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Amanda V. Leland

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A NEW APEX PREDATOR IN THE GULF OF MAINE?
LARGE, MOBILE CRABS (*CANCER BOREALIS*)
CONTROL BENTHIC COMMUNITY STRUCTURE

By

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B.S. Purdue University, 1999

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

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(in Marine Biology)

The Graduate School

The University of Maine

December, 2002

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Thesis Advisor: Dr. Robert S. Steneck

An Abstract of the Thesis Presented
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Apex predators can control community structure by preying on strongly interacting species at lower trophic levels. Fishing of apex predators in the marine realm often results in herbivore dominated systems. In the Gulf of Maine, coastal subtidal communities became dominated by grazing green sea urchins (*Strongylocentrotus droebachiensis*) following the extirpation of large, predatory groundfish from coastal zones. Subsequent depletion of sea urchins since the late 1980s functionally eliminated this dominant herbivore from vast regions. Sea urchin recruitment is low or nonexistent in communities dominated by fleshy algae that have developed since the decline of sea urchin populations. We hypothesized that sea urchin populations would be restored if grazing pressure resumed.

We moved adult sea urchins to a site where they had been abundant but were virtually absent by the late 1990s. During a two year study, 51,000 urchins were relocated to the shallow subtidal zone at Cape Elizabeth, ME (3000 urchins (35 – 45 mm

test diameter) to 8 replicate plots in 2000, and 3000 urchins (50 – 71 mm test diameter) to 9 replicate plots in 2001). We monitored population changes in fleshy algae, urchins and urchin predators. Urchin grazing denuded fleshy algae from May through July in 2001, while crab predator (*Cancer* spp.) abundances remained low. In August and September, predation by migratory populations of large Jonah crabs (*C. borealis*) decimated relocated urchin populations and restored fleshy-algal dominance at these locations. In laboratory experiments, we confirmed that sea urchin grazing decreases algal biomass and that Jonah crabs are stronger sea urchin predators than rock crabs (*C. irroratus*).

Historical and present-day evidence describes Atlantic cod (*Gadus morhua*) and other groundfish as important Jonah crab predators. NMFS trawl data showed a 4-fold increase in Jonah crab abundance in 2000 and 2001 in the Gulf of Maine which may be related to a continuing decline in Gulf-wide fish predator populations. We speculate that highly mobile Jonah crabs at high densities may have become apex predators since their release from predatory control by groundfish (e.g. cod) in some shallow subtidal zones of the Gulf of Maine.

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INTRODUCTION

Predation is a top-down force that can exert strong control over community structure (Hairston et al. 1960, Paine 1969, Power 1992, Menge 1995, Pace et al. 1999, Polis et al. 2000, and see reviews in Schmitz et al. 2000, Terborgh et al. 2001). Hairston et al. (1960) hypothesized that the world is vegetated because predators limit herbivore abundance. This paradigm of predator control was seemingly at odds with observations of sea urchins dominating subtidal marine systems in which macroalgae and most highly edible seaweeds were rare (Kitching and Ebling 1961, Paine and Vadas 1969, Himmelman and Steele 1971, Camp et al. 1973, Ogden et al. 1973, and reviewed in Lawrence 1975, Scheibling 1986, Fujita 1998, Macia and Lirman 1999). Sea urchin grazing often induces a benthic phase shift (*sensu* Done 1992) from a community dominated by fleshy macroalgae to one with crustose-coralline algae (also called ‘barrens’) or corals (Himmelman and Steele 1971, Carpenter 1981, Sammarco 1982, Scheibling 1986). But in accordance with the “vegetated world” hypothesis of Hairston et al. (1960), the strong role of predators in regulating urchin demography could not be overlooked (Muntz et al. 1965, Mann and Breen 1972, Estes and Palmisano 1974).

‘Apex predator’ species are not subject to predation themselves and shape the structure of the community by preying on species at lower trophic levels. Sea otter (*Enhydra lutris*) predation on sea urchins (*Strongylocentrotus* spp.) in the northeast Pacific is a well known large-scale example of an apex predator species controlling shallow subtidal community structure by preying on dominant herbivores (Estes and Palmisano 1974, Simenstad et al. 1978, Estes and Duggins 1995, Estes et al. 1998). In

addition, fishes have been cited as apex predators of sea urchins in the Mediterranean (Sala and Zabala 1996, Sala 1997), Caribbean (Carpenter 1984), western Indian Ocean (McClanahan and Muthiga 1989), eastern North Pacific (Cowen et al. 1982), and western North Atlantic (Keats et al. 1987, Ojeda and Dearborn 1991, Vadas and Steneck 1995).

Historical and present-day evidence suggests that Atlantic cod (*Gadus morhua*) and other predatory groundfish were apex predators in nearshore regions of the Gulf of Maine in the western North Atlantic (Witman and Sebens 1992, Vadas and Steneck 1995, Jackson et al. 2001, Steneck et al. 2003). Fleshy macroalgae were abundant in the shallow subtidal and intertidal zones (Johnson and Skutch 1928b, a) before coastal cod populations were functionally extirpated in the 1930s (Steneck 1997). By the 1960s, the shallow subtidal zone of the Gulf of Maine was a mosaic of coralline barrens dominated by sea urchins (*Strongylocentrotus droebachiensis*) and kelp beds (W. Adey, personal communication). Grazing by sea urchins continued to dominate benthic communities such that by the 1980s ‘barrens’ were prominent and sea urchins became viewed as pests (Pringle et al. 1980). Intense commercial fishing of this sea urchin since 1987 has extirpated *S. droebachiensis* in large regions (J. Vavrinec, unpublished data, McNaught 1999.). Urchin populations have not recovered despite over 5 years without fishing and an abundant larval supply (J. Vavrinec, unpublished data). Micropredation by amphipods, and newly settled and juvenile cancerid crabs on settling sea urchins prevents their recruitment in fleshy algae beds and perpetuates an urchin-free state (McNaught 1999). These regions in the Gulf of Maine have once again become vegetated but this time probably due to the removal of dominant species (e.g. cod and sea urchins) by intense fishing pressure.

In this study, we initially set out to test the hypothesis that sea urchin populations would be restored if grazing pressure was reinstated (i.e., we did not test the hypothesis indicated in the title). We theorized that urchin recruitment would recover following a decline in fleshy algae because micropredators would be rare. In a large-scale field experiment, we relocated adult sea urchins to an area where they had been extirpated, and we monitored changes in algal, urchin, and urchin predator populations. Surprising results from the first urchin relocation revealed strong predation on adult urchins by large *Cancer* spp. Thus, we modified our objectives to include describing the role of predation by rock and Jonah crabs (*Cancer irroratus* and *C. borealis*, respectively) on relocated sea urchin populations. Laboratory experiments examining urchin grazing rates on kelp (*Laminaria saccharina*) and predation rates of rock and Jonah crabs on urchins were conducted to validate our field results. We also examined Gulf-wide Jonah crab demographic patterns to highlight the possible importance of crab predation in controlling urchin populations at both spatial and temporal scales.

METHODS

Patterns of a trophic cascade

Study site

Field experiments were conducted at Cape Elizabeth, ME (N 43°34.0', W 70°11.5') in 2000 and 2001 (Fig. 1). Study plots were located along two ledge systems that run northeast from the eastern edge of Cape Elizabeth at depths ranging from 9m - 15m. Each plot was 100 m from its nearest neighbor and sand channels and shore provided lateral buffer zones. Bottom water temperatures were recorded every 30 minutes from 26 June to 14 November 2001 at one plot using calibrated temperature loggers (Hobo-temp, Onset Corp., Pocasset, MA, USA).

The area was characterized by common Gulf of Maine flora and fauna. The species composition of algae was similar at all plots and included canopy forming species: *Laminaria saccharina*, *Laminaria digitata*, *Agarum clathratum*, *Desmarestia viridis*; understory species: *Chondrus crispus*, *Callophyllis cristata*, *Phycodrys rubens*, *Ptilota serrata*, *Polysiphona* spp., *Bonnemaisonia hamifera*, *Ceramium nodosum*, *Corallina officinalis*; and encrusting algae: *Hildenbrandia rubra*, *Lithothamnion* spp., *Phymatolithon* spp., *Clathromorphum circumscriptum*. Horse mussels (*Modiolus modiolus*), seastars (*Asterias* spp. and *Henricia sanguinolenta*), American lobsters (*Homarus americanus*), rock crabs (*Cancer irroratus*), Jonah crabs (*C. borealis*), pollock (*Pollachius virens*), and a few cunner (*Tautoglabrus adspersus*) composed the macroinvertebrates and fishes that were most commonly seen during sampling. According to local urchin harvesters this area had large urchin populations historically,

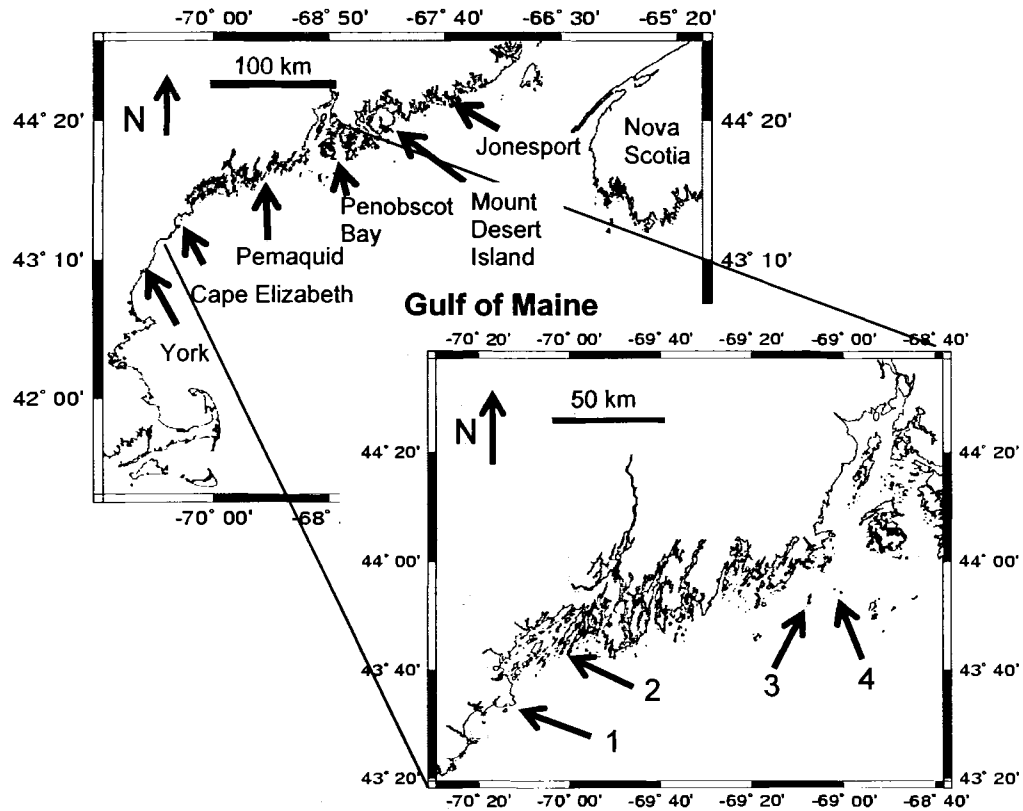


Figure 1: Regions of the Gulf of Maine and sea urchin collection sites. Sea urchin collection sites were: (1) West Cape Elizabeth and Richmond Island, (2) Land's End and Jaquish Ledge, (3) Metinic Island and (4) Large Green Island.

but our initial surveys in both years found none. In January 2001, the Maine Department of Marine Resources closed a large region surrounding and including Cape Elizabeth to urchin harvesting for five years.

