

Differential regulatory roles of crustacean predators in a sub-arctic, soft-sediment system

Pedro A. Quijón^{1,3,*}, Paul V. R. Snelgrove^{1,2}

¹Ocean Sciences Centre and Biology Department, Memorial University of Newfoundland, St. John's, Newfoundland A1C 5S7, Canada

²Canada Research Chair in Boreal and Cold Ocean Systems

³Present address: Institute of Marine and Coastal Sciences, Rutgers University, 71 Dudley Rd, New Brunswick, New Jersey 08901-8521, USA

ABSTRACT: The role of predation in structuring soft-sediment communities varies as a function of the number and composition of predators that co-occur in a given habitat. In Bonne Bay, Newfoundland, contrasting abundances of predators in different areas of the bay may contribute to different regulatory roles of predators on infauna. To test this hypothesis, results from a field exclusion experiment were compared with 5 laboratory experiments that measured the individual effects of the main crustacean predators of the bay: snow crab, rock crab, and toad crab. In the field experiment, the exclusion of predators generated clear differences in infaunal composition, and 2 species (the polychaete *Pholoe tecta* and the clam *Macoma calcareea*) dominated exclusion treatments. Predator exclusion also resulted in a significant increase in density, but only a modest increase in infaunal diversity. In the laboratory, fresh, undisturbed sediment cores were paired with similar cores, protected by mesh and exposed to each crab species in order to test for their potential effects on infaunal communities. Results indicate that snow crab and rock crab have clear effects on species composition and, as was the case with the field experiment, the infaunal species *P. tecta* and *M. calcareea* dominated exclusion treatments for both predatory crabs. These predators also reduced total infaunal density, but only rock crab significantly reduced species richness. In contrast, toad crab effects were not significant. Given that snow crab and rock crab are both targeted by commercial fisheries in Atlantic Canada, our results suggest that crab fishery removal may have multiple indirect effects on infaunal communities.

KEY WORDS: Predation · Sediment · Sub-arctic · Exclusion · Diversity

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Two general conclusions have emerged from studies on predation in soft-sediment communities: exclusion of predators tends to enhance total infaunal density, but density increases do not result in competitive exclusion of some species (Peterson 1979, Wilson 1991, Olafsson et al. 1994, Lenihan & Micheli 2001). These conclusions have often been used to predict changes in benthic communities as a consequence of natural or artificial variation in numbers of predators (Hall et al. 1990). Although predation at the local scale often pro-

duces a change in prey communities (Seitz & Lipcius 2001), this prediction may not be sufficiently specific or informative (Hilborn & Mangel 1997). Our inability to accurately predict the outcome of exclusion experiments (Thrush 1999) is related to the web of indirect interactions among infaunal species (Ambrose 1984, Posey & Hines 1991, Kneib 1991), and to the natural variability of predators co-occurring in a given area (Hines et al. 1990, Davis et al. 2003). Different predators likely have different prey preferences, rates of predation (Davis et al. 2003), and degrees of sediment/habitat alteration (Palomo et al. 2003). Regard-

*Email: quijon@marine.rutgers.edu

less, most experimental studies continue to analyze the role of predation by manipulating a single predator species (Sih et al. 1998).

Studies on the role of predatory crustaceans at boreal and sub-arctic latitudes ($>35^{\circ}\text{N}$) have lagged in the use of experimental approaches (Beal et al. 2001), particularly in sedimentary habitats as deep as 30 m. Literature describing predation effects on benthic communities has largely been restricted to correlative studies and stomach content analyses (Scarrat & Lowe 1972, Hudon & Lamarche 1989, Lefevre & Brêthes 1991, Stehlik 1993). A notable exception is the work on individual predator-prey interactions, particularly on the rock crab *Cancer irroratus*. This work has shown that rock crab feeding rates exhibit a broad range of variation that depends on site, temperature, and season, and also depends on type, size, behavior, density, and even odor plumes of prey (Elner & Jamieson 1979, Drummond-Davis et al. 1982, Barbeau & Scheibling 1994a,b, Salierno et al. 2003). If such variation occurs at the population level, at least the same degree of variation should be expected in comparing the predation effects of different crab species. For instance, based on feeding rates alone, the potential effects of rock crab are clearly different from those of the snow crab *Chionoecetes opilio*, and *Hyas* spp. toad crab (Thompson & Hawryluk 1989, Nadeau & Cliche 1998).

