

# **Reseeding the Green Sea Urchin in Depleted Habitats**

Final Report to the Maine Department of Marine Resources

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## SUMMARY

Overfishing extirpated the green sea urchin (*Strongylocentrotus droebachiensis*) from large areas of Maine's coast west of Penobscot Bay. Without their grazing, dense algal beds have developed and replaced the coralline "barren grounds" in western Maine. Dense algal beds prohibit urchin recruitment because they harbor micropredators of newly settled sea urchins. We examined the hypothesis that adult urchins, relocated to an area where they had been depleted, could aid in population recovery by directly increasing grazing pressure and indirectly increasing urchin recruitment. In two separate trials (August 2000 and April/May 2001), we relocated 3000 adult urchins to each of 8 sites in 2000 and 9 sites in 2001 at Cape Elizabeth, Maine. In July 2001, relatively low fleshy algal cover (< 50 %) was quantified at plots with urchins. In both trials, sea urchin abundances declined dramatically in the latter part of August and early part of September. We attributed these abrupt declines to massive predation by large, migratory Jonah crabs (*Cancer borealis*). Both trials had a significantly higher density of Jonah crabs at plots with urchins when compared to plots without. Therefore Jonah crab predation on urchins prevented the successful reestablishment of sea urchins in a depleted area.

Future fisheries population models need to increase natural mortality rates as barrens phase-shift to algal beds. This means the proportion of total mortality shifts from being primarily fisheries-based (i.e., "F") to being primarily natural mortality ("M"). Our outcome of massive mortality of adult urchins due to predation by large crabs coupled with the past finding of mortality of newly settled urchins due to predation by small micropredators, results in a remarkably stable urchin-free (algal dominated) state that shows no sign of recovery. This fishery must be managed to maintain the ecological function of herbivory if it is to be harvested sustainably.

## INTRODUCTION

### Purposes of the Project

The Sea Urchin Zone Council asked the scientific community to determine the feasibility of reestablishing sea urchin populations in order to help guide future fishery management decisions. We sought out to reestablish sea urchin populations by moving adult urchins to an area where they had been overharvested. We broke down this overall research goal into four smaller objectives.

**A) To determine if relocated sea urchins population densities persist over time and at what density.**

That urchin populations persisted at the sites they were relocated to was necessary for grazing pressure to remain high. Therefore we quantified urchin and urchin predator abundances over time post-relocation.

**B) To determine mortality rates associated with the collection and transportation of relocated urchins.**

In order to quantify urchin survival following relocation we needed to account for urchin mortality due to handling. Thus we measured survival of sea urchins post-relocation in laboratory tanks with no predators.

**C) To determine the rate of algal biomass removal due to grazing by relocated urchins.**

High grazing rates should have ensured the deforestation of fleshy algae and the creation of coralline barrens. Consequently we assessed the change in algal abundance over a three month period of presumably high grazing pressure.

**D) To determine if settlement success is measurably greater in areas with relocated urchins than in adjacent control areas.**

Post-settlement mortality should have been greater in fleshy algal beds than in coralline barrens (McNaught 1999). As a result we quantified urchin recruitment at plots with relocated urchins (barrens) and plots without urchins (algal beds).

## **Background**

Over the last 15 years populations of the green sea urchin (*Strongylocentrotus droebachiensis*) have declined dramatically along the coast of Maine (McNaught 1999). Intense fishing of cod and other predatory groundfish in the Gulf of Maine released sea urchins to become one of the most abundant species of shallow subtidal macroinvertebrates in the 1970s and 1980s (Steneck et al. 1994, Vadas and Steneck 1995, Steneck 1997). A fishery developed in 1987 and rapidly expanded to become the second most valuable wild fishery in Maine. Urchin landings peaked in 1993 and 1994 (at about 45 metric tons) and have been declining since (DMR 2000). Fisheries-independent SCUBA surveys have documented this rapid decline in sea urchin populations that has led to the depletion of urchins in vast regions west of Penobscot Bay (McNaught 1999).

The green sea urchin is *the* dominant benthic grazer in the shallow subtidal zones of the Gulf of Maine, and as such has the ability to denude the benthos of erect fleshy algae leaving little but encrusting coralline algae (often termed 'barrens') (Scheibling 1986, Steneck and Dethier 1994, Scheibling et al. 1999). Therefore as urchin populations have declined so have grazing rates, and fleshy macroalgal beds have become established. For example, fleshy algal beds have dominated in York, ME since urchins were extirpated in 1998 (J. Vavrinec, unpublished data). These algal beds persist because they harbor small predators (amphipods and newly settled *Cancer* crabs) of newly settled and juvenile sea urchins (McNaught 1999). Thus natural sea urchin recruitment is indirectly prevented by dense fleshy algae despite an abundant larval supply.

In this study we examined the feasibility of reestablishing sea urchin populations in areas where they once had been abundant but later were depleted and dense fleshy algal beds now dominate. In particular, we hypothesized that (1) adult sea urchins relocated to a depleted area would graze down the fleshy algae and create a barrens; and (2) natural sea urchin recruitment would be restored because micropredators of newly settled sea urchins would be scarce. To determine if sea urchin populations would recover following restoration of grazing pressure, we repeatedly quantified the survival of sea urchins after relocation to Cape Elizabeth, ME in two trials. In the second trial we also determined the change in algal abundance due to sea urchin grazing. Following unexpected urchin mortality early in the first trial, we modified our goals also to include quantifying population density of predatory crabs (*Cancer* spp.) as a possible cause of the urchin mortality. Sea urchin post-settler densities were quantified in the winter following the relocation of urchins in 2001.

## METHODS

### Study Site

In order to accurately ascertain the feasibility of reestablishing sea urchin populations in an area where they had been depleted we used a site that met the criteria listed below. The northeast corner of Cape Elizabeth, ME (N 43°34' W 70°11.5'; Fig. 1):

- (1) Was located in western-coastal Maine where vast areas were devoid of urchins and settlement was high (McNaught 1999);
- (2) Had a flat-ledge substrate which aided in accurately quantifying urchin densities post-relocation;
- (3) Was devoid of urchins at the beginning of the experiment which minimized confounding effects;
- (4) Had a relatively uniform cover and composition of benthic macroalgae;
- (5) Was contained within a fishery closed area that was enforceable by marine patrol on both land and sea;
- (6) Had been a productive urchin harvesting area historically.

The surrounding urchin fishery closed area was regulated in January 2001 for 5 years.

Therefore, the area was open to fishing following the first urchin relocation trial (August 2000) but urchins under the legal size (between 35 and 45mm TD) were used to avoid mortality due to harvesting.

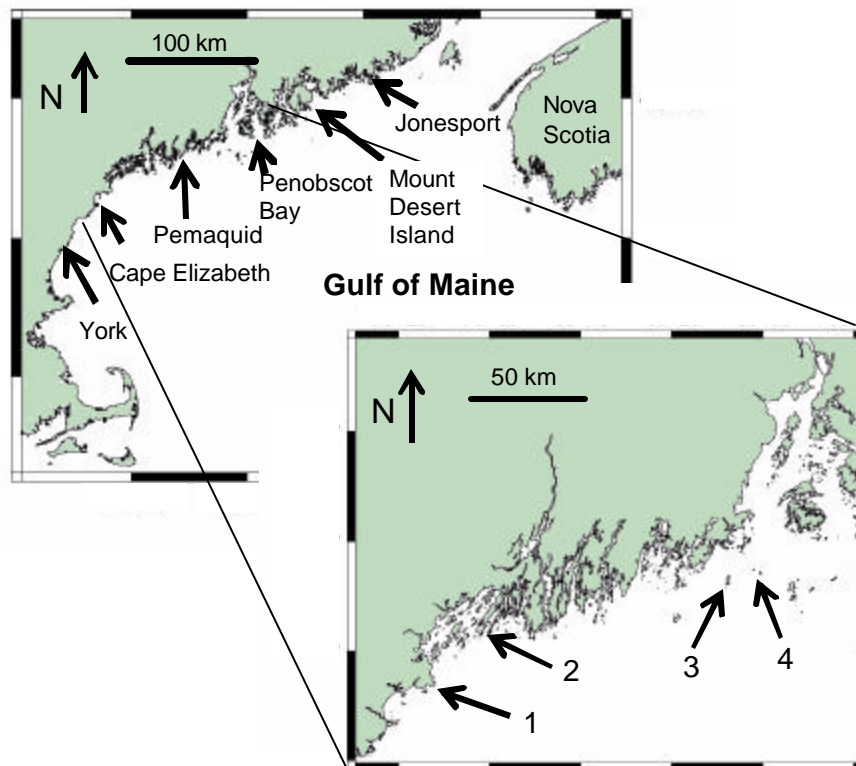


Fig. 1: Regions of the Gulf of Maine and sea urchin collection sites. Sea urchin collection sites were: (1) west Cape Elizabeth and Richmond Island, (2) Land's End and Jaquish Ledge, (3) Metinic Island and (4) Large Green Island.