Sea urchin relocation experiment

To determine if sea urchin populations would recover following restoration of grazing pressure, we quantified the survival of sea urchins after relocation to Cape Elizabeth 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 to also include quantifying predatory crab (*Cancer* spp.) abundances. Sea urchin recruitment was quantified but are presented elsewhere (Leland et al. 2002), because high levels of adult urchin mortality in both trials presumably ended grazing control of fleshy algal beds which probably allowed recolonization of juvenile sea urchin predators.

The urchin relocation experiment was set up as a randomized block design such that each block was a replicate of all treatment combinations. One of each treatment combination was randomly assigned within each block. The experimental design included two urchin treatments (– U, + U) × two fleshy macroalgae treatments (– A, + A) × four replicates. In 2001, the design was unbalanced because one block 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 densities at plots with relocated urchins (+ U) and without (– U). In both trials, fleshy algae were removed (– A) from the central areas of plots (Fig. 2) using paint

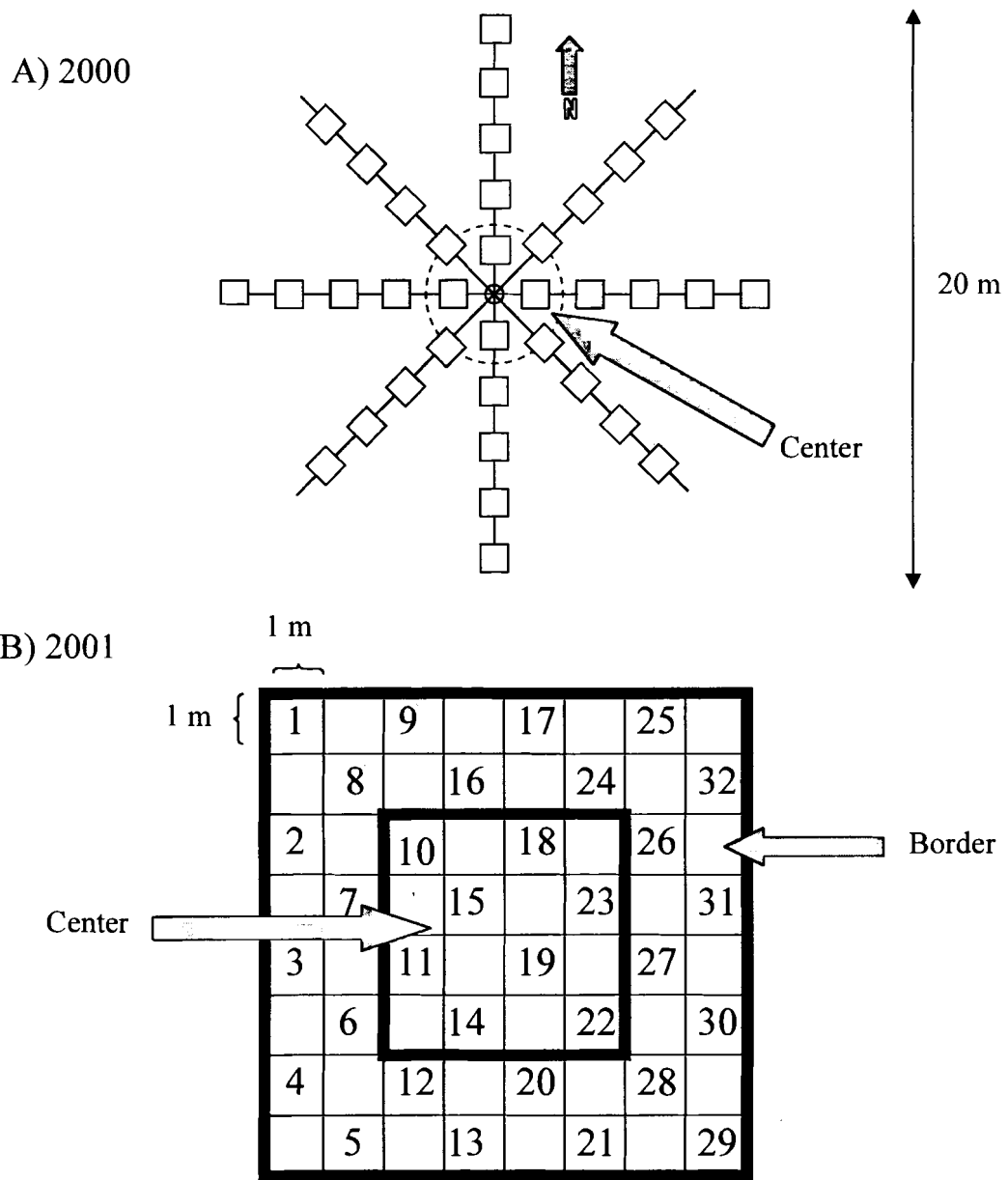


Fig. 2: Two sampling designs at Cape Elizabeth in years 2000 (A) and 2001 (B). A & B) Small squares represent 1 m^2 quadrats where urchin abundances were sampled many times. B) Percent cover of fleshy algae was sampled in all unnumbered quadrats in July. The central 2.5 m radius circle (A) was cleared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

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 previously (– 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.

The experiment was conducted 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, \geq 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 m³ 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 m² area of the two southernmost plots on 26 April and the rest of the plots on 4 May.

Sea urchins (n = 186) that were haphazardly subsampled from those collected at Large Green Island on 4 May 2001 and brought to the Flowing Seawater Lab at the Darling Marine Center 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 haphazardly 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 m² quadrats that were placed regularly along radial transect lines separated by 45° (n = (36) 1 m² quadrats per plot; Fig. 2A). In 2001, urchins, Jonah crabs and rock crabs at each plot were tallied in 1 m² quadrats placed regularly in a 64 m² sampling grid (n = (32) 1 m² quadrats per plot; numbered quadrats in Fig. 2B). Jonah and rock crabs were measured (carapace width (CW) in 5 mm size bins) in 2001.

Macroalgal 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 m² quadrats (McNaught 1999). Algal percent cover was assessed in quadrats placed regularly in both the border areas (n = (24) 1 m² quadrats) and center areas (n = (12) 1 m² quadrats) of plots (all unnumbered quadrats in Fig. 2B).

Per capita Jonah crab predation rates

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 plot⁻¹ to m⁻² estimate. The change in average urchin density (m⁻²) between each of five consecutive sampling dates (14 July to

5 November) was divided by the change in average Jonah crab density (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 from 4 May until 25 September 2001. The temperature of each tank was assessed using a calibrated YSI meter when urchins were counted.

Data analyses

Statistical analyses were performed using the SAS version 6.07 (SAS Institute 1999) statistical package. Each year was analyzed as a separate experiment because the 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 abundance data for both years were square root transformed prior to analyses. Crab densities and per Jonah crab predation rate 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 abundance was estimated repeatedly during both trials of the urchin relocation experiment. For each sampling date, the total number of urchins counted per

plot (half of total area) was doubled to estimate the density 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 either trial, 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 abundance was 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^2 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. No significant differences in the percent cover of fleshy algae in the border areas of all plots were detected 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 as 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 Jonah crab predation rate on urchins was 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. Significance levels were adjusted to $\alpha = 0.01$ to account for the nonrandom nature of the factor time. The variances of per Jonah crab predation rate among replicates were heterogeneous (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.

Quantifying processes

Urchin grazing rates

Grazing rates of urchins on kelp were determined experimentally at the Darling Marine Center, Walpole, ME. Fifteen urchins within a 50 to 60 mm TD size range were hand collected on 16 May 2001 from Pumpkin Cove, on the east side of Pemaquid Point, ME. Following collection, urchins were haphazardly placed into individual transparent aquaria with flowing seawater and constant aeration.

Laminaria saccharina, a common canopy-forming kelp, was offered to the urchins as food. At the start of the experiment, *L. saccharina* was collected from Pumpkin Cove, the floating dock at the Darling Marine Center (Damariscotta River), and off of anchor lines in the harbor. Following collection, fronds were cut into smaller pieces (about 60 g), epiphytes and conspicuous invertebrates were removed, and pieces were wet weighed. Wet weight was determined by lightly shaking (20 times) and weighing algae on a calibrated mass balance. Once the weights were recorded, algae were placed into each tank with an urchin. After 10 days, one urchin was removed permanently from three aquaria ($n = 12$ tanks with urchins, $n = 3$ tanks without urchins) to test for changes in algal biomass not associated with urchin grazing. All pieces of algae were reweighed and replaced at least every three weeks. Temperature was also recorded in each aquarium at least once a week using a YSI meter. Kelp replacement marked the beginning of a new trial. Six trials with both treatments (urchins and no urchins) were completed.

The average change in kelp biomass was estimated by subtracting the final kelp weight from the initial weight in each tank and dividing by urchin exposure time. Kelp

biomass differences in tanks without urchins were log-transformed, grouped by trial, and analyzed with a one-way ANOVA with trial as the main factor. No difference among trials was detected ($F_{5,12} = 1.38, p = 0.3358$), so kelp biomass difference estimates were pooled for all trials and averaged (0.0716 g of kelp). This average was subtracted from estimates of average change in kelp biomass in aquaria with urchins to control for alterations in algal biomass not due to grazing (e.g. growth). Grazing rate was regressed against temperature using SigmaPlot 5.00 (SPSS Corp.). Model assumptions of normality (Kolmogorov-Smirnov test) and homogeneity of variances (Levene Median test) were met.

Crab predation rates

Predation rates of rock and Jonah crabs on urchins also were estimated experimentally. Eighteen rock crabs, 18 Jonah crabs, and 150 urchins were collected on 4 August 2001 from Pumpkin Cove and under the Darling Marine Center floating dock. Urchin sizes ranged between 35 and 45 mm TD, and crabs were between 90 to 122 mm CW. Each crab was haphazardly assigned to one of 36 aquaria. Crabs had unknown feeding histories at the start of this experiment. Thirty six urchins were each assigned to an aquarium haphazardly, while the other urchins were placed in a holding tank to be used as replacements later in the study.

Aquaria were checked daily for temperature and evidence of crab predation on the available urchin. When an urchin was penetrated by a crab (either a cracked test or a hole in the peristomial membrane), it was collected from the aquarium and replaced with an urchin from the holding tank. Temperature was measured with a YSI meter everyday in

six randomly assigned aquaria. The main water valve broke on day 7 of the experiment which prevented observations from being made that day.

By day 19, it became apparent that some crabs were not even attempting to prey on the urchin, while others had preyed at least once and some were preying regularly. We refer to the crabs as having no history of urchin predation (never preyed) or a history of urchin predation (preyed at least once) throughout the study. We explored the role of chemical stimulation in crab feeding behavior by moving non-feeding crabs into the aquaria that had housed feeding crabs and vice-versa. Dead urchins were not replaced on days 20 and 21 of the experiment in order to allow for a longer soak of urchin scent in the aquaria. Aquaria had different levels of residual urchin scent when crabs were relocated due to the variation in time and flow rates since the last predation event. All crabs were relocated to the appropriate aquaria on day 21, and all predated urchins were replaced with healthy ones. Daily observations of the frequency of crab predation on urchins and temperature were made for 11 days.

To test for each crab's potential to actively feed (but especially those that had not preyed over the entire length of the experiment), urchins in all aquaria were cut in half with a knife on day 31. All aquaria were checked the next day for evidence of foraging on urchin soft tissue. We refer to crabs that foraged only on an urchin that was cut open for them as scavengers, and those that had preyed on an urchin at least once as predators.

Predation frequency was determined by the percent of the total number of crabs in each species that preyed each day. Two Jonah crabs were omitted from analyses because one molted and one died during the experiment. Predation frequencies of all crabs with unknown feeding histories, and crabs with and without a history of feeding on urchins

were regressed over time. Model assumptions of normality (Kolmogorov-Smirnov test) and homogeneity of variances (Levene Median test) were met.

