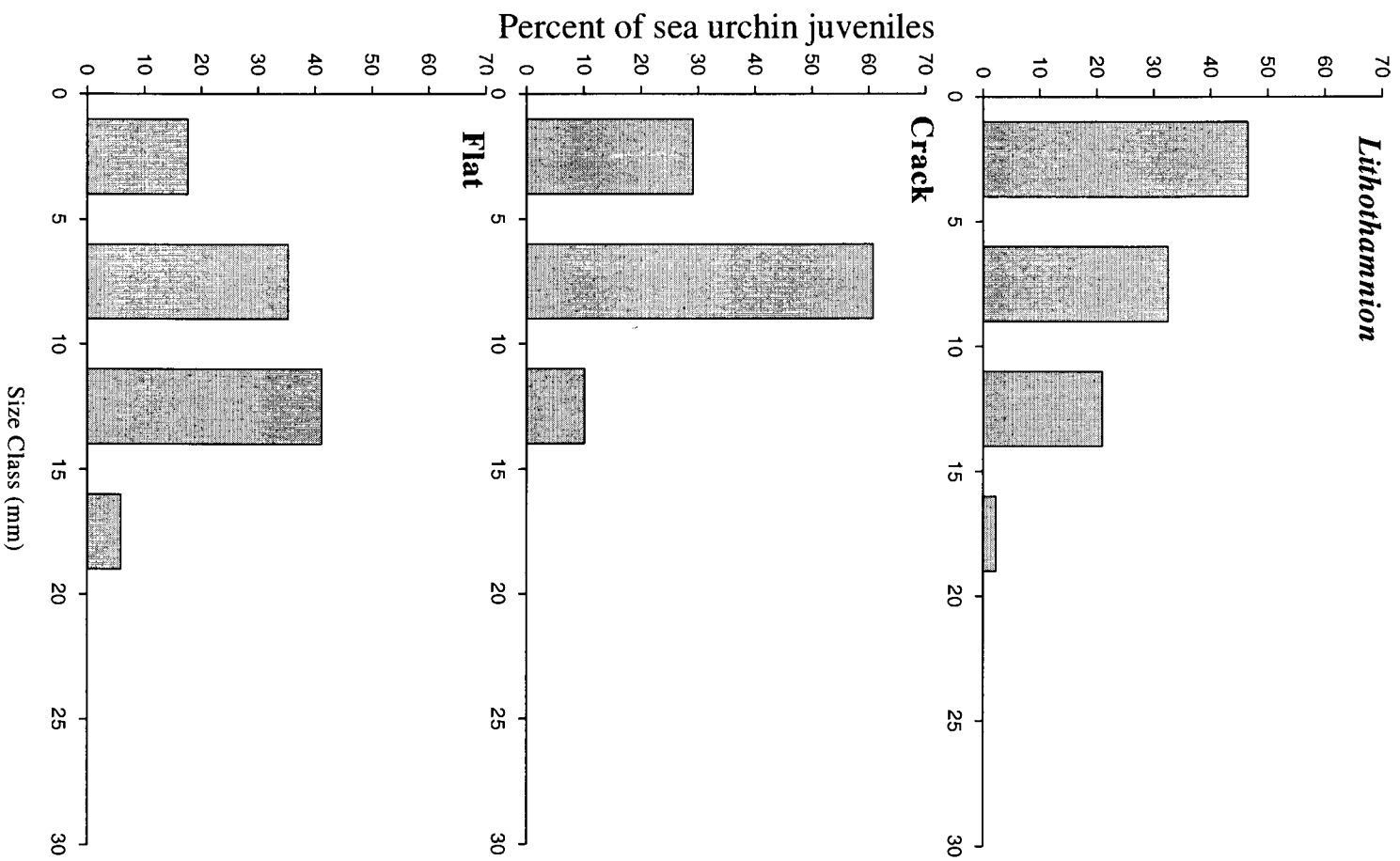
Figure 4.6. Natural size frequency distribution of juvenile sea urchins on the different substrate types. All data are drawn from wild sea urchins found in the open.