## Urchin relocation

The urchin relocation experiment was setup as a randomized block design such that each block was a replicate of all treatment combinations. The experimental design included two urchin treatments (- U, + U)  $\times$  two fleshy macroalgae treatments (- A, + A)  $\times$  four replicates. In 2001, the design was unbalanced because one replicate had two plots with urchins and without fleshy algae (+ U - A) but lacked a plot without urchins and without algae (- U - A). The main effect of the urchin treatment tested for differences in urchin and crab abundances at plots with relocated urchins (+ U) and without (- U). In both trials, divers removed fleshy algae (- A) from the central areas of plots (Fig. 2) using paint scrapers prior to the urchin relocation. Therefore, the main effect of the algae treatment (A) tested for differences in fleshy algae abundances at plots that had been cleared of fleshy algae at the beginning of the experiment (- A) versus those that had not (+ A). The interaction of both treatments (U  $\times$  A) tested for differences in urchin and crab abundances due to the presence (+ A) or absence (- A) of algae. In addition, the interaction effect (U  $\times$  A) tested for differences in algal abundance due to the presence (+ U) or absence (- U) of urchins.

We conducted the experiment over two trials. The first trial occurred between 8 August and 17 September 2000, and the second took place between 21 April and 5 November 2001. Initial urchin abundance was quantified prior to the urchin relocation in both trials. Initial crab abundance was counted prior to the urchin relocation in the second trial only. In both trials, urchin and crab abundances were measured periodically following the urchin relocation. Algal abundance was quantified once following the urchin relocation (14 July) in 2001.

Sea urchins (*S. droebachiensis*) were relocated to Cape Elizabeth from other areas. In 2000, urchins were collected from four locations (Fig. 1): Richmond Island (N 43°32.5', W 70°14.0'), southwest Cape Elizabeth (N 43°33.5', W 70°13.0'), Jaquish Ledge (N 43°42.5', W 70°00.0') and Land's End (N 43°43.0', W 70°00.0'). In 2001, all urchins were collected from Metinic Island (N 43°53.0', W 69°07.5') and Large Green Island (N 43°54.0', W 69°00.5') in outer Penobscot Bay (Fig. 1). Urchins were hand harvested using traditional methods and sorted out of water to include only healthy urchins within a specific size range (35 to 45 mm test diameter (TD) in 2000, = 50 mm TD in 2001).

From 14 - 17 August 2001, 24000 urchins were relocated to 8 plots (3000 per plot) at Cape Elizabeth. Sorted urchins were held in mesh bags on the bottom of the sea until they were transported in covered plastic boxes without water to plots at Cape Elizabeth. Divers released the urchins into the central 2.5 m radius area (Fig. 2) of appropriate plots. The southern plots were the first to receive urchins and the northern plots were the last.

In 2001, 27000 urchins were relocated to 9 plots (3000 per plot) at Cape Elizabeth in early spring. Sorted urchins were placed into mesh bags and held in 1.21 m<sup>3</sup> covered plastic boxes on the deck of the boat (R/V *Ira C.*, Darling Marine Center). The urchins were provided with flowing seawater and constant aeration during an overnight transit to Cape Elizabeth and were placed on plots the following morning. Urchins were released by divers into the central 16 m<sup>2</sup> area of the two southernmost plots on 26 April and the rest of the plots on 4 May.

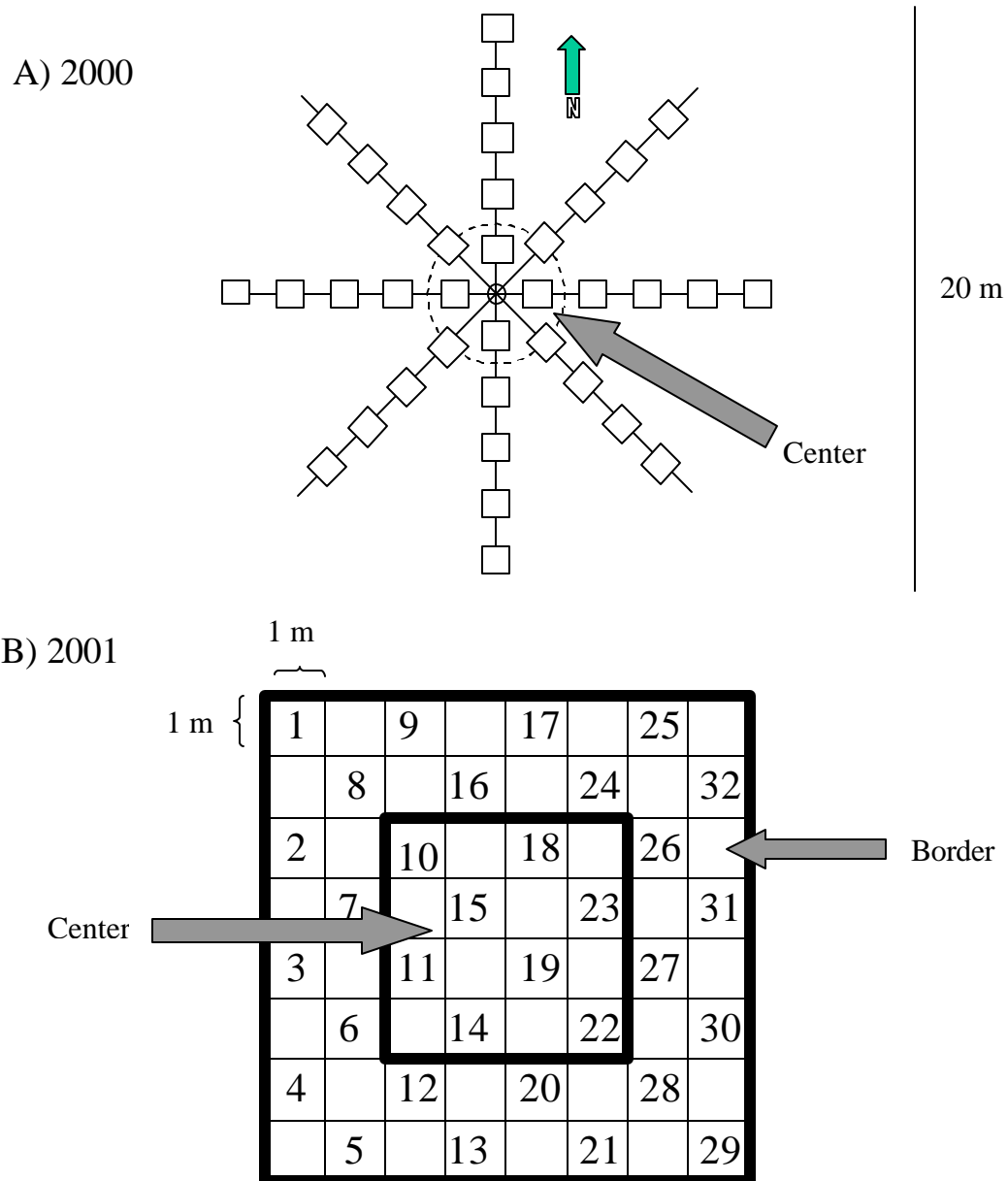


Fig. 2: Two sampling designs at Cape Elizabeth in years 2000 (A) and 2001 (B). A & B) Small squares represent  $1 \text{ m}^2$  quadrats where urchin abundances were sampled many times. B) Percent cover of fleshy algae was sampled in all unnumbered quadrats in July. The central 2.5 m radius circle (A) was cleared of fleshy algae at predetermined plots in 2000, while the central  $4 \text{ m} \times 4 \text{ m}$  square (B) was cleared in 2001.

On 4 May 2001, sea urchins ( $n = 186$ ) were haphazardly subsampled from those collected at Large Green Island such that a few sea urchins were collected from most harvester collection bags, and then they were brought to the Flowing Seawater Lab at the Darling Marine Center. These urchins were tested for survival over time under predator-free conditions. No urchins were subsampled from Metinic Island because of low urchin abundance. Urchins were measured (mm test diameter (TD)) for size information and randomly placed into one of six holding tanks ( $n = 36$  urchins per tank). Each tank had constant water flow and aeration. Urchins were fed *Laminaria saccharina ad libitum* until their release on 25 September 2001.