The probability of predation was determined by regressing the probability of a predation event the next day against the number of previous predation events for each crab. The number of previous predation events was defined as previous sequential daily predation events. Also, the probability of predation was tested with regression using SigmaPlot 5.00 (SPSS Corp.). Model assumptions of normality (Kolmogorov-Smirnov test) and homogeneity of variances (Levene Median test) were met for the probability of Jonah crab predation, but variances of the probability of rock crab predation were heterogeneous (failed the Levene Median test). Therefore, the probability of rock crab predation should be interpreted with caution.

Patterns of Jonah crab distribution and abundance in the Gulf of Maine

NMFS bottom trawl surveys

Jonah crab and rock crab abundance data in fall bottom trawl surveys in the Gulf of Maine were collected and compiled by the NOAA/Northeast Fisheries Science Center, Woods Hole, MA (see Reid et al. 1999 for survey sampling design, execution, and efficiency). All surveys consisted of a stratified (depth and latitude) random sampling design. At each station, a bottom trawl (36 Yankee or similar) was deployed and towed for 30 min. at a speed of $6.5 \text{ km} \cdot \text{h}^{-1}$. All crabs, regardless of size, sampled from complete tows at all stations within the limits of N 41°00.0' to N 44°30.0' and W 66°00.0' to W 71°00.0' were included to quantify annual abundance since 1975.

Coastal submarine surveys

Jonah crab distribution and abundance was sampled at four regions in the Gulf of Maine ($n = 6$ at Pemaquid, $n = 5$ at Mount Desert Island, $n = 3$ at Jonesport, and $n = 6$ at Nova Scotia; Fig. 1) using submarine video transects (R/V *Edwin Link*, Harbor Branch Oceanographic Institute) in September, 1997. Video was taken at the 50 m to 120 m depth isobaths in these regions. Jonah crab density (m^{-2}) was determined by counting the total number of Jonah crabs in a transect line and dividing by the video path area (m^{-2}). Average density per region was pooled for all sampled depths, habitats, and crab sizes.

Shallow subtidal SCUBA surveys

Jonah crab and rock crab distribution and abundance were sampled in 1997 also by SCUBA divers in five regions of the Gulf of Maine (York, Pemaquid, Penobscot Bay, Mount Desert Island, Jonesport; Fig. 1). Sites and methods are described in Palma *et al.* (1999). Average Jonah crab density per region was pooled for all crab sizes but was sorted by habitat (e.g. sediment, boulder, and ledge).

RESULTS

Patterns of a trophic cascade

Interactions between relocated urchins and benthic fleshy algae

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 were ranged from 50 mm to 71 mm TD (Fig. 3).

Urchins were never observed at plots without relocated urchins (– U) during either trial. Urchin population densities 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). Urchin abundance did not depend on the percent cover of fleshy algae in 2001 (Table 1B). In 2001, urchin populations persisted for nearly 3 months prior to their decline.

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. 5A) and therefore was considered 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. 5B).

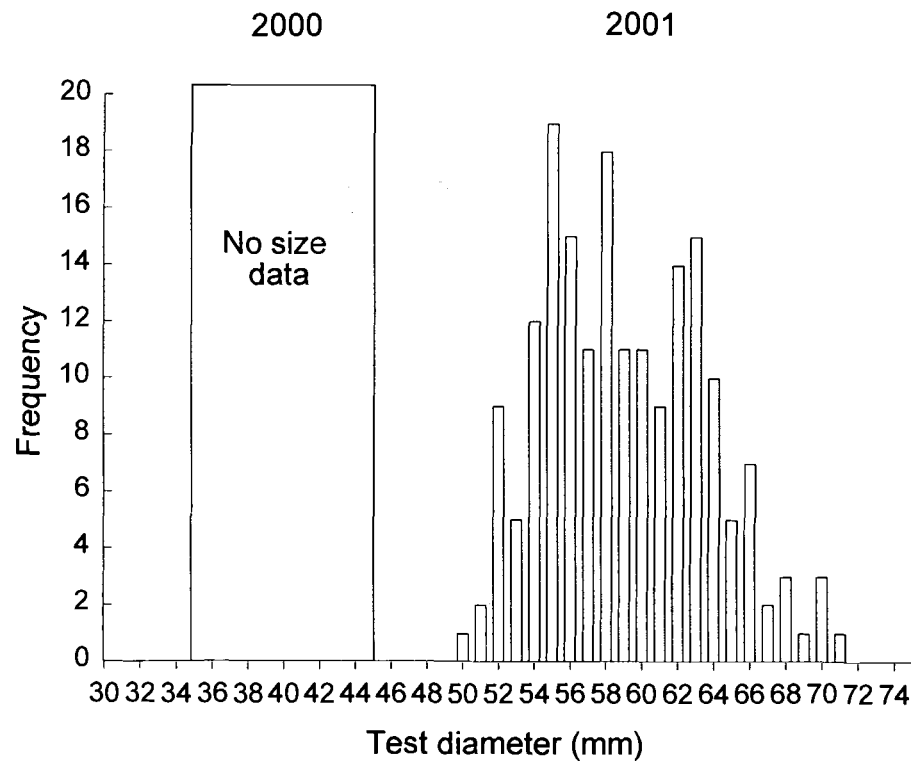


Fig. 3: Size distributions of urchins relocated to Cape Elizabeth in 2000 and 20001. No frequency data is available for 2000, but all 24,000 urchins were measured within 35 mm and 45 mm test diameter.

Table 1. Repeated measures ANOVA tables of urchin abundance (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 \times Algae	3	468.995	3.67	0.0277
Time	3	2230.93	17.46	0.0001
Algae \times 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 \times Algae	3	78.452	1.32	0.2797
Time	7	3151.752	52.98	0.0001
Algae \times 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 $\alpha = 0.05$.

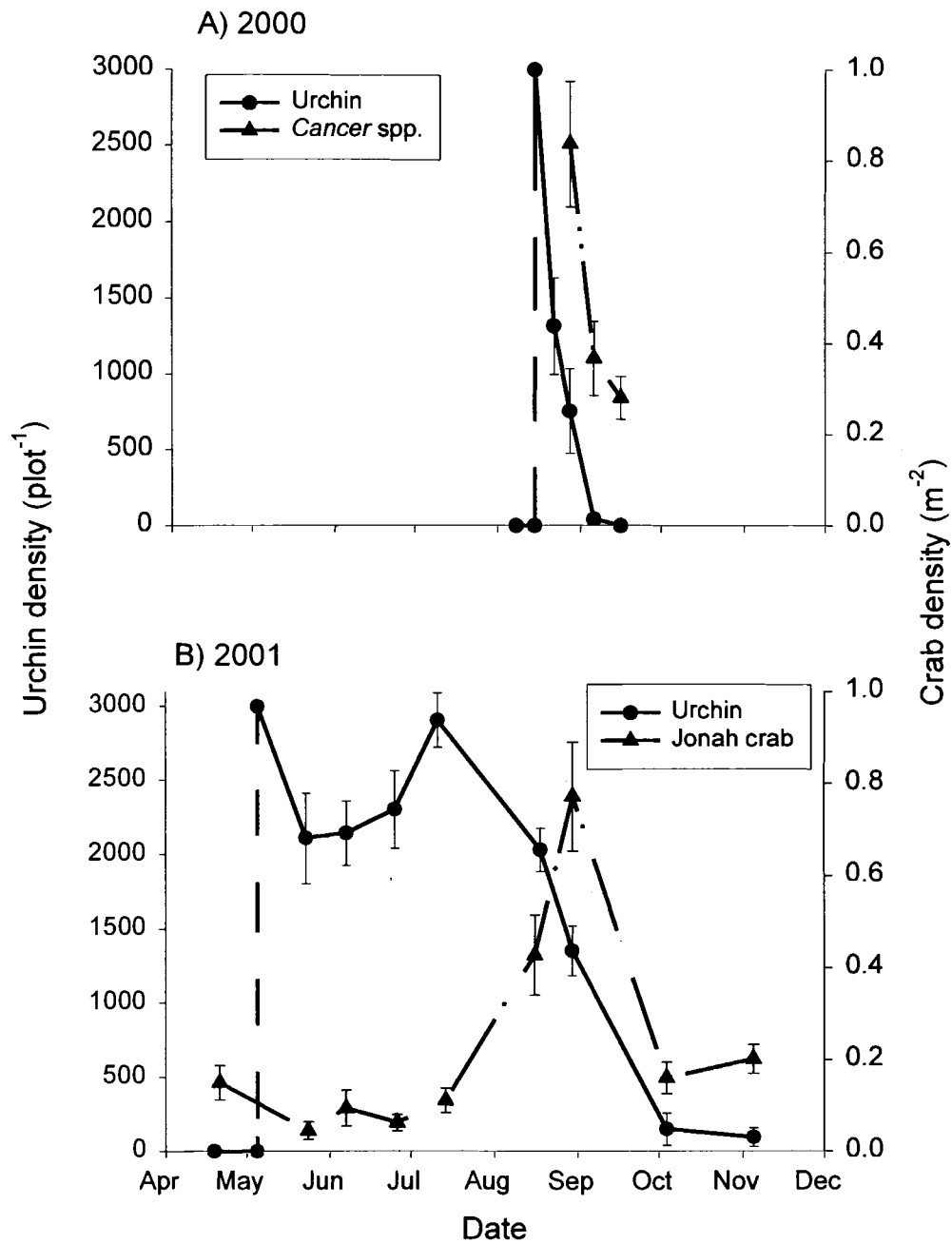


Fig. 4: Urchin and crab population trends at Cape Elizabeth, ME in A) 2000 and B) 2001. Data were pooled for fleshy algae treatments (+ A, - A) ($n = 8$ in 2000 and $n = 9$ in 2001). Error bars are ± 1 SE. (A) *Cancer* spp. density is reported. (B) Only Jonah crab (*C. borealis*) density is reported.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

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	0.0064
Algae	1	0.00146	6.05	0.0362
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 $\alpha = 0.05$.

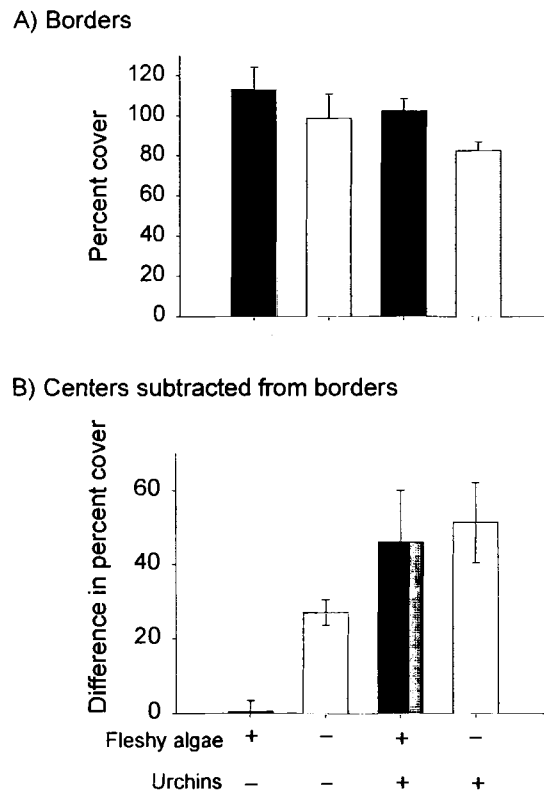


Fig. 5: Percent cover of all fleshy macroalgae in the border areas of plots only (A) and the paired difference in the central versus border areas of plots (B) in July 2001. Treatments are noted as having an initial presence (+ U) or absence (– U) of relocated urchins and fleshy macroalgae in the central area at the beginning of the experiment in March. Error bars are ± 1 SE.