Table 4.2. Multiple Kolmogorov-Smirnov tests on the size-frequency distributions for sea urchins found on three different substrate types (*Lithothamnion*, cracks, and flat corallines). Data are based on those presented in Fig. 4.6. We calculated a significant α = 0.0167 by applying the Dunn-Bonferroni procedure to control for Type I errors (Winer et al.).

Substrate	Mean ($\pm$ SD) mm	n
Lithothamnion	0.893 (0.418)	103
Crack	0.885 (0.316)	100
Flat	1.175 (0.422)	100

Comparison	p value
Lithothamnion x Crack	$p > 0.1$
Lithothamnion x Flat	$p < 0.001$***
Crack x Flat	$p < 0.001$***

habitat micro-complexity. The average number of sea urchins on the early postsettlement plates was greater in the coralline community than in the macroalgal bed (Fig. 4.7a). Additionally, within the coralline community, there were higher YOY numbers on the plates with the higher complexity (i.e. *Lithothamnion* mimic) when compared to the flat plates but no difference could be detected between micro-complexity types in the macroalgal bed (Fig. 4.7a, Table 4.3a.).

This pattern did not hold for the late postsettlement YOY collectors retrieved on 12 August 2002. Plates in the coralline community still had significantly more YOY urchins, but there was no longer a difference between plate complexities (Fig. 4.7b, Table 4.3b). Differences between the habitat types were probably resulted from the initial settlement since all treatments averaged ~ 50% YOY survival during the 48 days the
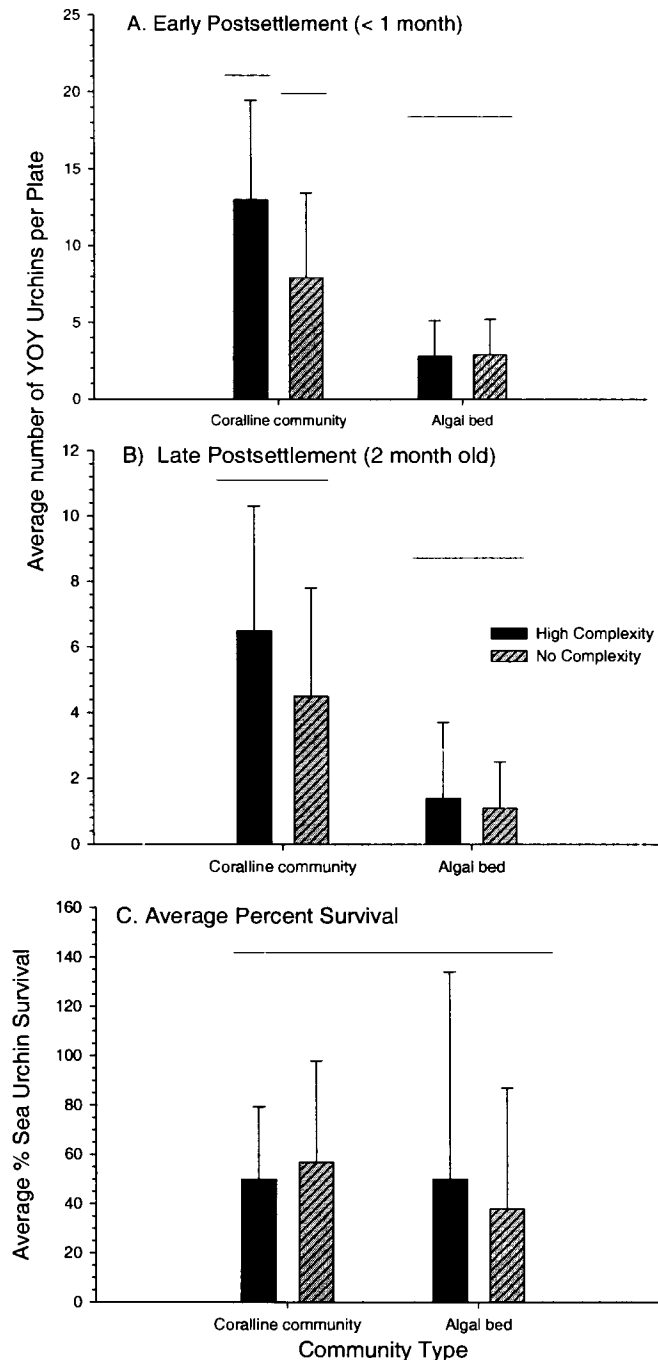
Figure 4.7. Results from the complexity plates (both high complexity and flat plates) placed at Pumpkin Cove inside an urchin-dominated coralline community and a fleshy macroalgal bed. Continuous lines above the columns indicate no statistical difference based on Fisher's LSD *post hoc* test (on square-root transformed data). A) Average number of sea urchin settlers found on the plates after five weeks (early postsettlement; retrieved on 26 June 2002). B) Average number of urchins per plate on plates after 12 weeks (late postsettlement; retrieved 12 August 2002). C) Average survival of sea urchin juveniles to 12 August 2002.