#### *Urchin and Cancer spp. densities*

In all replicates, divers estimated urchin and crab densities weekly in 2000 and at least monthly in 2001 following the relocation of urchins. Urchin densities were estimated prior to the relocation of urchins in both trials. Crab densities were estimated prior to urchin relocation in 2001 only. In 2000, urchins and *Cancer* spp. at each plot were counted in  $1 \text{ m}^2$  quadrats that were placed regularly along radial transect lines separated by  $45^\circ$  ( $n = (36) 1 \text{ m}^2$  quadrats per plot; Fig. 2A). In 2001, urchins, Jonah crabs and rock crabs at each plot were tallied in  $1 \text{ m}^2$  quadrats placed regularly in a  $64 \text{ m}^2$  sampling grid ( $n = (32) 1 \text{ m}^2$  quadrats per plot; numbered quadrats in Fig. 2B). Jonah and rock crabs were measured (carapace width (CW) in 5 mm size bins) in 2001.

#### *Macroalgae abundances*

In 2001, the percent cover of benthic macroalgae was estimated in all plots on 14 July. Divers visually estimated the percent cover of all macroalgae at three different spatial tiers in  $1 \text{ m}^2$  quadrats (McNaught 1999). Algal percent cover was assessed in quadrats placed regularly in both the border areas ( $n = (24) 1 \text{ m}^2$  quadrats) and center areas ( $n = (12) 1 \text{ m}^2$  quadrats) of plots (all unnumbered quadrats in Fig. 2B).

#### *Per capita predation rates of Jonah crabs*

Per capita predation rates of Jonah crabs on urchins were estimated as  $\text{urchins} \cdot \text{crab}^{-1} \cdot \text{d}^{-1}$  in 2001. The average urchin density at each plot with relocated urchins ( $+ U$ ) was transformed from a  $\text{plot}^{-1}$  to  $\text{m}^{-2}$  estimate. The change in average urchin density ( $\text{m}^{-2}$ ) between each of five consecutive sampling dates (14 July to 5 November) was divided by the change in average Jonah crab density ( $\text{m}^{-2}$ ) during these same intervals. This value was divided by the time (days) that had passed between each interval. Data prior to 14 July were not used due to large variation in estimated urchin abundances.

#### *Urchin survival in controlled conditions*

The number of urchins in each of six laboratory tanks was counted weekly to estimate urchin survival from 4 May until 25 September 2001. The temperature of each tank was assessed using a calibrated YSI meter when urchins were counted.

#### *Sea urchin post-settler densities*

In 2001, urchin post-settler densities were quantified using suction sampling to determine if post-settlement mortality was enhanced where urchins had grazed down fleshy algae. We suctioned within a  $0.0625 \text{ m}^2$  square quadrat at some plots. Details of the suction sampler unit and general methods can be found in McNaught (1999). We suctioned eleven plots in three

replicate blocks between December 2001 and March 2002. We took four replicate suction samples at each plot, except one in which we suctioned three replicates. In all cases, flat ledge substrate was suctioned as near to the center eyebolt (the middle of each plot) as possible. Samples were frozen on return to the lab and processed under a dissecting microscope as described in McNaught (1999).

### *Data analyses*

Data analyses were performed using the SAS version (SAS Institute 2001) statistical package. Both years were analyzed as separate experiments because their experimental designs were different. Sampling of plots rarely was completed within one day so sample dates were averaged for each period; these average sample dates are presented in the results. Urchin abundances for both years were square root transformed prior to analyses. Crab densities and per capita predation rates of Jonah crabs were log transformed. The paired differences of the percent cover of fleshy algae data in center areas of plots versus the border areas were arcsine transformed. Assumptions of normality and homogeneity of variances were examined in all analyses using the Shapiro-Wilk test and Levene Median test respectively.

Urchin abundances were estimated repeatedly during both trials of the urchin relocation experiment. For each sampling date, the number of urchins counted per plot (in half of the total plot area) was doubled to estimate the total abundance of urchins per plot. These values were used in all analyses. Because no urchin was observed at any plot that did not receive relocated urchins at any sampling date in both trials, this treatment (- U) was not included in analyses of urchin abundance over time. Data were analyzed in a randomized block split-plot ANOVA such that fleshy algae (+ A, - A) and replicate formed the main plot factors and time and the interaction of time  $\times$  algae formed the "sub-plot" factors. Hypotheses were tested using the replicate  $\times$  algae mean square value as the error term for both main plot factors.

Although crab densities were also quantified repeatedly during both trials of the urchin relocation experiment, these data were not analyzed using a randomized block split-plot ANOVA. In analyses of both trials, crab abundance data violated normality and homogeneity of variance assumptions despite log-transformation. Instead, total crab density summed over eight sampling dates was analyzed in a randomized block ANOVA with replicate, urchin (U), and algae (A) as main factors. In 2000, the total number of *Cancer* spp. per plot on each sampling date was converted to a density per m<sup>2</sup> estimate. The same was done in 2001 except that the densities were separated by species (Jonah crabs and rock crabs). These densities were added for all sampling dates except 30 August 2001 when all plots were not sampled.

The percent cover of fleshy algae was sampled in the border and center areas (Fig. 2) of all plots about three months following the relocation of urchins in 2001. The average percent cover of fleshy algae was determined for the center and border areas separately for each plot. We failed to detect differences in the percent cover of fleshy algae in the border areas of all plots when analyzed using a randomized block ANOVA with replicate, urchin (U), and algae (A) as main factors, so the percent cover of fleshy algae in each border area was used a paired control (e.g. no impacts) for each plot. The average percent cover of fleshy algae in the center area was subtracted from the average percent cover of fleshy algae in the border area for each plot. These paired differences were arcsine-transformed and analyzed in a randomized block ANOVA with replicate, urchin (U), and algae (A) as main factors.

Per capita predation rates of Jonah crabs on urchins were estimated for each plot that received relocated urchins during four sampling intervals in 2001. These data were analyzed



using a randomized block split-plot ANOVA with replicate and algae (+ A, - A) as the two main factors and time and the interaction of time  $\times$  algae as “sub-plot” factors. Hypotheses were tested using the replicate  $\times$  algae mean square value as the error term for both main plot factors. The variances of per Jonah crab predation rate among replicates were heterogenous (failed Levene’s test), and therefore probabilities close to  $\alpha = 0.01$  in this analysis should be interpreted with caution.

For each sampling date, the survival of urchins held in controlled conditions was averaged. Average water temperature for all tanks on each sampling date was also calculated. No statistical analyses of urchin survival were performed because urchin survival remained very high throughout the experiment.

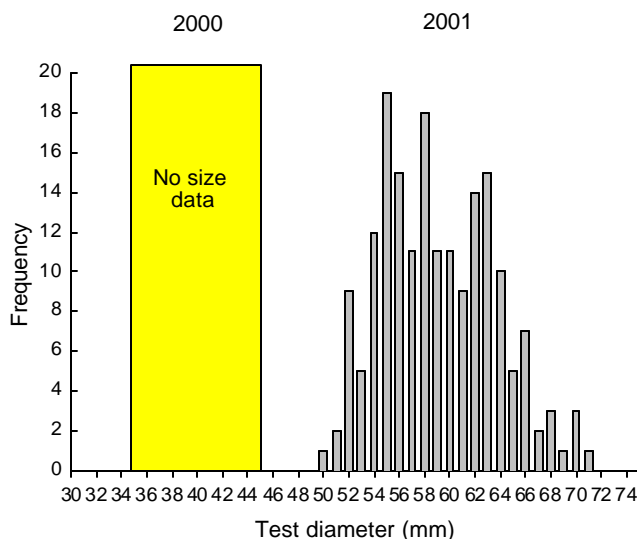
Urchin post-settler density in each replicate suction sample was square root transformed and all replicates were averaged for each plot. Post-settler density at each plot was analyzed in a randomized block ANOVA with replicate, urchin (U), and algae (A) as main factors.

## RESULTS

### Relocated sea urchin populations

#### *Survival*

In both trials, sea urchins were relocated to predetermined plots (+ U) above natural population biomass estimates found in urchin feeding fronts (Breen and Mann 1976, Scheibling et al. 1999). In 2000, all relocated urchins were between 35 mm and 45 mm TD, while in 2001 urchins ranged from 50 mm to 71 mm TD (Fig. 3). Urchins were never observed at plots without relocated urchins (- U) during both trials.



**Fig. 3:** Size distributions of urchins relocated to Cape Elizabeth in 2000 and 2001. No frequency data is available for 2000, but all 24,000 urchins were measured within 35 mm and 45 mm test diameter.

Urchin populations persisted for different durations during the two years of the study (as they were relocated in different months), but strong seasonal (August and September) declines occurred in both years (Table 1, Fig. 4). In 2000, urchin abundances declined rapidly following relocation to Cape Elizabeth (Fig. 4A). Surveys one week after relocation revealed 50% mortality (1500 plot<sup>-1</sup>) of relocated urchins. Urchins were extirpated from all plots within one month of relocation in 2000 (mid-September). In 2001, urchin populations persisted for about 3 months prior to declines (Fig. 4B), but urchins were very low (100 plot<sup>-1</sup>) at most plots by the beginning of October. Urchin abundance did not depend on the percent cover of fleshy algae in 2001 (Table 1B).