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) and initially lacked fleshy algae (- A) (personal observation).

Interactions between predatory crabs and relocated sea urchins

Demographic trends in sea urchins and crabs

In 2000, urchin abundance declined rapidly following relocation to Cape Elizabeth (Fig 4A). Surveys one week after relocation revealed 50% mortality (1500 plot^{-1}) of relocated urchins. All urchins were extirpated from all plots within four weeks of the relocation. 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. Surveys two, three and four weeks

following relocation revealed declining *Cancer* spp. density (0.8 m^{-2} dropped to 0.3 m^{-2}) at plots with urchins (+ U) concomitant with declining urchin populations. In contrast, crab densities at plots without urchins (- U) were similar (0.25 m^{-2}) for the three sampling dates (Fig. 6A). The highest crab density (0.8 m^{-2}) was observed at plots with urchins on 28 August (Fig 6A). Crab (*Cancer* spp.) densities were similar at all plots (0.3 m^{-2}) once all urchins were eliminated. When summed across all sampling dates, crabs were significantly more abundant at plots that did not have fleshy algae initially (- A) when than in plots that did (Table 3A). In addition, crab density totaled over all sampling dates were significantly higher for plots with urchins (+ A) than those without. No

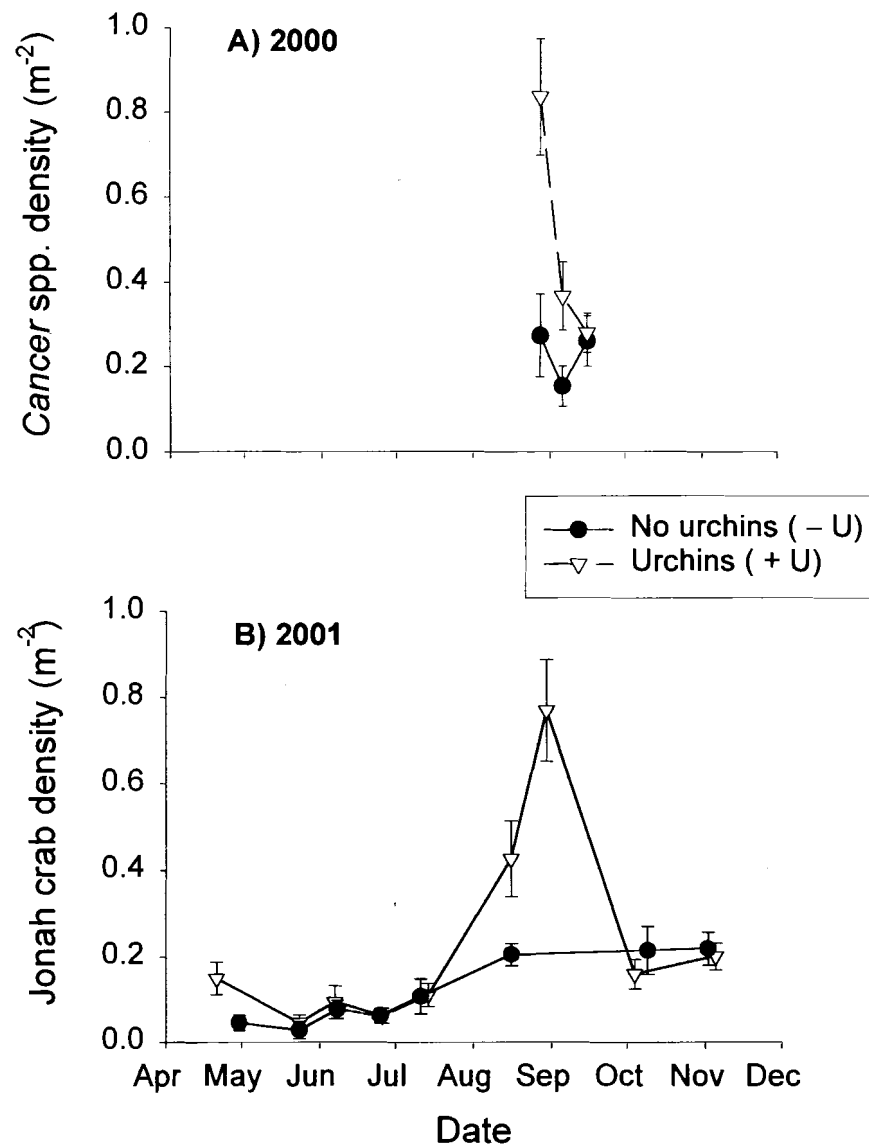


Fig. 6: Crab densities at plots with (+ U) and without urchins (- U) in 2000 (A) and 2001 (B) at Cape Elizabeth, ME. (A) *Cancer* spp. density is reported. (B) Only Jonah crab (*C. borealis*) density is reported. Data were pooled for fleshy algae treatments (+ A, - A) such that in A) $n = 8$ for plots 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 ± 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	0.0061	
Urchin	1	0.656	25.1	0.0007	+ U > – U
Algae	1	0.248	9.47	0.0132	– 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	0.0025	+ 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 $\alpha = 0.05$.

significant Urchin \times Algae interaction was detected for crab density summed over all sampling dates in 2000.

The decline in sea urchin densities in August 2001 coincided with an increase in Jonah crab densities (Fig. 4B) and observations by divers that Jonah crabs were feeding on the urchins. While urchin abundance was high (2100 plot^{-1} to 2900 plot^{-1}) from May through mid-July, Jonah crab densities were low (0.1 m^{-2}) at all plots. Crab densities peaked at 0.78 m^{-2} by the end of August only at plots with declining urchin abundance (+ U), and they remained low (0.2 m^{-2}) at plots without urchins (- U; Fig. 6B). Jonah crab densities were low again (0.2 m^{-2}) at all plots by early October when urchins were scarce (100 plot^{-1} ; Figs. 3B & 6B). Jonah crab densities summed over all sampling dates were significantly greater at plots with urchins (+ U) than without (Table 3B). Neither the initial presence or absence of algae (+ A, - A) nor the interaction of Urchin \times Algae significantly affected the total Jonah crab abundance at each plot in 2001.

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. 7). Densities of Jonah crabs in this size range peaked at 0.4 m^{-2} in August but were less than 0.1 m^{-2} in all other months. The density of Jonah crabs greater than 100 mm CW also peaked in August (0.15 m^{-2}) despite densities less than 0.05 m^{-2} in every other month.

Increases in Jonah crab densities in 2001 occurred when bottom water temperatures were warming (Fig. 8). Water temperature and Jonah crab density peaked in late August (14.5°C and 0.78 m^{-2} , respectively; Fig. 8). Water temperature was high again in late September (14.2°C). In early October, Jonah crab densities were low (0.2 m^{-2}) but water temperatures were still relatively high (13.5°C).

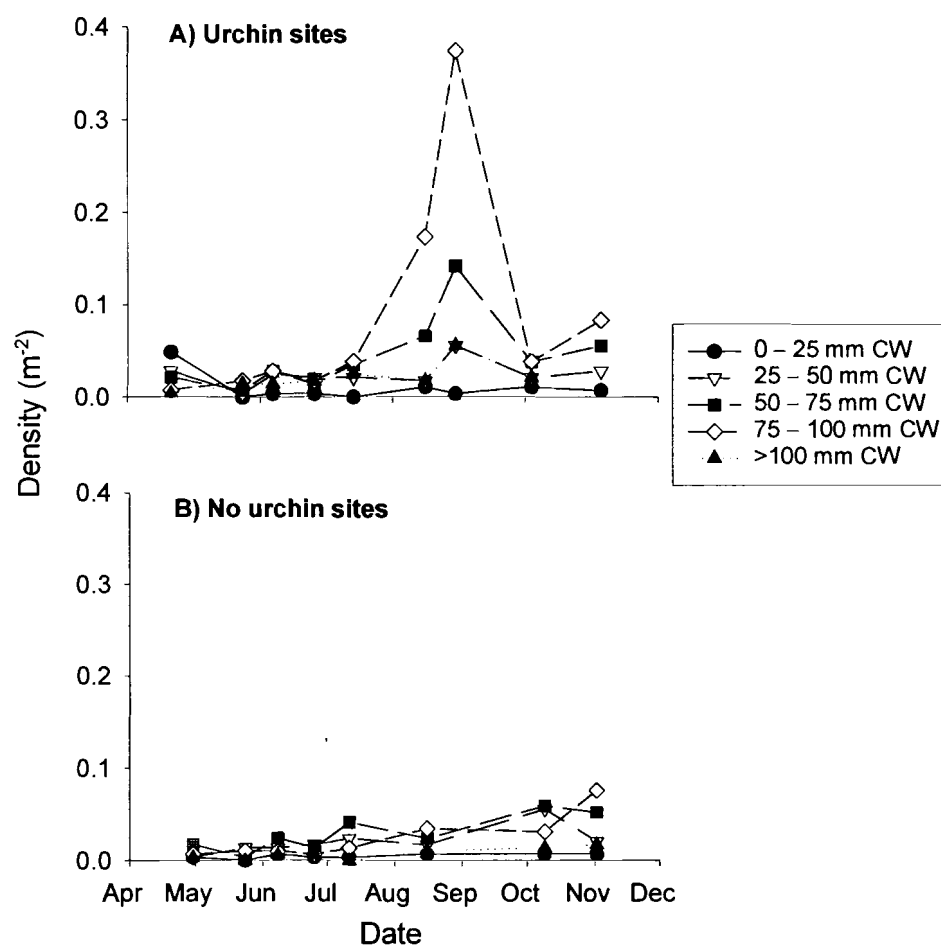


Fig. 7: Average density of Jonah crabs in 25 mm carapace width (CW) size bins at plots with urchins (A) and plots without urchins (B) at Cape Elizabeth, ME in 2001. Data were pooled for fleshy algae treatments (+ A, - A; (A) $n = 9$ and (B) $n = 7$).

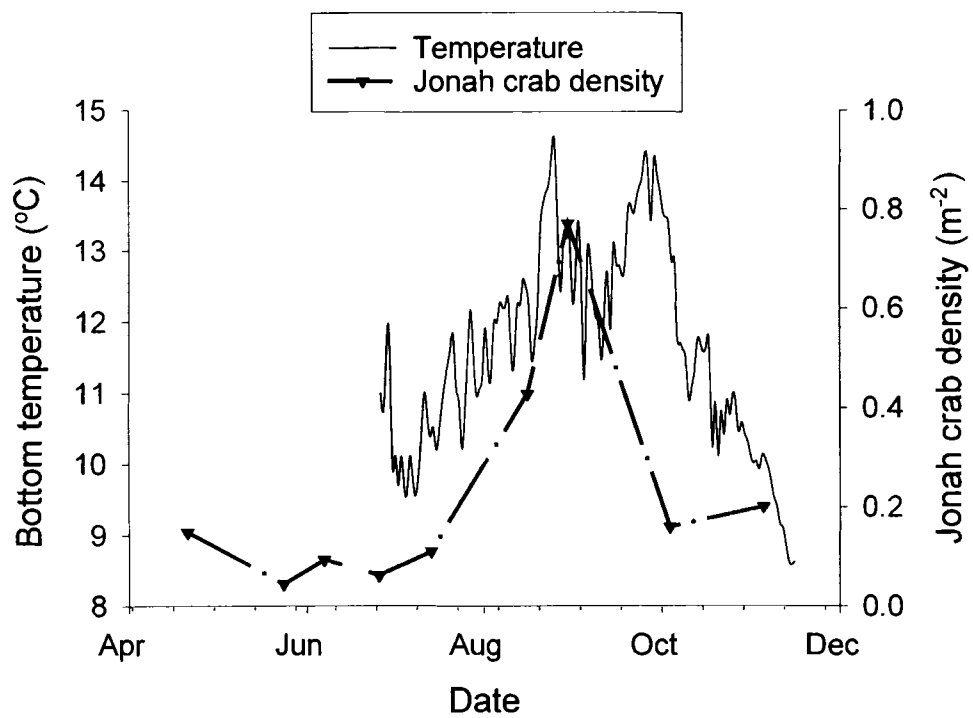


Fig. 8: Average Jonah crab density at plots with urchins (+ U, - U) and bottom water temperature at Cape Elizabeth, ME in 2001.