Table 4.3. ANOVA results for the habitat complexity plate experiment corresponding with Fig. 4.7. The effects are complexity (high or none) and habitat (coralline community or algal bed). All data were square-root transformed. A) Average number of sea urchin settlers found on the plates after five weeks (retrieved on 26 June 2002). B) Average percent of sea urchin juveniles surviving to 12 August 2002.

A. Settlement

Effect	df	SS	F	p
Complexity	1	1.5446	2.4046	0.12997
Habitat	1	20.2387	31.5078	<0.0001***
Complexity * Habitat	1	1.9201	2.9893	0.1923
Error	36	23.1242		

B. Recruitment

Effect	df	SS	F	p
Complexity	1	65.2	0.0212	0.8848
Habitat	1	905.4	0.2956	0.5899
Complexity * Habitat	1	905.4	0.2956	0.5899
Error	36	11.236.6		

plates were in the field (Fig. 4.7c, Table 4.3b). Variability was very high in the samples, especially in the macroalgal bed, and may have obscured real trends in the data.

In the laboratory, the sea urchin YOY did not choose the higher micro-complexity when given a choice of substrates (Fig. 4.8). The average number of urchins using each degree of complexity was similar in all cases, but the highest complexity (*Lithothamnion* mimic) attracted the fewest urchins. There was no consistent trend over the micro-complexity gradient (Fig. 4.8, Table 4.4). The highest numbers of YOY urchins were found on the wall of the aquaria, which was similar to the results of the spine canopy experiment using larger juveniles.
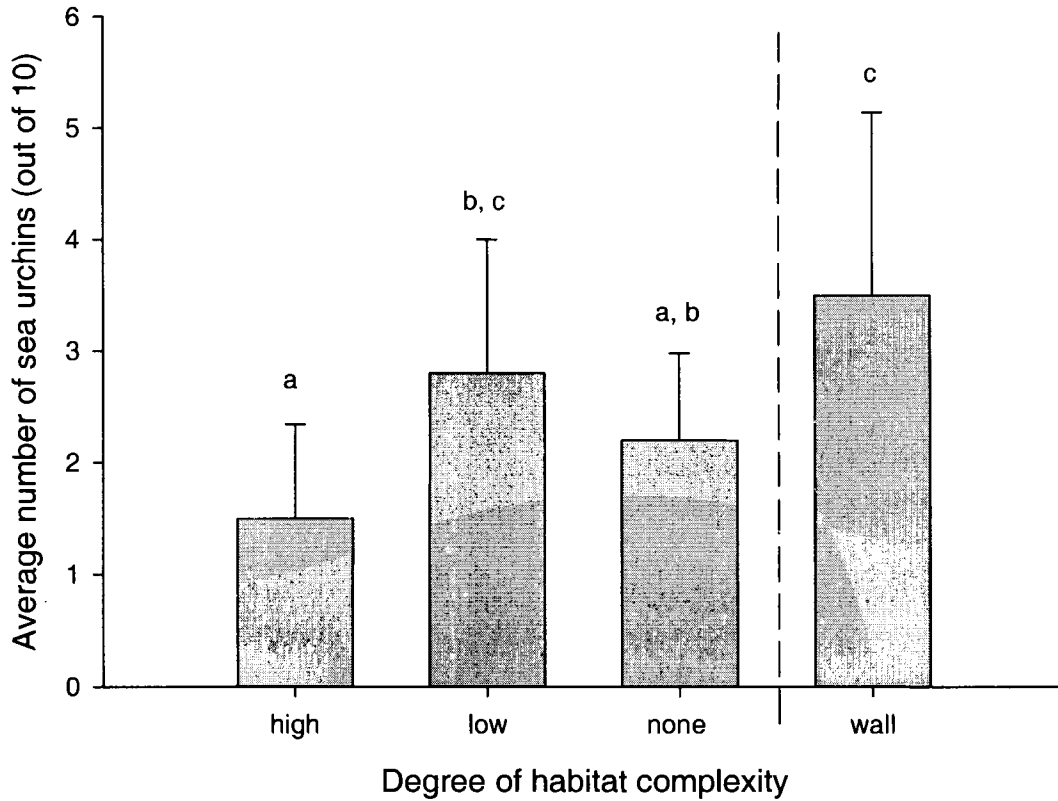
Figure 4.8. Average number of young of the year sea urchins ($\pm$ SD) found on each of the habitat complexity types (high, low, and none/flat) in laboratory experiments. "Wall" indicates sea urchins were found on the vertical wall of the aquaria (not part of the original microcomplexity experiment). Identical letters above error bars indicate no statistical difference based on a Fisher's LSD *post hoc* test (on square root-transformed data).