**Table 1.** Repeated measures ANOVA tables of urchin abundances (square root transformed) at plots with relocated urchins (+ U) in A) 2000 and B) 2001. Replicates were blocks for treatments. Treatments were the presence or absence of fleshy algae in the center areas of each plot (see Fig. 2) at the beginning of the experiment. Experimental units for Time are nested within those for Algae in a split-plot design.

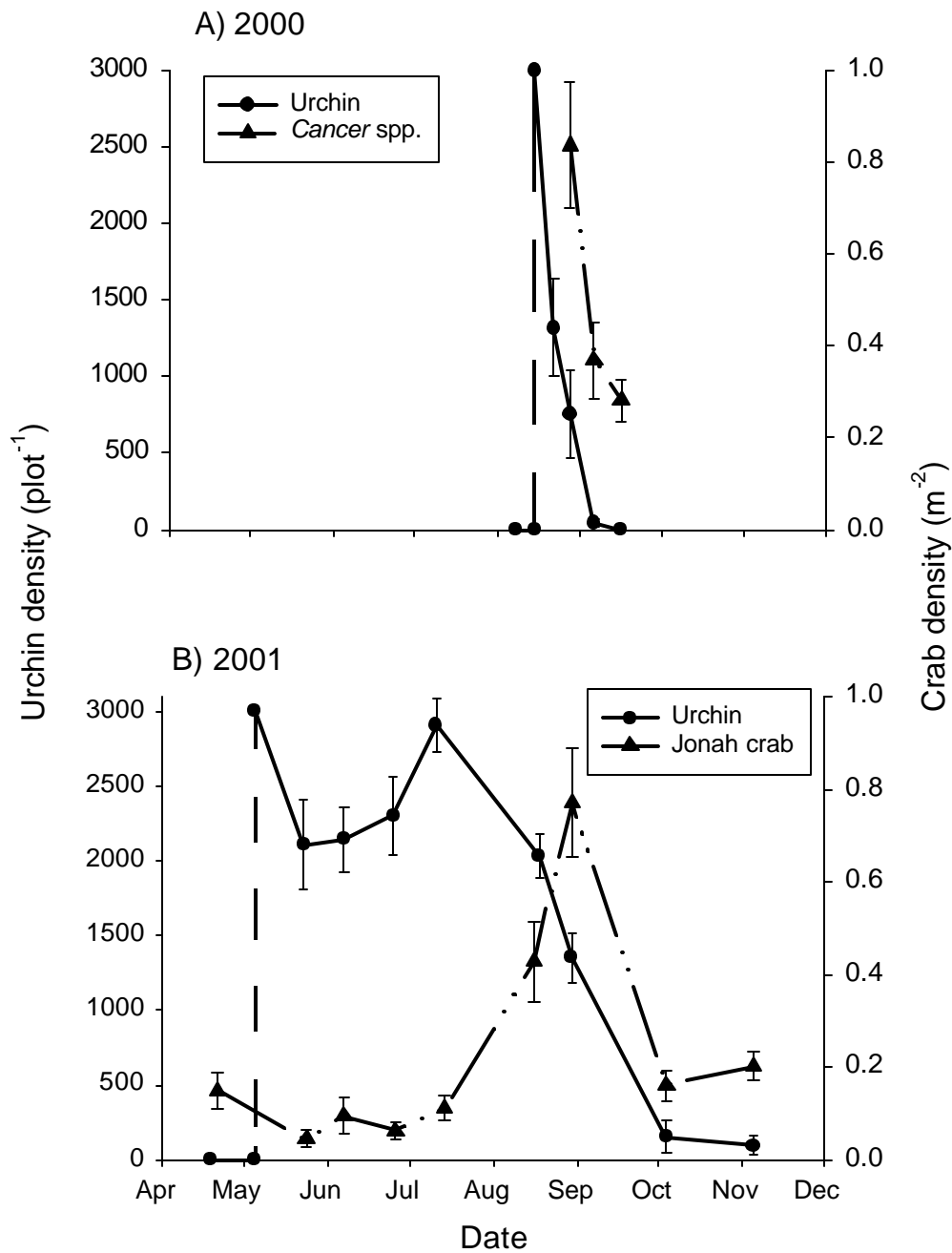
**A) 2000**

Source	df	MS	F	<i>p</i>
Replicate	3	10.735	0.02	0.9944
Algae	1	82.716	0.18	0.7028
Error 1: Replicate × Algae	3	468.995	3.67	<b>0.0277</b>
Time	3	2230.93	17.46	<b>0.0001</b>
Algae × Time	3	11.988	0.09	0.9626
Error 2	22	127.751		

**B) 2001**

Source	df	MS	F	<i>p</i>
Replicate	3	156.796	2	0.2920
Algae	1	288.583	3.68	0.1509
Error 1: Replicate × Algae	3	78.452	1.32	0.2797
Time	7	3151.752	52.98	<b>0.0001</b>
Algae × Time	7	78.125	1.31	0.2657
Error 2	46	59.49		

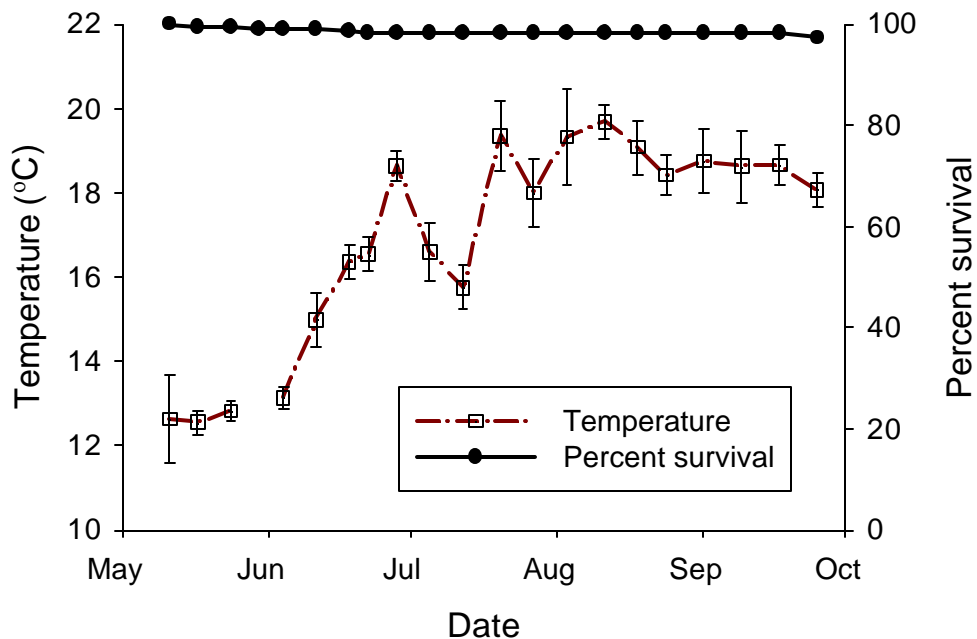
*Notes:* Data met normality (Shapiro-Wilk test) and homogeneity of variance (Levene Median test) assumptions. Boldface *p* values indicate significance at  $\alpha = 0.05$ .



**Fig. 4:** Urchin and crab population trends at Cape Elizabeth, ME in A) 2000 and B) 2001. Data were pooled for fleshy algae treatments (+ A, - A) (n = 8 in 2000 and n = 9 in 2001). Error bars are  $\pm 1$  SE. (A) *Cancer* spp. density is reported. (B) Only Jonah crab (*C. borealis*) density is reported. The hatched portion of the urchin trends denotes the time when 3000 urchins were relocated to each plot.

### Handling mortality

The survival of sea urchins relocated to the laboratory and maintained in predator-free, controlled conditions remained high throughout the experiment in 2001. On average, less than 3% of 186 sea urchins in each aquarium ( $n = 7$ ) died from May through September despite water temperatures approaching 20°C (Fig. 5).



**Fig. 5:** Percent survival of relocated sea urchins maintained under controlled conditions and flowing seawater temperatures ( $n = 7$  aquaria with 186 urchins each) in 2001. Error bars are  $\pm 1$  SE.

### Urchin grazing

Rates of herbivory were high enough in the urchin relocation areas (+ U) in 2001, so that fleshy algae were grazed down and maintained at low percent cover. Fleshy algal cover was high ( $> 80\%$ ) in the border areas of all plots in July 2001 (Table 2A, Fig. 6A) and was used as a paired control for each plot. Low fleshy algal cover in the center areas of plots when compared to their border areas was due to treatment differences in the initial fleshy algal (+ A, - A) and urchin abundances (+ U, - U) (Table 2B), but plots with urchins (+ U) showed the largest paired differences in algal cover (center subtracted from border; Fig. 6B) regardless of the initial fleshy algal cover.