Rock crab density remained relatively low for the duration of the experiment in 2001 (Fig. 9). Rock crab density was greatest (0.035 m^{-2}) 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. 9). 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 \times Algae interaction (Table 3C).

Per capita Jonah 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 ($2.37 \text{ urchins} \cdot \text{crab}^{-1} \cdot \text{d}^{-1}$) but were not significantly different from predation rate estimates from 14 July to 16 August and from 30 August to 4 October ($\approx 1.5 \text{ urchins} \cdot \text{crab}^{-1} \cdot \text{d}^{-1}$; Tables 4 & 5). From October to November per capita predation rates of Jonah crabs significantly decreased to $0.22 \text{ urchins} \cdot \text{crab}^{-1} \cdot \text{d}^{-1}$ (Tables 4 & 5).

Sea urchin survival under controlled conditions

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

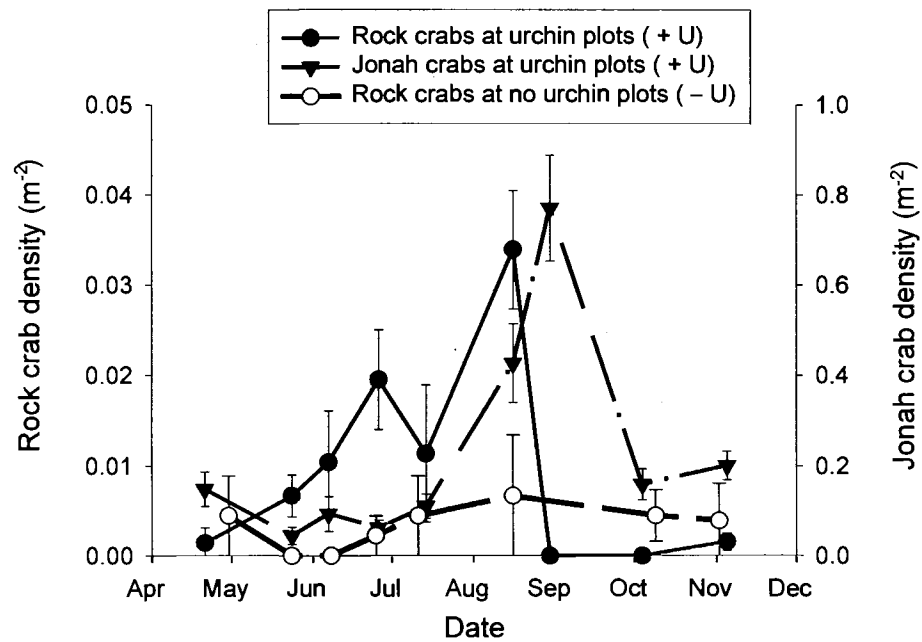


Fig. 9: Temporal trends in rock crab densities at plots with urchins (+ U) and without urchins (- U) and Jonah crab densities at plots with urchins (+ U) at Cape Elizabeth, ME in 2001.

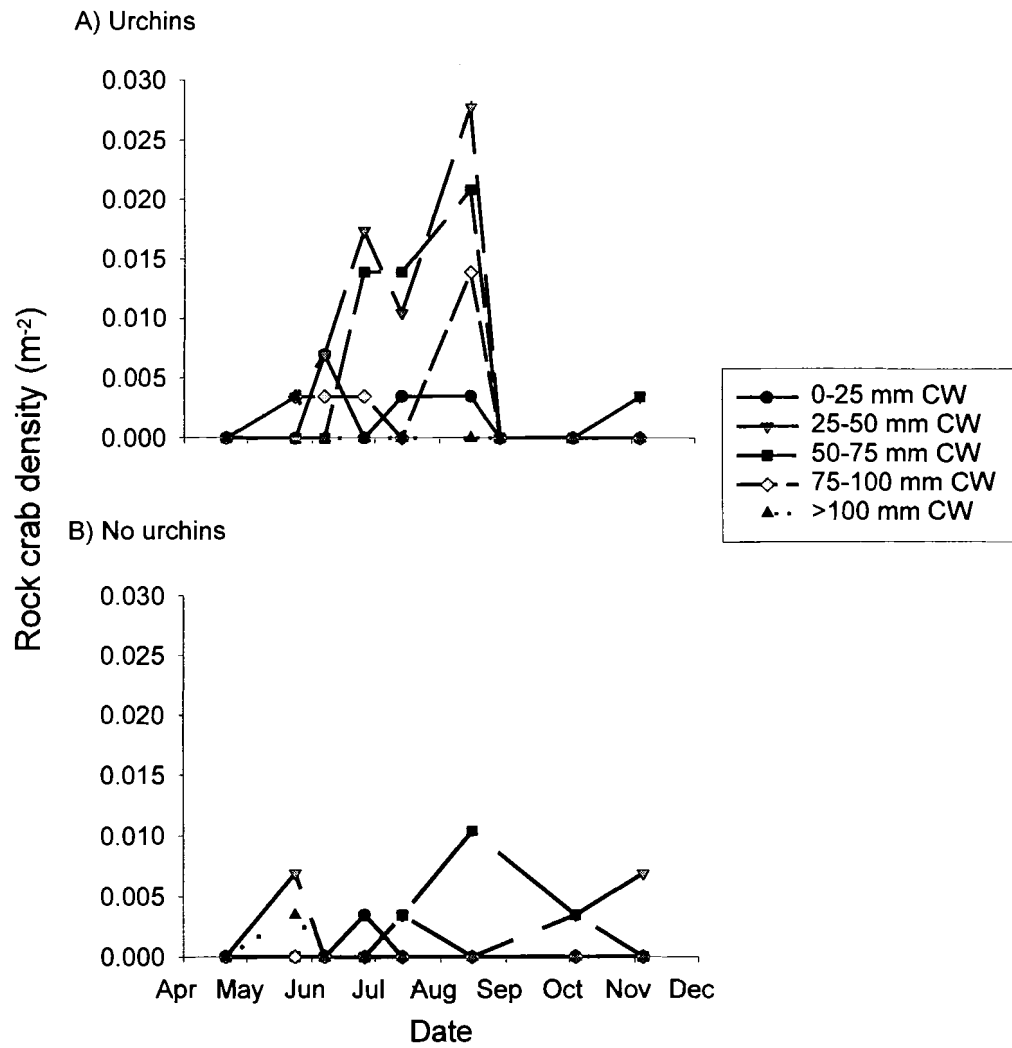


Fig. 10: Average density of rock crabs in 25 mm carapace width (CW) size bins at A) plots with urchins (+ U) and B) plots without urchins (- U) at Cape Elizabeth, ME in 2001. Data were pooled for fleshy algae treatments ($n=9$ in A and $n=7$ in B).

Table 4. Repeated measures ANOVA of per capita 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	<i>p</i>
Replicate	3	0.293	1.61	0.3533
Algae	1	0.734	4.02	0.1385
Error 1: Replicate \times Algae	3	0.182	1.27	0.3093
Time	3	0.293	10.32	0.0002
Algae \times Time	3	0.5	3.48	0.0331
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⁻¹ \cdot d⁻¹) 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

September despite water temperatures approaching 20°C (Fig. 11).

Quantifying processes

Urchin grazing rates

Grazing rates in the laboratory were measured at temperatures ranging between 12 °C and 20°C from late May through August. Grazing rates ranged between 1 g to 2.1 g *Laminaria saccharina* · urchin⁻¹ · d⁻¹ and appeared to be temperature dependent (Fig. 12). Grazing rate declined only at water temperatures exceeding 17°C.

Crab predation rates

The proportion of captive Jonah and rock crabs feeding on sea urchins increased over the duration of the feeding experiment (Fig. 13). Predation rates by Jonah crabs were greater than that of rock crabs. During the first trial of the experiment, the frequency of Jonah crab predation increased to 0.6 urchins · crab⁻¹ · d⁻¹, while the frequency of rock crab predation reached only 0.2 urchins · crab⁻¹ · d⁻¹ (Fig. 13). Water temperature ranged from 17-21°C during the experiment and did not appear to correlate with predation rates for either species (Fig. 13).

Patterns of predation of crabs that had a known history of predation and had been relocated to an aquarium without residual urchin scent did not change in either species (Fig. 14). Jonah crabs that had preyed on at least one urchin in the first trial of the experiment (i.e. unknown feeding history trial) maintained a 0.8 urchins · crab⁻¹ · d⁻¹ predation frequency throughout the second trial. Rock crabs with a known history of predation did not maintain a consistent predation frequency but averaged close to

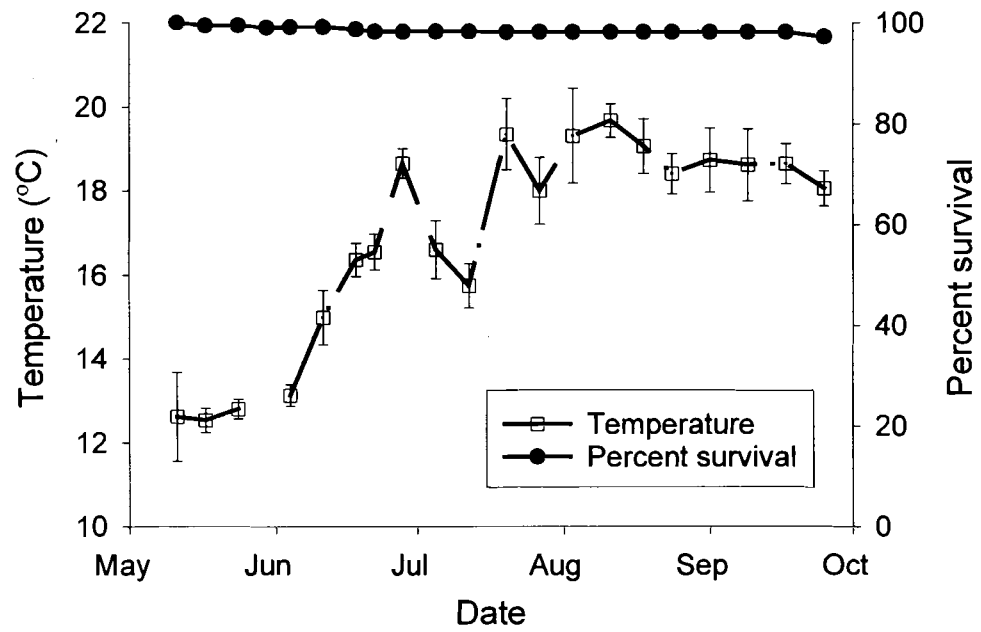


Fig. 11: Percent survival of relocated sea urchins maintained under controlled conditions and flowing seawater temperatures ($n = 7$ aquaria with 186 urchins each) in 2001. Error bars are ± 1 SE.