Table 4.4. ANOVA table for laboratory experiment to determine the habitat complexity preference of YOY sea urchins (data shown in Fig. 9).

Effect	SS	df	MS	F	p
Complexity	1.81	3	0.60	5.11	0.004**
Error	4.25	36	0.11		

Results of our last experiment suggested that YOY urchins may be susceptible to cannibalism by larger adults. In the 10 trials conducted, no urchins were missing in the treatments with the high complexity or the controls without adult sea urchins (Fig. 4.9). Four flat substrate trials, however, were missing one or two urchins. A Mann-Whitney U test revealed a significant difference between the two habitat complexities (Fig. 4.9).

Discussion

Our data suggest that habitat heterogeneity does impact the distribution of sea urchins at different scales. In the wild, juvenile sea urchins were more likely to find, or persist in, areas of higher micro-complexity like cracks, although use of this micro-complexity appeared to be dependent on the size of the sea urchin and the interstitial spaces of the benthos. This would imply that the *Lithothamnion* provides nursery grounds for smaller sea urchins as suggested by Keats et al. (1985) and Himmelman (1986). Our laboratory experiments did not indicate that the YOY actively choose these sites, thus the distribution in nature may be due to differential survival; i.e. the sea urchins are found in all habitats but have lower mortality in sites with higher micro-complexity. The sea urchins probably outgrow the interstices of the *Lithothamnion* and
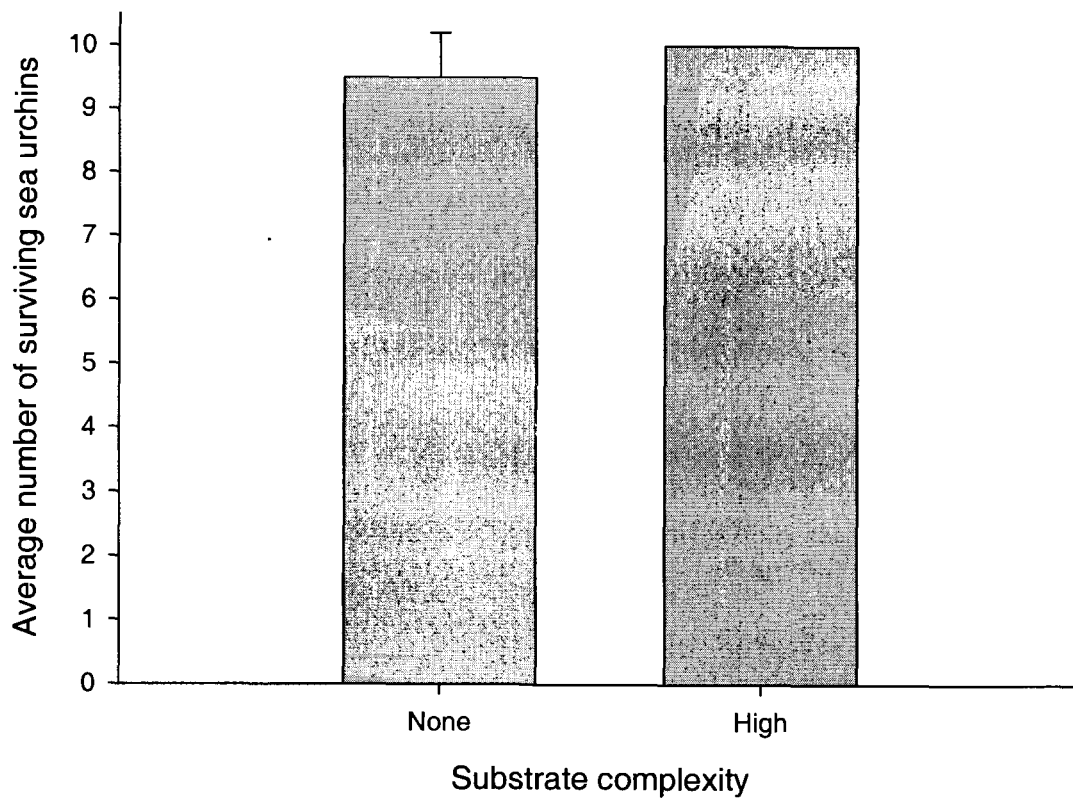
Figure 4.9. Average number of surviving (initial = 10) YOY sea urchins ($\pm$ SD) in each degree of substrate complexity in laboratory experiments with adult sea urchins as a potential predator. No YOY sea urchins were lost in control treatments without adult sea urchins. Averages are statistically different between the substrates (z = 2.169, p = 0.03, Mann-Whitney U Test)