Urchin population densities declined by mid-August 2001 (Fig. 4B). Herbivory undoubtedly declined as well. By October 2001 urchins were functionally absent, and macroalgae were regrowing in the central areas of plots that had received relocated urchins (+ U) (personal observation).

**Table 2.** ANOVA tables of the percent cover of fleshy algae in July 2001. A) Percent cover of fleshy algae in border areas alone. B) Paired differences between the percent cover of fleshy algae (arcsine-transformed) in the center versus the border areas. Replicates were blocks for treatments. Treatments were the presence or absence of urchins (+ U, - U) and fleshy algae (+ A, - A) in the center areas (see Fig. 2) at the beginning of each trial.

A) Borders only

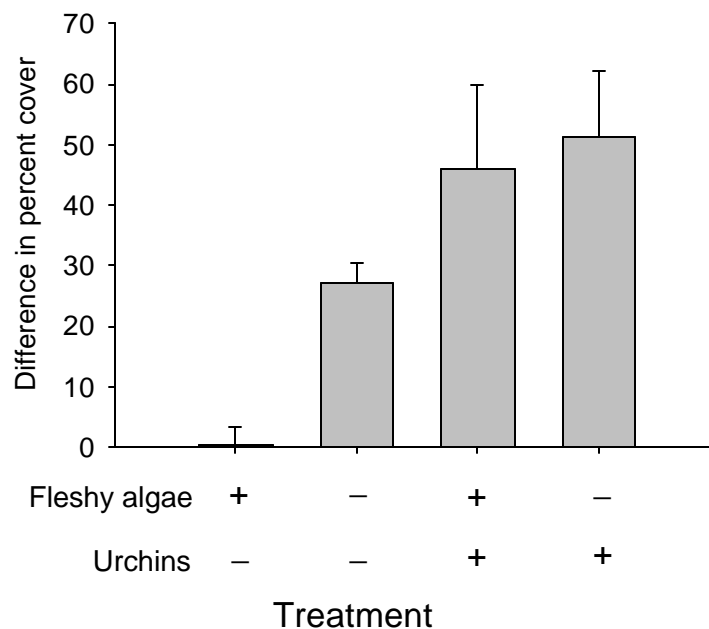
Source	df	MS	F	<i>p</i>
Replicate	3	369.1050	1.47	0.2868
Urchin	1	722.9298	2.88	0.1239
Algae	1	1081.4632	4.31	0.0677
Urchin × Algae	1	52.3072	0.21	0.6588
Error	9	250.9338		

B) Paired differences between borders and centers

Source	df	MS	F	<i>p</i>
Replicate	3	0.00066	2.75	0.1046
Urchin	1	0.00301	12.5	<b>0.0064</b>
Algae	1	0.00146	6.05	<b>0.0362</b>
Urchin × Algae	1	0.00007	0.29	0.6052
Error	9	0.00216		

Notes: Data met normality (Shapiro-Wilk test) and homogeneity of variance (Levene Median test) assumptions. Boldface *p* values indicate significance at  $\alpha = 0.05$ .

**Fig. 6:** Percent cover of all fleshy macroalgae in the border areas of plots only (A) and the paired difference in the central versus border areas of plots (B) in July 2001. Treatments are noted as having an initial presence (+ U) or absence (- U) of relocated urchins and fleshy macroalgae in the central area at the beginning of the experiment in March. Error bars are  $\pm 1$  SE.

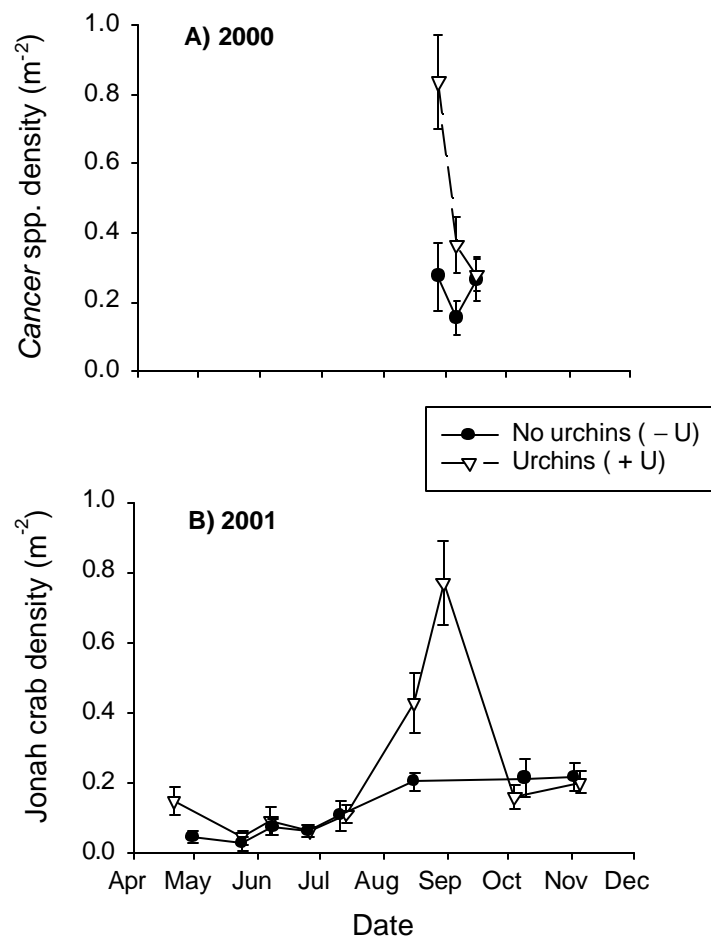


## Predatory crab populations

### Demographic patterns

In 2000, divers observed crabs (*Cancer* spp.) feeding on sea urchins one week after the relocation of sea urchins, but they were unable to determine if crabs were actively preying on or scavenging unhealthy urchins. Crab density surveys were then conducted two, three and four weeks following relocation and revealed declining *Cancer* spp. abundances ( $0.8 \text{ m}^{-2}$  to  $0.3 \text{ m}^{-2}$ ) at plots with urchins (+ U) concomitant with declining urchin populations (Fig. 4A). In contrast, crab densities at plots without urchins (- U) were similar ( $0.25 \text{ m}^{-2}$ ) for the three sampling dates (Fig. 7A). The greatest crab densities ( $0.8 \text{ m}^{-2}$ ) were observed at plots with urchins on 28 August (Fig 6A). Crab (*Cancer* spp.) densities were similar at all plots ( $0.3 \text{ m}^{-2}$ ) once all urchins were absent. When summed across all sampling dates, crabs were significantly more abundant at plots that did not have fleshy algae initially (- A) when compared to plots that did (Table 3A). In addition, crab abundances totaled over all sampling dates were significantly higher for plots with urchins (+ A) than those without. No significant Urchin  $\times$  Algae interaction was detected for crab densities summed over all sampling dates in 2000.

**Fig. 7:** Crab densities at plots with (+ U) and without urchins (- U) in 2000 (A) and 2001 (B) at Cape Elizabeth, ME. (A) *Cancer* spp. density is reported. (B) Only Jonah crab (*C. borealis*) density is reported. Data were pooled for fleshy algae treatments (+ A, - A) such that in A)  $n = 8$  for plots both with and without urchins (+ U, - U) and in B)  $n = 9$  at plots with urchins (+ U) and  $n = 7$  at plots without urchins (- U). Error bars are  $\pm 1$  SE.



**Table 3.** ANOVA tables of crab abundance summed over the entire sampling period (log-transformed data) for two trials. A) *Cancer* spp. abundance in 2000. B) *Cancer borealis* abundance in 2001. C) *Cancer irroratus* abundance in 2001. Replicates were blocks for treatments. Treatments were the presence or absence of urchins (+ U, - U) and fleshy algae (+ A, - A) in the center areas (see Fig. 2) at the beginning of each trial.