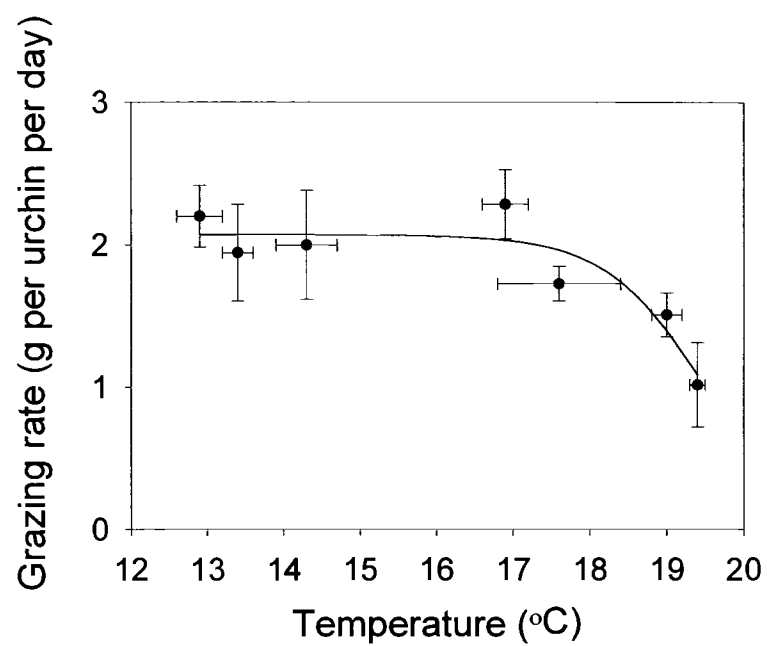


Fig. 12: Urchin grazing rate as a function of temperature. Data are fitted with a sigmoidal curve ($y = 2.071 / 1 + \exp(-(x - 19.47) / -0.64)$; $R^2 = 0.85$; $F_{2,6} = 11.30$; $p = 0.023$). Error bars are ± 1 SE.

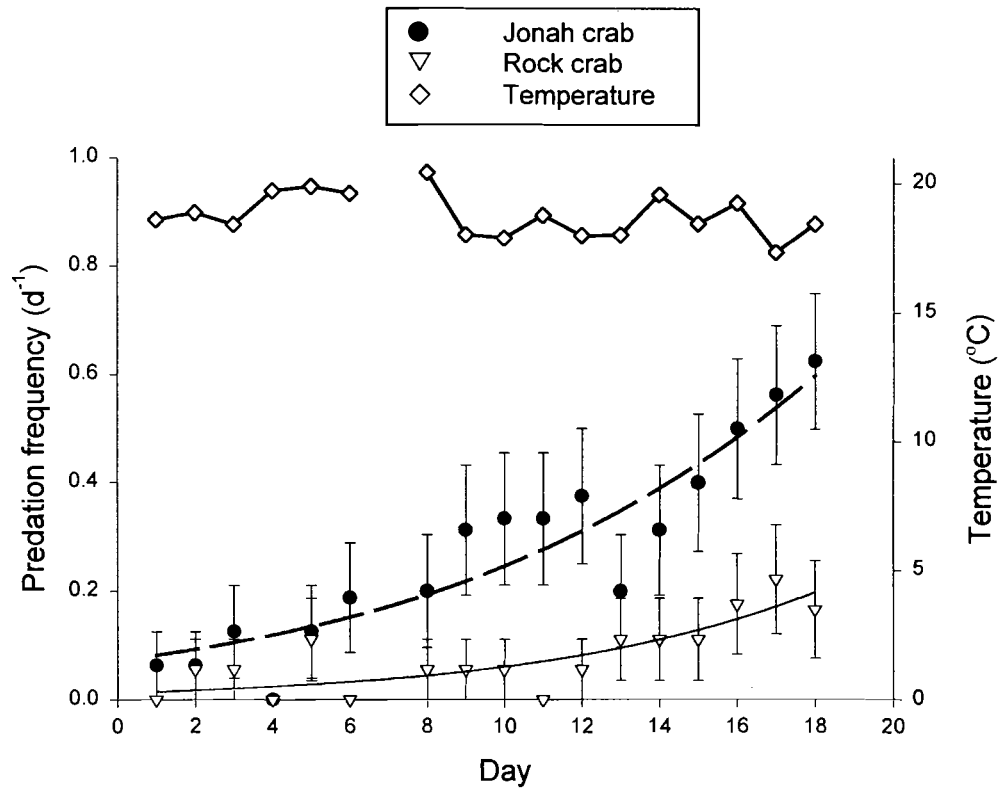


Fig. 13: The frequency of predation of Jonah and rock crabs feeding on urchins and seawater temperature during a laboratory experiment. Predation frequency denotes the average number of crabs that consumed an urchin each day ($n=16$ for Jonah crabs and $n=18$ for rock crabs). Crabs had unknown feeding histories. Error bars are ± 1 SE. Data for both species fit sigmoidal curves (Jonah crab: $y = 2.8463 / (1 + \exp(-(x - 28.2728) / 7.7436))$, $R^2 = 0.86$, $F_{2,14} = 43.84$, $p < 0.0001$; rock crab: $y = 2.2412 / (1 + \exp(-(x - 32.7816) / 6.3411))$, $R^2 = 0.68$, $F_{2,14} = 39.60$, $p = 0.0003$).

0.4 urchins \cdot crab⁻¹ \cdot d⁻¹ during that trial. Crabs of both species that had not preyed on an urchin during the unknown feeding history trial maintained low predation frequencies during the second trial despite being stimulated with residual urchin ‘scent’ (Fig. 14).

All crabs fed on an urchin when it was cut in half for them. The soft-tissue of cracked urchins was consumed within one day by all crabs, regardless of each crab’s previous urchin feeding history. Twenty-five percent of Jonah crabs and 61% of rock crabs were classified as scavengers, because they fed only on cracked urchins.

The propensity to prey based on previous feeding experience increased exponentially for both Jonah and rock crabs (Fig. 15). Following four sequential predation events, Jonah crabs exhibited about an 88% probability of preying on an urchin while rock crabs exhibited about a 62% chance of continued predation.

Large-scale spatial and temporal Jonah and rock crab patterns

NMFS bottom trawl surveys

Jonah crab abundance increased in fall groundfish surveys in 2000 and 2001 (Fig. 16A). Between 1973 and 1999 Jonah crab abundance had been relatively constant (1 per tow) but was estimated at 4.5 per tow in 2001. In contrast, rock crabs were more abundant than Jonah crabs in most years, but had a much larger inter-annual variation than Jonah crabs (Fig. 16B).

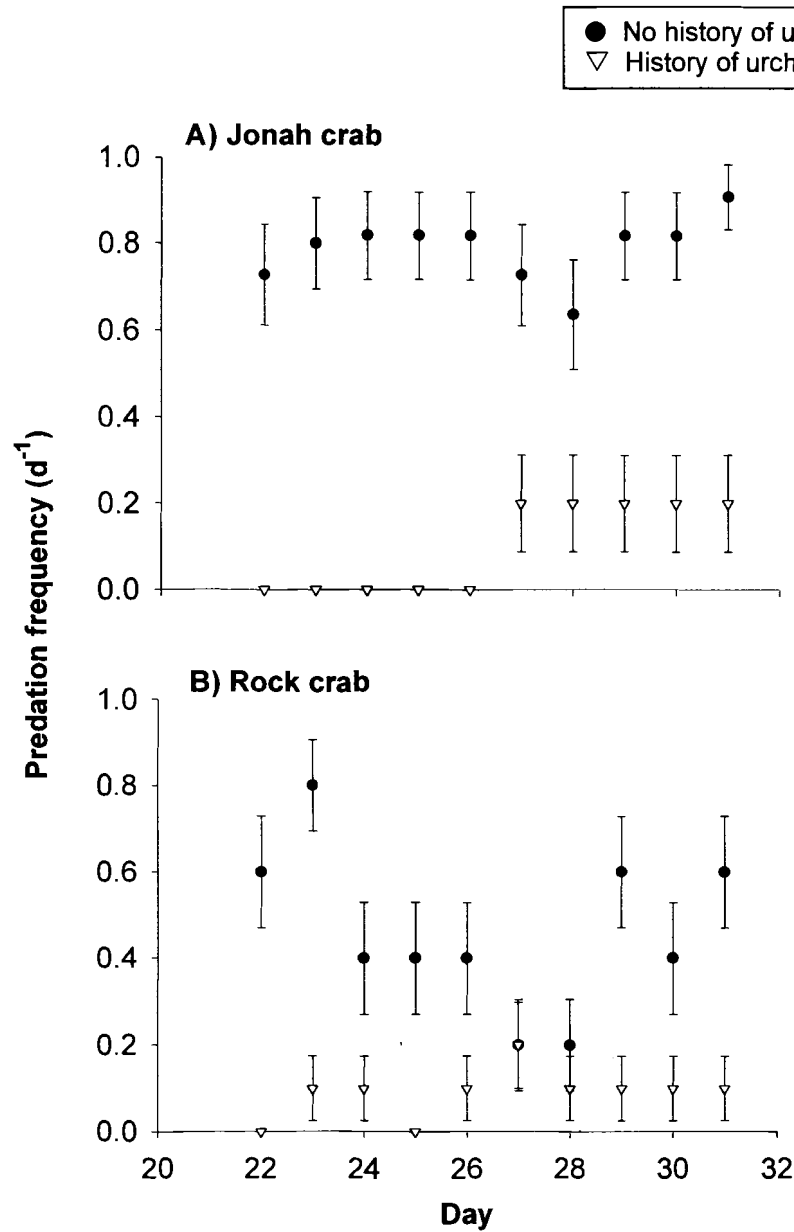


Fig. 14: Proportion of crabs with different feeding histories feeding on urchins: A) Jonah crabs and B) rock crabs. Predation frequency denotes the total number of crabs that consumed an urchin each day ($n=16$ for Jonah crabs and $n=18$ for rock crabs). Crabs with a history of predation were placed into aquaria with clean (unscented) water on day 21. Crabs with no history of predation were placed into aquaria with urchin scented water. Neither crab species showed a marked change in feeding behavior following a change in ambient urchin scent.

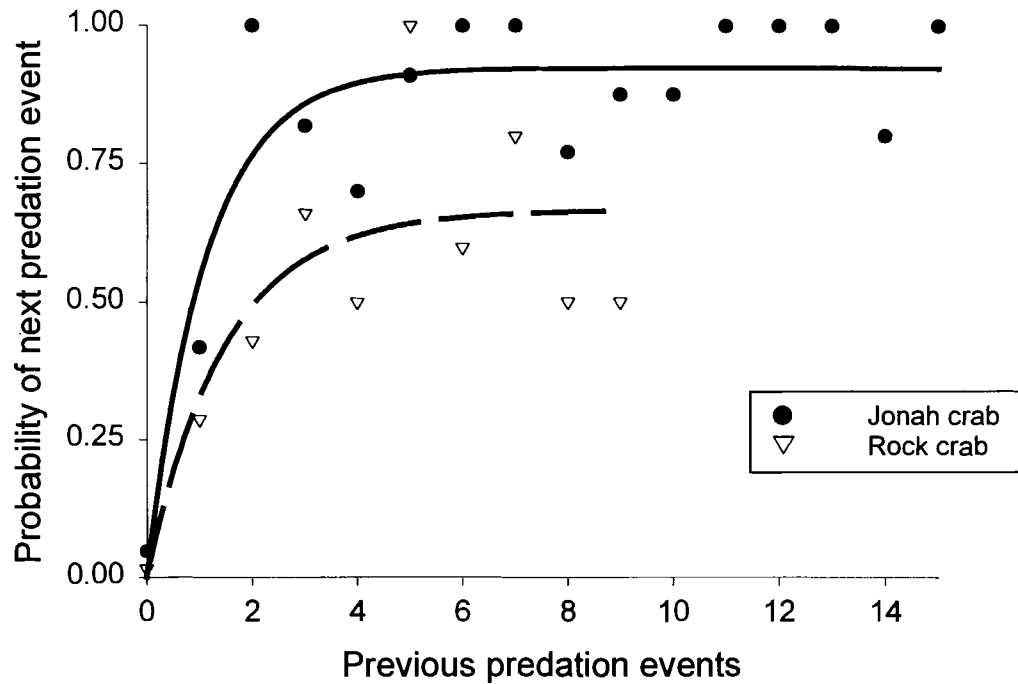


Fig. 15: Propensity to prey based on previous feeding experience for Jonah and rock crabs. The number of previous predation events is defined as the number of days in a row that a crab preyed on an urchin. The probability to prey again was determined by whether or not each crab preyed on an urchin following previous predation events. Data for both species were fitted with exponential curves (Jonah crab: $y = 0.922 (1 - \exp(-0.89x))$, $R^2 = 0.81$, $F_{1,15} = 60.08$, $p < 0.0001$; rock crab: $y = 0.67 (1 - \exp(-0.67x))$, $R^2 = 0.65$, $F_{1,15} = 14.6$, $p = 0.0051$ (but failed the Levene Median test)).