move to areas with more space, like cracks in the ledge. Eventually the juvenile sea

urchins either outgrow the cracks or, more likely, their increased size offers some

protection from predation, and more can move about on the areas with very little micro-

complexity. Therefore microhabitat use is probably dependent on size and susceptibility

to predation and can become a bottleneck determining population structure (Himmelman

1986, Scheibling and Hamm 1991).

These experiments do not show if the initial selection of micro-complexity is due

to differential settlement or survival. Early postsettlement of sea urchins in coralline

communities was greater on the plates with more complexity than on the flat plates (Fig

8a). It is possible that the increased structural complexity changed local hydrodynamics,

therefore improving settlement (Eckman 1983, Wethey 1986). Alternatively, it is also

possible that during the time settlers were on the plate post-settlement mortality could

have differed for the various complexities. The higher complexity plates could have

afforded an early protection from predation for the settlers, especially predation from fish

such as cunner. Predation from adult urchins (most likely incidental ingestion) was also

possible since the plates were intentionally placed flush to the substrate, and substrate

complexity was shown to protect juvenile urchins from cannibalism. The increased

complexity could also have allowed better purchase and protection for the juvenile

urchins during the storms encountered during the month of June (see Chapt. 3).

Additionally, various objects such as lobster traps could have abraded the plates, and had

a greater effect on the flat plates where there was no place to hide.

Results from the second late postsettlement plates would suggest that differences

in the settlement plates are due primarily to larval delivery mechanisms rather than

differential YOY mortality. There were no significant differences in post-settlement

mortality on these plates for the remainder of the summer (Fig. 8b). Rates of mortality

could have changed during the two trials, however, in two possible ways. First, if the

trend of higher settlement on higher micro-complexity was due to size dependent

mortality (e.g. smaller sea urchins have a reduced ability to adhere during a storm) we

would expect to see a shift in mortality later in the summer as the settlers grow (i.e.

higher mortality on the smallest sea urchins, lower rates later on larger YOY). Second, if

the agent of mortality changes and is not hindered by increased habitat complexity,

changes in the survival rates might occur. Until now, we have mostly considered larger

predators such as cunner (Keats et al. 1985, Ojeda and Dearborn 1991) and large urchins

that would have problems getting into the smaller spaces of more complex habitats.