A) *Cancer* spp. in 2000

Source	df	MS	F	<i>p</i>	
Replicate	3	0.215	8.22	<b>0.0061</b>	
Urchin	1	0.656	25.1	<b>0.0007</b>	+ U > - U
Algae	1	0.248	9.47	<b>0.0132</b>	- A > + A
Urchin × Algae	1	0.065	2.48	0.1498	
Error	9	0.026			

B) Jonah crabs in 2001

Source	df	MS	F	<i>p</i>	
Replicate	3	0.005	0.22	0.8825	
Urchin	1	0.416	17.1	<b>0.0025</b>	+ U > - U
Algae	1	0.009	0.37	0.5585	
Urchin × Algae	1	0.016	0.64	0.4435	
Error	9	0.024			

C) Rock crabs in 2001

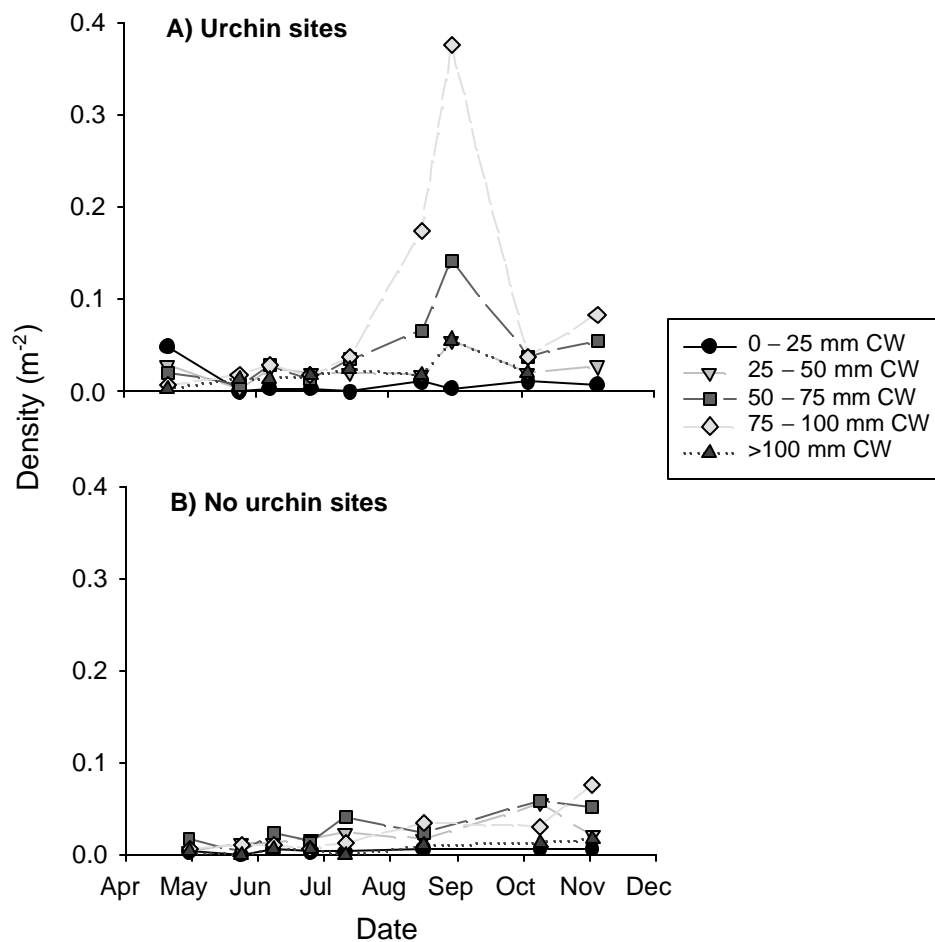
Source	df	MS	F	<i>p</i>
Replicate	3	0.0027	1.34	0.3211
Urchin	1	0.0077	3.83	0.0820
Algae	1	0.0002	0.12	0.7388
Urchin × Algae	1	0.0003	0.14	0.7202
Error	9	0.0020		

Notes: Data met normality (Shapiro-Wilk test) and homogeneity of variance (Levene Median test) assumptions. Boldface *p* values indicate significance at  $\alpha = 0.05$ .

In 2001, the decline in sea urchin abundances in August coincided with an increase in Jonah crab densities (Fig. 4B) and diver observations that Jonah crabs were feeding on the urchins. While urchin abundances were high (2100 plot<sup>-1</sup> to 2900 plot<sup>-1</sup>) from May through mid-July, Jonah crab densities were low (0.1 m<sup>-2</sup>) at all plots. Crab densities peaked at 0.78 m<sup>-2</sup> by the end of August only at plots with declining urchin abundances (+ U), and they remained low (0.2 m<sup>-2</sup>) at plots without urchins (- U; Fig. 7B). Jonah crab densities were low again (0.2 m<sup>-2</sup>) at all plots by early October when urchins were scarce (100 plot<sup>-1</sup>; Figs. 3B & 6B). Jonah crab

densities summed over all sampling dates were significantly greater at plots with urchins (+ U) than without (Table 3B) but differences were not detected for the initial presence or absence of algae (+ A, - A) and an Urchin  $\times$  Algae interaction.

The Jonah crab population density peak in August 2001 at the plots with urchins was composed primarily of individuals between 75-100 mm CW (Fig. 8). Densities of Jonah crabs in this size range peaked at  $0.4 \text{ m}^{-2}$  in August but were less than  $0.1 \text{ m}^{-2}$  in all other months. The density of Jonah crabs between 50-75 mm CW also peaked in August ( $0.15 \text{ m}^{-2}$ ) despite densities less than  $0.05 \text{ m}^{-2}$  in every other month.

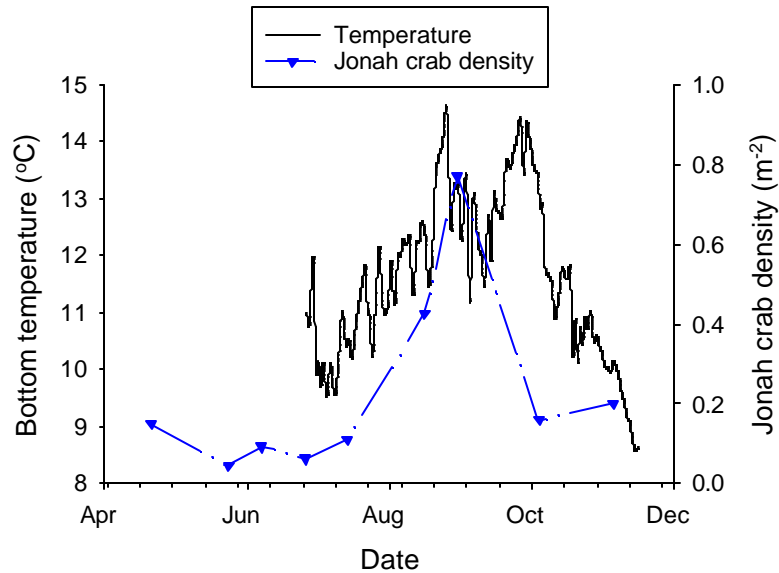


**Fig. 8:** Average density of Jonah crabs in 25 mm carapace width (CW) size bins at plots with urchins (A) and plots without urchins (B) at Cape Elizabeth, ME in 2001. Data were pooled for fleshy algae treatments (+ A, - A; (A) n = 9 and (B) n = 7).



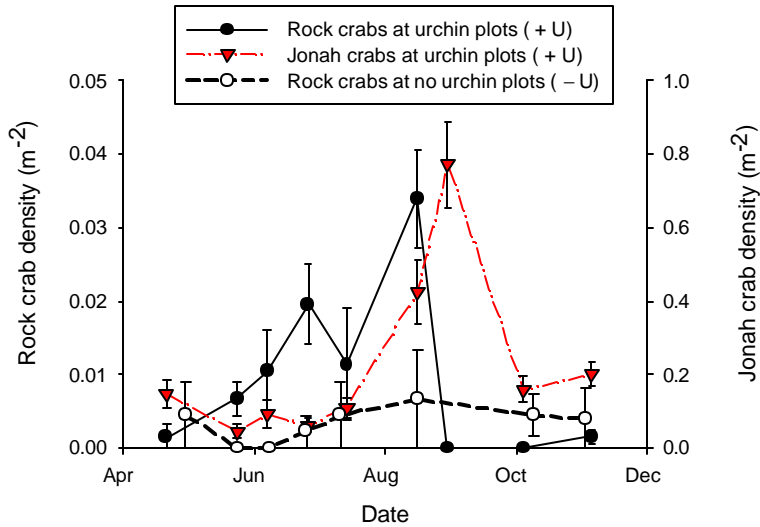
Increases in Jonah crab densities in 2001 occurred when bottom water temperatures were warming (Fig. 9). Water temperature and Jonah crab density peaked in late August (14.5 °C and 0.78 m<sup>-2</sup>, respectively; Fig. 9). Water temperature was high again in late September (14.2 °C). In early October, Jonah crab densities were low (0.2 m<sup>-2</sup>) but water temperatures were still relatively high (13.5 °C).

**Fig. 9:** Average Jonah crab density at plots with urchins (+ U, - U) and bottom water temperature at Cape Elizabeth, ME in 2001.



Rock crab densities remained relatively low for the duration of the experiment in 2001 (Fig. 10). Rock crab density was greatest (0.035 m<sup>-2</sup>) in mid-August at plots with relocated urchins (+ U) and was not composed of a distinct size class (Figs. 9 & 10). Declines in rock crab abundance at plots with urchins (+ U) in late August occurred when Jonah crabs were most abundant (Fig. 10). Total rock crab abundance at each plot (summed across all sampling dates) did not differ significantly based on the initial presence or absence of fleshy algae (+ A, - A), the presence or absence of relocated urchins (+ U, - U), or an Urchin × Algae interaction (Table 3C).