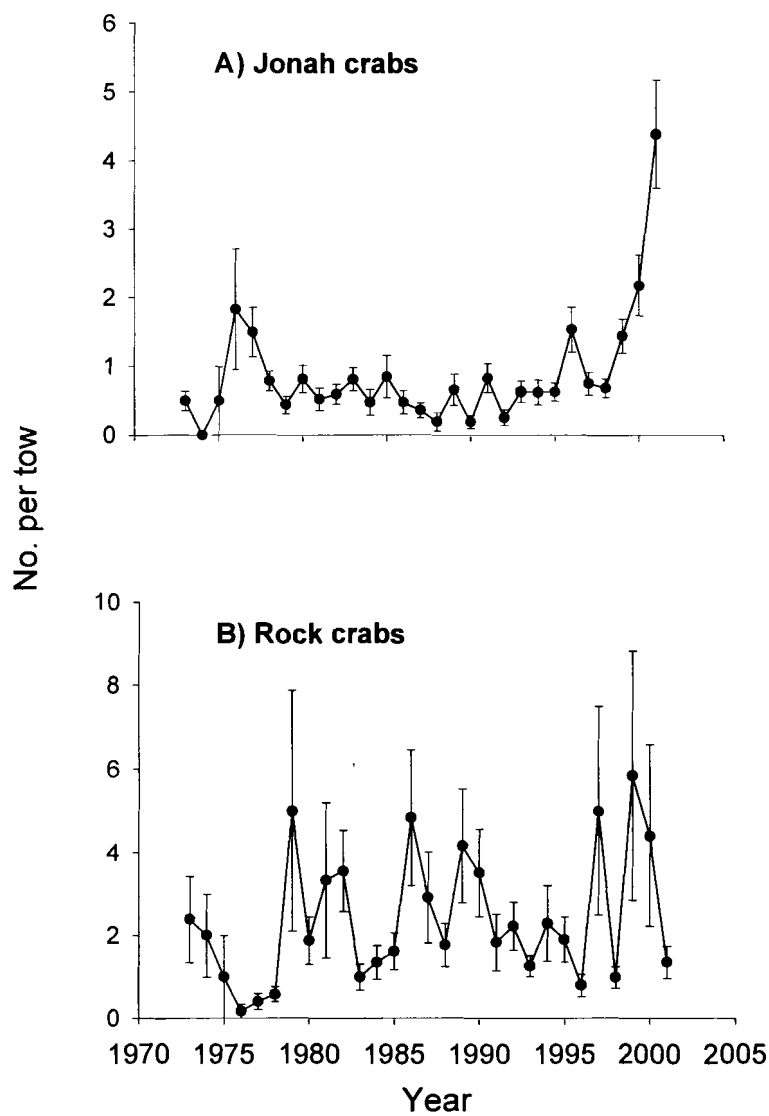


Fig. 16: Average number of Jonah crabs (A) and rock crabs (B) in NMFS fall groundfish surveys in the Gulf of Maine. Error bars are ± 1 SE. Stations varied between years but were all within the limits of N 41°00.0' to N 44°30.0' and W 66°00.0' to W 71°00.0'.

Coastal submarine surveys

Jonah crabs were observed in four Gulf of Maine regions that were sampled using a submersible in 1997 (Fig. 17). Jonah crabs were most abundant (0.008 m^{-2}) in the Mount Desert Island region, and they were least abundant offshore of the southern coast of Nova Scotia (0.0001 m^{-2}). Jonah crabs were equally abundant in the deeper waters off of Pemaquid and Jonesport (0.00025 m^{-2}).

Shallow subtidal SCUBA surveys

Jonah crabs were ubiquitous in the shallow subtidal zone along the Maine coast in 1997, but the highest abundance (0.12 m^{-2}) was in the Pemaquid (mid-coast) region (Fig. 18). In all regions, Jonah crabs were most common in boulder habitats. Jonah crabs were least common in sediment when these habitats were sampled.

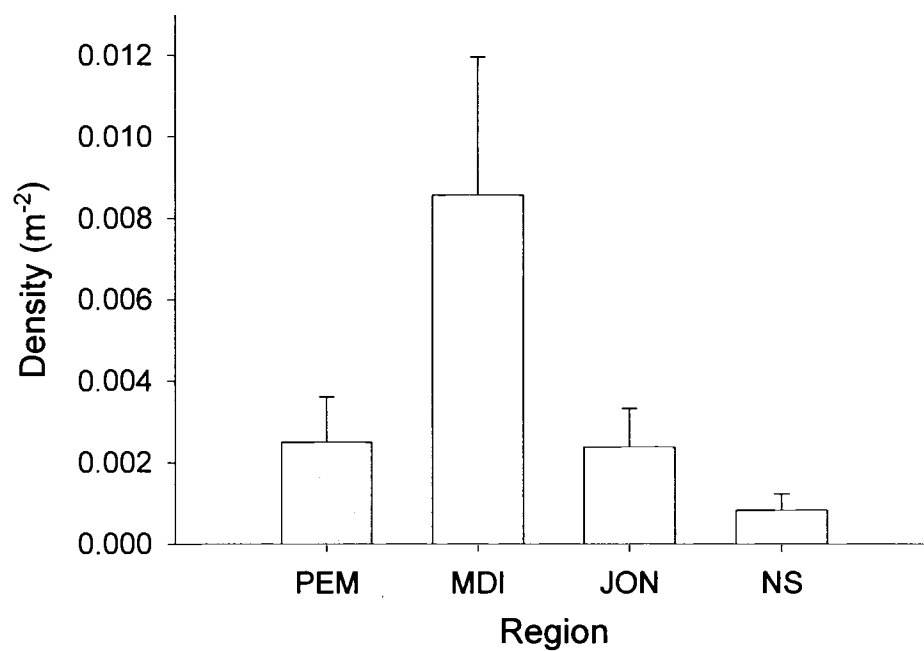


Fig. 17: Jonah crab density in 5 regions of the Gulf of Maine surveyed in 1997 using videos from submersible dives. Error bars are ± 1 SE. Regions are: PEM= Pemaquid, MDI= Mount Desert Island, JON= Jonesport, and NS= Nova Scotia. Data were pooled for all habitats.

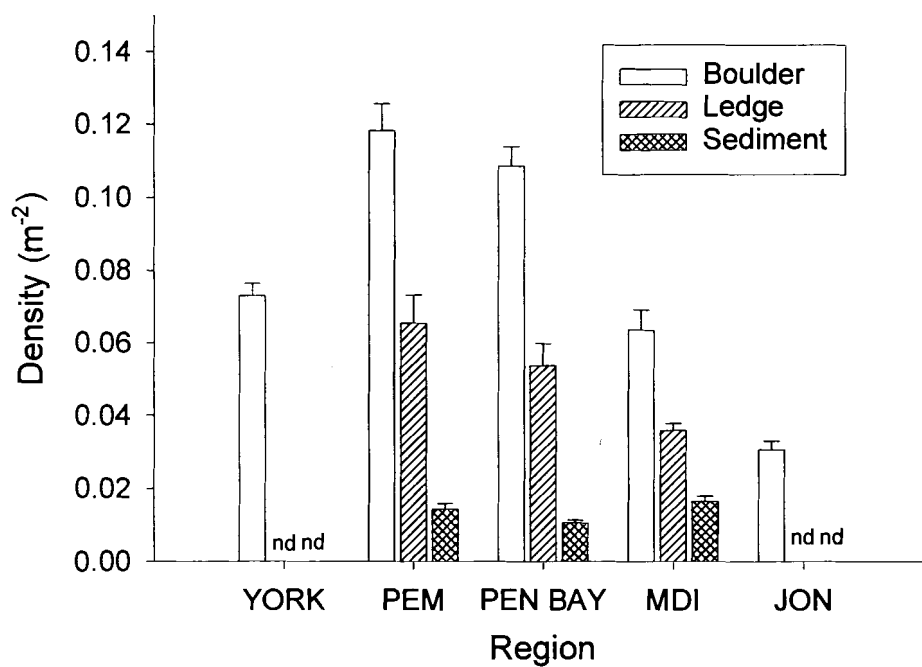


Fig. 18: Jonah crab density by substrate type in 5 regions in the Gulf of Maine in 1997. Surveys were conducted at 10 m depth using SCUBA. Error bars are ± 1 SE. ND = no data. Regions were: YORK, PEM = Pemaquid, PEN BAY = Penobscot Bay, MDI = Mount Desert Island, and JON = Jonesport.

DISCUSSION

Sea urchin grazing control of benthic fleshy algae

Grazing by green sea urchins induced a 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 ($\approx 50\%$ decrease in fleshy algae) regardless of whether the plot had fleshy algae or not (+ A, - A) prior to the relocation of urchins (Fig. 5B). We observed relatively few urchins (< 25) in the border of each plot, and most of the urchins in the center of plots were covered with drift algae in July (personal observation). This observation 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 but otherwise were temperature insensitive. When measured in the lab, urchin grazing rates were consistently about $2.1 \text{ g } L. \text{ saccharina} \cdot \text{urchin}^{-1} \cdot \text{d}^{-1}$ at temperatures ranging from 13°C until 17°C (Fig. 12). Grazing rates declined at temperatures above 17°C . 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. 8), and so we expect that changes in herbivory during this time were not influenced by water temperature.

Crab predatory control of sea urchins

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.) abundance (Fig. 4B). Second, there were more crabs at plots with urchins (+ U) than those without when urchin abundances were declining (Fig. 6B). Third, crab densities at plots with urchins (+ U) dropped from 0.8 m^{-2} to 0.3 m^{-2} 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^{-2}) on 28 August 2000 were similar to elevated Jonah crab densities (0.78 m^{-2}) 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. 6B). Following a classic predator-prey cycle, Jonah crab density 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 ≥ 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 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).

The mortality of urchins relocated to controlled conditions in the laboratory in 2001 remained very low during the experiment despite relatively warm water temperatures (Fig. 7). Moreover, these urchins showed no obvious signs of thermal stress (e.g. darkened spots on the epidermis and loss of spines). This suggests that relocated urchins at Cape Elizabeth probably did not die from elevated water temperatures in late summer.

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 abundances increased (Table 5, Fig. 8). Assuming that Jonah crabs were solely responsible for urchin mortality, individuals were feeding on over $2 \text{ urchins} \cdot \text{crab}^{-1} \cdot \text{d}^{-1}$ on average in mid- to late August, when Jonah crabs were anomalously abundant. Per capita predation rates when Jonah crab abundances were increasing and decreasing averaged about $1.5 \text{ urchins} \cdot \text{crab}^{-1} \cdot \text{d}^{-1}$. 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 are alike in their capacity (behavioral and mechanical) to prey on urchins, then no change in per capita predation rate is expected when density is 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 the laboratory predation experiment we performed in 2001 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 m^{-2} year round (Fig. 6). This density is close to that (0.10 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 effectively extirpated 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 75-100mm CW size range in August only (Fig. 7); thus the non-residents comprised a size cohort.