The guild of predatory crustaceans that dominates the Canadian Maritimes to the Eastern sub-arctic comprises snow crab, rock crab, toad crab, pandalid shrimp (*Pandalus borealis*, *P. montagui*), and crangonid shrimp (*Crangon septemspinosa*) among others (cf. Squires 1996). Several members of this guild have increased in commercial importance and apparently in numbers and distribution over the last 2 decades (Mallet & Landsburg 1996, Bundy 2001). For instance, increasing landings of snow crab have paralleled an increase in numbers and distribution on the Scotian and Newfoundland shelves since the late 1980s (Tremblay et al. 1994, Sainte-Marie 1997). Similar increases are also apparent in the Gulf of St. Lawrence and other sub-regions, but the lack of long-term data-sets precludes the description of more conclusive trends in this and other less-studied species. Correlative studies have started to link these historical changes in crustacean populations to temperature regime shifts (cf. Gilbert et al. 1996, Colbourne et al. 2002), reduced cannibalism and increased recruitment (eg. in snow crab, Dutil et al. 1997, Lovrich & Sainte-Marie 1997), the collapse or reduction of cod (*Gadus morhua*) and other major predators on large decapod crustaceans (eg. Robichaud et al. 1991, Worm & Myers 2003), and the interaction of these factors. Snow crab and other decapod crustaceans primarily feed on bottom dwelling organisms such as polychaetes, clams, and per-

acarid crustaceans (Scarrat & Lowe 1972, Brêthes et al. 1984, Stehlik 1993, Squires & Dawe 2003). As cod and other major fish predators are largely pelagic, the current dominance of decapod crustaceans suggests that the western North Atlantic shelf ecosystem has experienced a switch in predator regimes from primarily pelagic to bottom-feeding predators. Irrespective of the relative contribution of cod and other major predators to the spatial-temporal patterns exhibited by decapod crustaceans, this switch may have cascading effects on benthic community structure (Quijón & Snelgrove in press).

In order to evaluate the generality of this hypothesis, studies are needed to examine the individual effects of different predators. Such studies could clarify the multiple influences of incipient small-scale fisheries targeting some species (e.g. rock crab and toad crab) and a large-scale fishery targeting others (e.g. snow crab) (cf. Mallet & Landsburg 1996, Sainte-Marie 1997, Paul et al. 2001). This study analyses the influence of snow crab, rock crab, and toad crab on shallow (~15 to 30 m deep), soft-sediment communities of Bonne Bay, a sub-arctic (~49°N) Newfoundland fjord. We used laboratory experiments to test for the individual effects of these 3 species on composition, richness, and density of macrobenthic organisms. We then manipulated snow crab and rock crab densities to reflect their variable abundance in different areas of the bay. We compared these results with a field exclusion experiment to determine whether results from the controlled, small-scale laboratory experiments were consistent with those observed at larger spatial and temporal scales in the field.

MATERIALS AND METHODS

Study area. Bonne Bay fjord is located in Western Newfoundland, NW Atlantic (Fig. 1). Sediment infaunal cores for the laboratory experiments were collected from Small Cove (~15 m deep; 49°28'84"N, 57°54'48"W), a protected site located in South Arm, which is one of the 2 main arms of the fjord. South Arm is a basin up to ~55 m deep, and opens to the waters of the Gulf of St. Lawrence (Gilbert & Pettigrew 1993). Small Cove sediments contain sparse gravel and pebble and are primarily fine sands (~60% in weight) with silt (~30%), and clay (~10%). C:N ratios average 15.9 (± 0.6 , 95% CI), a value relatively high in comparison to those reported for freshly settled detritus (~13; Blackburn et al. 1996), but low compared with other sites in East Arm (eg. 20.6 \pm 0.95 in South East Arm; Quijón & Snelgrove in press). The field experiment was carried out in close proximity to that area, at ~30 m depth. Preliminary sampling and analyses did not indi-