**Fig. 10:** Temporal trends in rock crab densities at plots with urchins (+ U) and without urchins (- U) and Jonah crab densities at plots with urchins (+ U) at Cape Elizabeth, ME in 2001.



#### Crab predation rates

Jonah crab predation rates on relocated sea urchins differed significantly over time in 2001 but not between plots initially with and without fleshy algae (+ A, - A) (Table 4). Per capita predation rates pooled for all plots with urchins (+ U) were greatest in late August (2.37 urchins · crab<sup>-1</sup> · d<sup>-1</sup>) but were not significantly different from predation rate estimates from 14 July to 16 August and from 30 August to 4 October (~ 1.5 urchins · crab<sup>-1</sup> · d<sup>-1</sup>; Tables 4 & 5). From October to November per capita predation rates of Jonah crabs significantly decreased to 0.22 urchins · crab<sup>-1</sup> · d<sup>-1</sup> (Tables 4 & 5).

**Table 4.** Repeated measures ANOVA of per Jonah crab predation rates on sea urchins (log-transformed data). Replicates were blocks for treatments. Treatments were the presence or absence of fleshy algae (+ A, - A) in the center areas (see Fig. 2) at the beginning of the experiment. Experimental units for Time are nested within those for Algae in a split-plot design.

Source	df	MS	F	p
Replicate	3	0.293	1.61	0.3533
Algae	1	0.734	4.02	0.1385
Error 1: Replicate × Algae	3	0.182	1.27	0.3093
Time	3	0.293	10.32	<b>0.0002</b>
Algae × Time	3	0.5	3.48	<b>0.0331</b>
Error 2	22	0.144		

Notes: Data met normality (Shapiro-Wilk test) and homogeneity of variance (Levene Median test) assumptions, except that per capita predation rates among replicates had heterogeneous variances. Boldface *p* values indicate significance at  $\alpha = 0.05$ .

**Table 5.** Per capita predation rates (urchins  $\cdot$  crab<sup>-1</sup>  $\cdot$  d<sup>-1</sup>) of Jonah crabs over time in 2001.

Sampling Interval	n	average	1 SE
14 July - 16 August	9	1.49	0.32
16 August - 30 August	9	2.37	0.66
30 August - 4 October	9	1.55	0.54
4 October - 5 November	9	0.22	0.16

### Sea urchin post-settlement survival

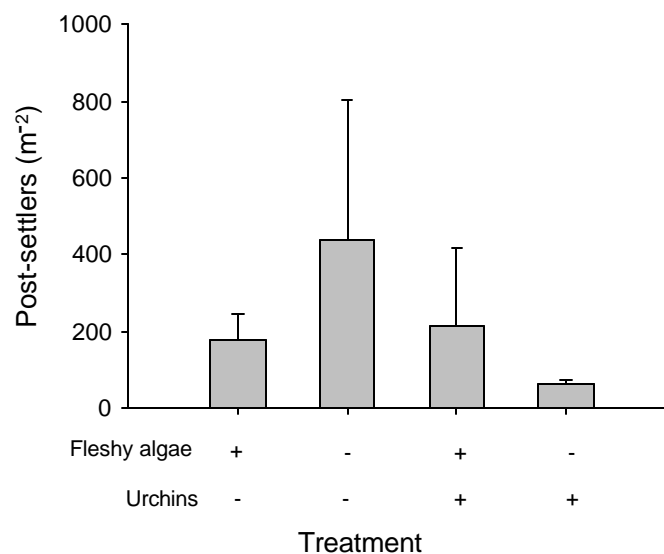
Urchin post-settler densities did not significantly vary by treatment (Table 6). On average, the most post-settlers were found at plots that initially did not have algae or urchins (- A, - U; Fig. 11). In contrast, average post-settler density was lowest at plots that did not have algae initially but did have urchins (- A, + U).

**Table 6.** ANOVA table of sea urchin post-settler densities at Cape Elizabeth in the winter following summer 2001 settlement. Replicates were blocks for treatments. Treatments were the presence or absence of urchins (+ U, - U) and fleshy algae (+ A, - A) in the center areas (see Fig. 2) at the beginning of the trial.

Source	df	MS	F	p
Replicate	2	5.666906	1.59	0.2916
Urchin	1	6.385502	1.79	0.2380
Algae	1	0.319516	0.09	0.7765
Urchin $\times$ Algae	1	2.839502	0.80	0.4126
Error	5	3.558274		

*Notes:* Data met normality (Shapiro-Wilk test) and homogeneity of variance (Levene Median test) assumptions. Boldface *p* values indicate significance at  $\alpha = 0.05$ .

**Fig. 11:** Densities of post-settled sea urchins sampled in the winter following summer 2001 settlement. Treatments were the presence or absence of urchins (+ U, - U) and fleshy algae (+ A, - A) in the center areas (see Fig. 2) at the beginning of the trial.



## DISCUSSION

### **Sea urchin grazing controlled benthic fleshy algae populations.**

Grazing by green sea urchins induced a benthic phase-shift from a fleshy macroalgal community to a coralline barrens within three months in 2001. The impact of sustained urchin grazing appeared to be equally effective (~ 50% decrease in fleshy algae) regardless of whether the plot had fleshy algae or not (+ A, - A) prior to the relocation of urchins (Fig. 6B). We observed relatively few urchins (< 25) in the borders of each plot, and most of the urchins in the center of plots were covered with drift algae in July (personal observation). This coupled with similarities in the percent cover of fleshy algae in the border areas of plots in July suggests that urchins did not move far into the surrounding algal bed because food was not limiting (Mattison et al. 1977, Harrold and Reed 1985).

Grazing rates probably would not have declined during the summer and early fall had sea urchin populations remained stable. In the laboratory, urchin grazing rates declined at high temperatures (> 17°C) but otherwise were temperature insensitive (13°C to 17°C; Leland 2002). Average daily bottom water temperatures at Cape Elizabeth from late July through early October stayed within a 12°C to 14.5°C range (Fig. 9), therefore suggesting that changes in herbivory during this time were not influenced by water temperature.

### **Sea urchins survived hand harvesting methods.**

There was probably little mortality associated with harvesting and handling of sea urchins during relocation to Cape Elizabeth, ME in 2001. Sea urchins survived for over two months *in situ* following relocation and for the entire sampling period (five months) in predator-free laboratory tanks (Figs. 4 & 5). Moreover, these urchins showed no obvious signs of stress (e.g. darkened spots on the epidermis and loss of spines). These results suggest that another agent of mortality was responsible for eliminating the relocated sea urchins in both 2000 and 2001.

### **Crab predation controlled relocated sea urchin populations.**

#### *Jonah crab predation on relocated sea urchins*

Many pieces of evidence suggest that predatory control by crabs of relocated urchin populations occurred in August 2000. First, dramatic urchin mortality in August and September 2000 coincided with high crab (*Cancer* spp.) density (Fig. 4B). Second, there were more crabs at plots with urchins (+ U) than those without when urchin abundances were declining (Fig. 7B). Third, crab densities at plots with urchins (+ U) dropped from 0.8 m<sup>-2</sup> to 0.3 m<sup>-2</sup> once all urchins were extirpated. Fourth, we observed crabs feeding on the relocated sea urchins.

Predation by Jonah crabs probably extirpated relocated sea urchin populations in 2001. Despite differences in experimental designs in 2000 and 2001, the interactions were similar. Following four months of high survival of relocated urchins, intense mortality occurred in August and September which coincided with anomalously high Jonah crab densities and observations of Jonah crabs feeding on relocated sea urchins (Fig. 4A). High crab densities (0.8 m<sup>-2</sup>) on 28 August 2000 were similar to elevated Jonah crab densities (0.78 m<sup>-2</sup>) quantified on 30 August 2001, suggesting that the majority of crabs sampled in 2000 were Jonah crabs. There was relatively little change in Jonah crab density at plots without urchins (- U) throughout the experiment (Fig. 7B). Following a classic predator-prey oscillation, Jonah crab

densities declined as urchins became rare. The faster decline in urchin abundance in 2000 could have been due to differences in sizes of relocated urchins. Urchins were smaller in 2000 (35 mm to 45 mm TD) than in 2001 (all  $\geq 50$  mm TD; Fig. 3) and probably more easily preyed on by crabs (Juanes 1992). Subsequently, Jonah crab densities returned to similar values ( $0.2 \text{ m}^{-2}$ ) as were present from May through July at plots with urchins (+ U) and were present at plots without urchins (- U) throughout the experiment (Figs. 4B & 6B).