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 Jonah 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 great abundance of evidence supporting a migration hypothesis, no one has tested it directly.

Bottom water temperature was an environmental parameter that 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 mm to 100 mm CW cohort (Figs. 12 & 13, 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. We observed distinct differences in Jonah crab feeding behavior (e.g. predatory and scavenger) in relatively warm water (20°C; Fig. 9).

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 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.

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. 9), 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).

Learning in predatory crabs?

In the laboratory, the frequency of predation by Jonah and rock crabs on sea urchins increased over time (Fig. 8). This increase in predation rate could have been due to several factors. First, an increased predation rate could have been a function of increased hunger over time. Second, increased predation rate also could have indicated that the crabs needed time to acclimate to the aquaria before they could function. Third, predation rate may have increased with increasing water temperature. Fourth, predation rate may have depended on the strength of a chemical cue. In other words, as more urchin 'scent' was released into the aquarium the probability that the crab would prey again increased. Fifth, increased predation rate may have been a function of increased efficiency of prey handling.

If hunger or stress level was the cause of delayed predation then all crabs would prey after some period of starvation and acclimatization. This hypothesis was not supported because there was no pattern in either species for when date of first predation event occurred. At least one crab of each species preyed on an urchin by the second day,

and the numbers climbed steadily during the experiment. In addition, some individuals never preyed on an urchin (Fig. 9). We assumed that the crabs that never preyed on an urchin were hungry despite not demonstrating predatory behavior, because they all ate the soft tissue of an urchin that was cut in half for them.

Variation in water temperature did not measurably affect the predation rate of either crab species. Temperature has been shown to affect predation rates of the shore crab, *Carcinus maenas*, (Elner 1980, Sanchez-Salazar et al. 1987) and would likely affect predation by Jonah crabs (A. Leland, unpublished data). But temperature stayed within a narrow 3°C range (17.5°C to 20.5°C) for the duration of the experiment (Fig. 13), and predation frequencies were low when temperature was greatest.

Predation frequency did not appear to depend on the availability of a chemical cue, because predation by some individuals was elicited during each trial when no chemical cue existed. All crabs were housed in 'clean' aquaria (no residual scent from predation) at the start of the first trial, and many crabs of both species preyed on an urchin (Fig. 8). The crabs that preyed on an urchin in the first trial were relocated to another 'clean' aquarium on day 21, and most continued to prey on urchins (Fig. 9A). In contrast, those crabs that did not prey on an urchin in the first trial did not exhibit strong behavior changes when they were relocated to an aquarium with urchin-scented water (Fig. 9B). It is possible that the stimulus needed to be much stronger to induce predation in non-feeding crabs in the second trial (Finelli et al. 2000).

Increased predation efficiency through prey recognition and handling may be the most likely reason that predation frequency increased over time. Because crabs were offered only one urchin per day, predation frequency was based on the number of crabs

that successfully preyed on an urchin each day. (Note that per capita predation rate is different as it measures the total number of urchins preyed on by each crab per day.) Predation frequency increased because the number of feeding individuals increased (not because each predator was eating more). Most individuals that preyed a few days in a row remained active predators for the duration of the experiment. For example, Jonah crabs that preyed on an urchin three days in a row had close to an 88% chance of preying the fourth day (Fig. 10). In addition, rock crabs that had preyed three days in a row had a 62% chance of preying again the following day (Fig. 10). This relationship is indicative of increased handling efficiency of the prey item by the predator (Cunningham and Hughes 1984).

Crab predation was probably limited by recognition of the urchin as a possible prey item and by handling of the urchin (including attack and capture). Initially, we observed crabs trying to use urchins as shelter, which suggests that they were not being recognized as prey. We also observed crabs attempting to penetrate urchins which presumably meant that the crabs recognized the urchins as prey. For the most part, crabs that were feeding regularly attacked as soon as the urchin was replaced each day, while crabs that had previously preyed only once or twice took many hours before showing signs of attack (personal observation). Therefore, the efficiency of predation relied heavily upon previous experience. The crabs that preyed on an urchin early in the experiment may have had recent experience preying on urchins in nature. (One Jonah crab was collected while preying on an urchin.)

While an urchin chemical cue did not seem to directly elicit predatory behaviors in non-feeding urchins, some form of cue may have been involved in stimulating and

sustaining predatory behaviors in feeding crabs. Shore crabs, *Carcinus maenus*, transfer learned handling skills of prey they have been recently feeding on to similarly shaped novel prey items (Hughes and O'Brien 2001). This suggests that the crabs can recognize, or cue into, prey by shape. Rock crabs have been shown to differentiate between the odors of familiar and unfamiliar prey species, such that recently preyed on species are preferred (Ristvey and Rebach 1999). This lure of the rock crab to 'stick to what it knows' can explain why the probability of future predation increased with the number of historical predation events (Fig. 10). Maybe the same mechanism is operating in Jonah crabs.

Strength of predation in Jonah and rock crabs

Jonah crabs were stronger urchin predators than rock crabs in the laboratory experiment. The frequency of predation of Jonah crabs was three-fold higher than that of rock crabs by the end of the first trial (Fig. 8). Moreover, in the second trial, about 80% of Jonah crabs with a history of urchin predation were feeding each day while about 40% of rock crabs with a history of urchin predation were preying per day (Fig. 9A). We estimated that about 68% of Jonah crabs and 25% of rock crabs could be active urchin predators, when we assumed that the crabs used in this experiment approximated the feeding capabilities of natural crab populations. We also estimated that in populations of Jonah crabs and rock crabs, 30% of Jonah crabs and 75% of rock crabs could be scavengers.

Jonah crab control of benthic community structure

This is the first study to demonstrate that Jonah crab predation on urchins can be a strong interaction. Moreover, this is the first study that experimentally tested for this interaction. Overall, there is little mention in the literature that Jonah crabs consume urchins (Ojeda and Dearborn 1991). Rock crabs have been more commonly cited as possible predators (Himmelman and Steele 1971, Breen and Mann 1976, Drummond-Davis et al. 1982, Scheibling 1984, Vadas et al. 1986), but Miller (1985) pointed out that low frequency of occurrence of urchins in gut content studies, low preference for urchins in lab experiments, and low rock crab abundance *in situ* was insufficient to account for urchin population control. This study supports Miller's (1985) findings that rock crabs are not major urchin predators, but adds that Jonah crabs can be major urchin predators locally.

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 twice eliminated the dominant benthic herbivores from this system. Crabs are size-dependent predators (Moody and Steneck 1993) but no urchin size class was too large for the crabs as relocated urchins ranged from 35 mm to 71mm TD. The extirpation of grazers probably resulted in the re-creation of a vegetated system. Thus these crabs were apex predators that determined the distribution and abundance of fleshy macroalgae by limiting herbivores.

The importance of Jonah crab predation on urchins in other regions of the Gulf of Maine where natural populations still exist remains unknown. Jonah crabs were widely

distributed at low densities in video transects taken at about 100 m depth in the Gulf of Maine in 1997 (Fig. 17). In addition, pervasive Jonah crab abundance was found in benthic surveys of shallow subtidal zones along the Maine coast with greatest concentrations in the Pemaquid region (mid-coast) and in boulder habitats (Fig. 18). Jonah crabs were also commonly found on ledge habitat. Because sea urchins are less abundant on boulders and ledges in the shallow subtidal zones to the west of Pemaquid (J. Vavrinec, unpublished data), there still are large distribution overlaps with Jonah crabs. Sea urchin harvesters have provided anecdotal evidence that crab predation on sea urchins in the Pemaquid and Penobscot Bay regions has increased recently. Future studies need to address the generality of this interaction in a broader ecosystem.

Cascading system-wide changes

It is unlikely that Jonah crab predation on sea urchins was a strong interaction that went unnoticed until now. Instead, it is more likely that increased Jonah crab abundance in the Gulf of Maine since 2000 (Fig. 16) has forced crabs to feed on urchins. We speculate that relatively recent top-down changes in ecosystem structure and function may be driving the increased importance of crab predation on urchins.

Increased suitable recruitment habitat is one possible cause of increased Jonah crab abundance. Intense harvesting of sea urchins has expanded fleshy algal beds in the coastal zones of the Gulf of Maine in the last 10 years (Vavrinec, in prep., McNaught 1999). McNaught (1999) attributed differential urchin post-settlement survival to a compelling pattern of more juvenile rock crabs in fleshy macroalgal beds than in coralline barrens. He suggested that following urchin extirpation, fleshy macroalgal beds

persist because rock crab predation prevents urchin recruitment, which keeps grazing pressure fundamentally nonexistent. If Jonah crab juveniles follow a similar abundance pattern, then they facilitate their own population increase by removing grazing pressure from the system when they prey on urchins.

Currently, there is little information about the distribution and abundance of juvenile Jonah crabs in the Gulf of Maine. Krouse (1979) suggested that Jonah crab nursery habitats are in deep water because no Jonah crabs less than 67 mm CW were caught in lobster and research traps, but trap sampling may have selectively caught only large crabs. Palma *et al.* (1999) were unable to accurately sample Jonah crab settlement using the same methods that were effective for lobster and rock crabs in four regions of the Gulf of Maine. Jonah crab juveniles (< 10 mm CW) were sampled in the Gulf of Maine at 5 m depth from both a ledge dominated by macroalgae and a cobble-sand habitat (Williams and Wahle 1992). In addition, crabs less than 25 mm CW were sampled at 10 m depth at Cape Elizabeth (Fig 12). These sparse pieces of evidence suggest that at least some proportion of Jonah crabs settle in shallow water where they may feed on juvenile sea urchins.

In addition, groundfish including Atlantic cod (*Gadus morhua*) and haddock (*Melagrammus aeglefinus*) have been described historically as rapacious feeders that devour benthic fauna, including *Cancer* spp. (Collette and Klein-MacPhee 2002). Jonah crabs were “several times found in stomachs of cod taken on the Cod Ledges” (about 1 nm from Cape Elizabeth) in the mid 1800s (Smith 1879), and even today cod exhibit a high preference for *Cancer* spp. (Link and Garrison 2002). Predation by groundfish can significantly reduce populations of large, benthic invertebrates (Ojeda and Dearborn

1991, Witman and Sebens 1992, Vadas and Steneck 1995). Remaining cod populations in the Gulf of Maine have plummeted since 1991 (Collette and Klein-MacPhee 2002). *Cancer spp.* (in specific Jonah crabs) have been increasing concurrent with the continued decline of Gulf of Maine cod populations (Fig. 16, Link and Garrison 2002). Release from predatory control by cod and other predatory groundfish may be another cause of the current, anomalously high Jonah crab abundance in the Gulf of Maine.

Ecosystem baselines are changing rapidly in the Gulf of Maine as fishing continues to remove species. Because this is a relatively species depauperate system, there is little redundancy in important functions such as predation and grazing. Community phase-shifts are difficult to reverse in a low diversity system because few redundant species promote stability (May 1971). Therefore, it is not surprising that abundance changes in a few strongly interacting species (e.g. cod and sea urchins) can produce similar system-wide consequences as seen in the northeast Pacific (Estes and Palmisano 1974). But in contrast to the dynamics of the northeast Pacific, we have observed a shift in apex predator species in the Gulf of Maine that is probably more due to predator release of an otherwise weakly interacting species, rather than changing food resources (Estes et al. 1998). We hypothesize that Jonah crabs have become apex predators because functional elimination of predatory groundfish and benthic grazing sea urchins have created conditions that allowed a drastic population increase; and only at high density is this mesopredator able to effectively control benthic community structure.

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