McNaught (1999), however, found small, newly-settled crabs (*Hyas araneus* and *Cancer*

irroratus) were potentially important predators on settling sea urchins. These crabs

settled later in the summer after the first round of plates had been picked up (Palma et al.

1998). These small predators are appropriately sized to exploit many of the small refuges

larger predators would have difficulty accessing. Therefore, rates of mortality could

become equal between substrates of different micro-complexity.

Larger scales of heterogeneity (macro-complexity) also proved to be important to

young sea urchins. Macroalgal beds showed significantly lower settlement overall, a

trend also observed by Balch et al. (1998) but contrary to other studies (Harris and

Chester 1996, McNaught 1999). This may be due to the baffling effects of the algal bed.

Many have suggested that kelp beds may slow water and facilitate the settlement of

invertebrates on the edges of the bed, effectively filtering the interior of the kelp bed of

larvae (Eckman 1983, Jackson and Winant 1983, Jackson 1986, 1998). Lower settlement numbers in the algal beds may also be due to an increase in potential predators. Adult cunner are more numerous in Gulf of Maine algal beds (Levin et al. 1997), and fish recruitment may be dependent upon increased habitat complexity provided by the macroalgae (Levin 1991). Likewise, micropredators such as small crabs and amphipods may use the algal matrix of macroalgal beds to support higher densities (Hacker and Steneck 1990, McNaught 1999). Ironically, this larger-scale structure of the algae may overgrow the beneficial micro-scale habitat complexity that apparently facilitates sea urchin settlement in coralline communities (but not in the macroalgal bed; see Fig. 7a).

Macro-complexity afforded by adult spine canopies is not important juvenile habitat for *S. droebachiensis*. Fewer juveniles were found under adults than in the open, and this was the case for all sizes of juveniles. In fact, the area under adults was virtually the least likely place for juveniles in the laboratory, and a much lower percentage of the juveniles were found there than would have been expected from the field surveys. The field surveys included motile adults who may have moved around more than our snapshot of a survey could predict. Therefore juveniles could have found themselves unintentionally under adults when they obviously would not have chosen that site on their own (according to laboratory experiments; Fig. 6). Additionally, beneficial spine canopy effects are probably only seen when the adult sea urchins are basically sedentary (Day and Branch 2002), which is probably not the case in *S. droebachiensis* coralline communities (Harrold and Pearse 1987).

Urchins of all sizes appear to be drawn to cracks and corners in the substrate (Vadas et al. 1986, J. Vavrinec pers. obs.); thus, the higher proportion of juveniles found

in the field beneath adults (compared to laboratory experiments) could be due to adult movement rather than juvenile behavior. Both life stages could be drawn to the same complexity on the bottom and end up together by chance. It is interesting that there is a higher percent of urchins on flat (low complexity) corallines under the spine canopy than in the open. Perhaps some of the juveniles perceive the adults as structure and are less likely to seek out other refuges. It would be ironic, however, if this perceived refuge is also a potentially hostile environment where adult urchins cannibalize the young.

It would also appear that given a choice, juveniles prefer vertical surfaces or hard angles. In all laboratory experiments, juveniles were observed quickly moving to the sides of the aquaria. This behavior was also observed by Vadas et al. (1986) and Scheibling and Hamm (1991). The desire to wedge into a corner may explain the unexpected results when YOY did not choose more complex habitats. None of our complexity plates had hard angles; the juveniles may have simply traversed the substrate in search of a crack (negative vertical surface), a corner, or a wall. In a large coralline community this behavior may be a flight response to decrease the potential of predation from adult conspecifics and decapods (Scheibling and Hamm 1991), or it may be an artifact to the laboratory experiments since such vertical surfaces are rarer on natural ledges (Vadas et al. 1986).

In conclusion, habitat complexity may have varied effects on the recruitment of *S. droebachiensis* in the Gulf of Maine. Small scale micro-complexity definitely appears to act as nursery habitat, especially for smaller juveniles. As the juveniles grow, they are either excluded from these areas or attain a partial refuge in size and can become more mobile. Large scale macro-complexity may be beneficial when referring to large vertical

surfaces, but is probably detrimental when in the form of adult sea urchins (potential

predators) or fleshy macroalgae (probably harbors large populations of predators).

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