#### *Rock crab predation on relocated sea urchins*

Rock crabs were probably not an agent of measurable urchin mortality on urchins relocated to Cape Elizabeth. Although rock crabs appeared to be attracted to plots with urchins (+ U) until mid-August 2001 (Fig. 10), total rock crab abundance (summed over all sampling dates) was not significantly different at plots with and without urchins (+ U, - U; Table 4). Moreover, few rock crabs were observed at plots with urchins (+ U) after mid-August when urchin mortality was still high (Figs. 4 & 9). Rock crabs were rarely observed feeding on urchins throughout the experiment (personal observation). In addition, rock crab density was at least an order of magnitude less than Jonah crab density on most sample dates (Fig. 9).

#### *Non-resident, large Jonah crabs as dominant urchin predators*

Per capita predation rates of Jonah crabs on urchins relocated to Cape Elizabeth changed over time. Per capita predation rates increased while bottom water temperatures warmed and Jonah crab densities increased (Table 5, Fig. 9). Assuming that Jonah crabs were solely responsible for urchin mortality, individuals were feeding on over 2 urchins  $\cdot \text{crab}^{-1} \cdot \text{d}^{-1}$  on average in mid- to late August, when Jonah crabs were anomalously abundant. Per capita predation rates when Jonah crab densities were increasing and decreasing averaged about 1.5 urchins  $\cdot \text{crab}^{-1} \cdot \text{d}^{-1}$ . Because there was no sampling event in September, per capita predation rate was averaged over two months, which explains the larger variance for this interval. Nonetheless, average per capita predation rate of Jonah crabs may have been density dependent.

If all Jonah crabs were alike in their capacity (behavioral and mechanical) to prey on urchins, then no change in per capita predation rate was expected when density was varied, but instead changes in per capita predation rate occurred with changes in predator density. One possible explanation for increased per capita predation rate with crab density is that indirect positive interactions were operating as long as prey items were plentiful. Crustaceans are generally sensitive to the chemical stimuli of potential prey items (Finelli et al. 2000). Attacks on urchins may create 'scent' plumes that crabs can identify and seek out. As more predators are attracted to the urchins, more 'scent' is released making the stimulus stronger. Feeding response per predator may increase as more stimuli are released (Finelli et al. 2000), and any decline in per capita predation rate may be explained as competition among predators once prey became scarce. Results of a laboratory predation experiment examining Cancer crab predation on urchins (Leland 2002) suggest that waterborne urchin 'scent' probably did not stimulate predation on urchins at Cape Elizabeth because crab predation was not elicited in aquaria with urchin scented water.

A more likely explanation for per capita predation rate varying positively with Jonah crab density is that two different populations may have been present. As stated previously, there was a large influx of Jonah crabs to the plots with urchins (+ U) in August. Conversely there was no notable change in Jonah crab density at plots without urchins (- U) from April through

November. Therefore, we assumed that a resident population of Jonah crabs lives in the Cape Elizabeth area at a density of about  $0.15 \text{ m}^{-2}$  year round (Fig. 7). This density was close to that ( $0.10 \text{ m}^{-2}$ ) estimated by Palma *et al.* (1999) for Jonah crabs in the shallow subtidal zone of the Gulf of Maine in mid-summer. The crabs that preyed on the relocated urchins at Cape Elizabeth were probably non-residents with different predatory responses than the residents. This idea was supported by evidence that the majority of Jonah crabs at plots with urchins (+ U) were within the 75 - 100 mm CW size range in August only (Fig. 8) and were probably just reaching their first reproduction (Haefner 1977).

It is possible that different populations of crabs may have different foraging strategies. Resident crabs that are faced with the same food options everyday may have developed specialized prey handling capabilities, while migratory crabs may assume a more generalist feeding pattern as food choices change regularly with location (Micheli 1997). Evidence from predation studies in the laboratory suggest that individual crabs have different foraging histories that lead to different future feeding behaviors (Fig. 10, Ristvey and Rebach 1999, Hughes and O'Brien 2001). The same phenomenon might extend to the population level.

Evidence from previous studies support the hypothesis that some Jonah crabs migrate inshore in the late summer through early fall. Smith (1879) observed a drastic increase of intertidal Jonah crabs at Peak's Island, Maine (less than 4 nm from Cape Elizabeth) around the end of August and beginning of September. Likewise, Krouse (1979) measured a marked increase in Jonah crabs in August and September in the Boothbay Harbor, Maine region. Jonah crabs along the entire Northwest Atlantic shelf were collected in inshore trawl surveys more often in the fall than spring (Stehlik *et al.* 1991). Jeffries (1966) attributed migration to deeper, warmer water to the low abundance of Jonah crabs in Narragansett Bay in winter. Smith (1879), Haefner (1977), Krouse (1979) and Stehlik *et al.*, (1991), described late summer and fall inshore Jonah crab populations as dominated by females, while spring and early summer populations were composed mostly of males. Krouse (1979) suggested that this seasonal demographic shift is due to molting and copulation behaviors. But despite the preponderance of evidence supporting a migration hypothesis, no one has tested it directly.

Bottom water temperature was an environmental parameter that may have confounded the relationship between per capita predation rate and predator density. Changes in bottom water temperature tracked slightly with changes in per capita predation rate and density of Jonah crabs in the 75 - 100 mm CW size range (Figs. 8 & 9, Table 5) and may have affected both of these responses. Ambient water temperature has been shown to affect crab feeding rate (Elner 1980, Sanchez-Salazar *et al.* 1987), but there is limited evidence describing Jonah crab migration as temperature dependent (Jeffries 1966). The possibility that all Jonah crabs (both residents and non-residents) may have had elevated per capita predation rates in August due to increased water temperature cannot be ruled out, but water temperature alone may not sufficiently explain the increased per capita predation rate in August. For example, Leland (2002) observed distinct differences in Jonah crab feeding behavior (e.g. predatory and scavenger) in relatively warm water.

The importance of Jonah crabs as urchin predators appears to be largely seasonal. Whether bottom water temperatures (Jeffries 1966) or ambient light levels (Rebach 1987) drive migration, seasonality at least positions Jonah crabs in the same nearshore, shallow subtidal habitats as urchins for some period of time. This opens up the possibility of urchins as possible prey items for the non-resident crabs. While predation may be short-lived (e.g. August and September), it has a disproportionately large impact on the benthic community.

### **Sea urchin recruitment was not enhanced.**

Sea urchin post-settler densities were not enhanced following the relocation of adult sea urchins (Fig. 11). Post-settler densities did not vary consistently by replicate, initial algal cover (- A + A) or urchin abundance (- U + U; Table 6). Algal cover was low at plots with relocated urchins (+ U; Fig. 6) when urchin settlement probably peaked ((Lambert and Harris 2000), therefore we expect that post-settler survival was high because micropredator densities perhaps were low (McNaught 1999). By October, fleshy algae were regrowing following massive urchin mortality (personal observation), which may have led to increased micropredator densities and predation on urchin post-settlers. Therefore, any significant increase in post-settlement survival due to decreased algal abundance in summer and early fall would have been masked by winter when we sampled for urchin post-settler densities.

## **CONCLUSIONS**

Reintroducing adult sea urchins did not lead to the long-term reestablishment of urchin populations. In a few months, predation by non-resident Jonah crabs effectively extirpated 24,000 urchins in 2000 and 27,000 urchins in 2001, and in so doing eliminated the dominant benthic herbivores from this system twice. Crabs are size-dependent predators (Moody and Steneck 1993), but no urchin size class (35 – 71 mm TD) was too large for these crabs. The extirpation of grazers resulted in the recreation of an algal-dominated system. Presumably this system will be perpetuated due to *Cancer* spp. predation on urchins of all sizes. The strength of this interaction in other regions and other habitats (e.g. barrens) along the Maine coast remains uncertain, but the population distributions of Jonah crabs and urchins largely overlap (Leland 2002) so it is likely to be widespread. Moreover, Jonah crab abundance in the Gulf of Maine has increased four-fold in the last two years (Leland 2002) and a continued increase may lead to more urchin mortality due to Jonah crab predation. In vast areas of Maine, intense fishing has altered the benthic ecosystem so much that recovery of sea urchins seems impossible.

We recommend that urchin fishery managers and the Sea Urchin Zone Council act quickly to conserve what is left of this resource. Urchin population decreases are still initiating phase-shifts to algal beds in regions east of Penobscot Bay (J. Vavrinc, unpublished data). Based on the results presented herein and those found earlier we expect that recovery of urchin populations in these regions also will be prevented by crab predation. Thus, harvesting effort should be managed to maintain the ecological function of herbivory if this resource is to be harvested sustainably. In addition, we recommend that the fishery population models that are used to determine harvesting effort account for increased mortality rates in urchin-depleted areas. In these areas, the proportion of total mortality shifts from being primarily fisheries-based (i.e., “F”) to being primarily natural mortality (“M”). For this fishery in particular, we cannot assume that a release from harvesting pressure will result in an increase in the urchin resource over time.

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