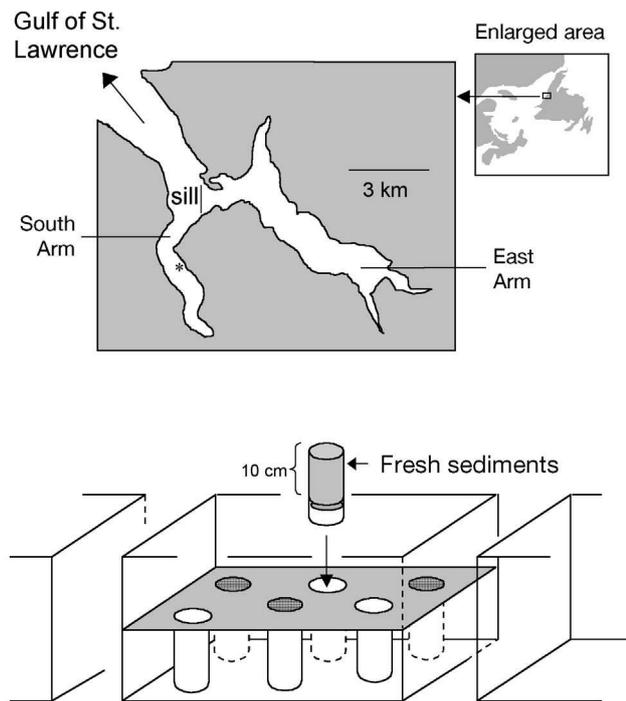


Fig. 1. Top: Bonne Bay, with the location of South Arm and Small Cove (indicated by *). Bottom: Experimental tanks showing the arrangement of sediment cores protected from (exclusion, with mesh top) and exposed to (predator, open cores) crab predation

cate any differences in benthic composition and overall abundance between the 2 depths, and samples from both locations were considered representative of the same infaunal community.

Prey and predators. Infaunal species composition for this and other areas of the fjord have been described by Wieckzoreck & Hooper (1995), and Quijón & Snelgrove (in press). The community includes a total of ~55 species, composed primarily by polychaetes (34 spp.), bivalves (10 spp.), amphipods (4 spp.), and cumaceans (3 spp.). The most abundant species are the polychaetes *Paradoneis lyra*, *Prionospio steenstrupi*, and the bivalves *Astarte* sp., *Thyasira flexuosa*, and *Cerastoderma pinnulisum* (see Fig. 3 for a comparison of relative abundances). Snow crab, rock crab, and toad crab are the most abundant and frequently collected predators in the experimental area (Quijón & Snelgrove in press), as shown by successive deployments of 60 × 40 × 30 cm traps fitted with ~1.5 cm mesh and baited with mackerel. Mesh size was appropriate for the retention of immature, adolescent (sensu Sainte-Marie et al. 1995), and small adult crabs that were representative of size composition at this depth and season, particularly for snow crab populations in the area (Comeau et al. 1998). Deployments were all carried out at 30 to 50 m depth approximately every 2 wk during

the summers of 1999 to 2001 (see comparison of densities in 'Discussion').

Field experiment. A field experiment including full cages or 'exclusions', partial cages or 'artifact treatments', and ambient undisturbed sediments or 'predation treatments' was deployed at ~30 m depth in Small Cove (Fig. 1). Each treatment included 4 replicates that were haphazardly interspersed on the seafloor. Cages (1 m diameter × 15 cm high, pushed 3 cm into the sediment) were circular in shape to minimize differential erosion or deposition of sediments in different areas of the cages. Each cage was anchored to the bottom by 4 legs that extended into the sediment. Plastic mesh (1 cm × 1 cm) covered full cages and 50% of the area of each artifact treatment (50% of top and sides). The design of the artifact treatments was intended to allow predators to access and potentially feed on infauna, while mimicking the effects of the full cages on the local hydrodynamics (see review by Olafsson et al. 1994).

Macrobenthic organisms were sampled with tube cores (7 cm diameter; 10 cm deep; 2 cores per sample) that were collected by scuba divers. Initial sampling ('before') took place on June 25 1999, immediately prior to deployment of full cages, artifact treatments, and ambient sediments. Cages were subsequently sampled after 4 (exclusion treatments) and 8 (exclusion treatments and artifact treatments) wk periods ('after'; see data analysis below). To minimize potential disturbance effects resulting in loss of independence between 4 and 8 wk treatments, cages were removed immediately after sampling and sampling was never repeated within a given caged or ambient location. This design allowed us to evaluate the influence of predation (predator versus exclusion) at 2 time periods (4 and 8 wk) and to evaluate the possibility of experimental artifacts only over the 8 wk period. For this last analysis, additional sediment cores were collected from all treatments and used to evaluate grain size distribution and CHN content. These analyses allowed us to evaluate possible sediment-mediated artifacts related to caging treatments.

Laboratory experiments. During the summers of 1999 and 2000, 5 laboratory experiments were conducted to evaluate the individual influence of snow crab (*Chionoecetes opilio* Fabricius), rock crab (*Cancer irroratus* Say), and toad crab (*Hyas* spp.). Fresh sediment cores (7 cm diameter) with intact infauna were collected by divers and carefully transported to the Bonne Bay Field Station (~1.5 km away). In the laboratory, experiments were established in a series of 3 flow-through tanks supplied with cold-water (1 to 2°C) from the bay. Six sediment cores were placed in each tank (18 cores per experiment) so that the upper lip of the cores was flush with a plastic plate that

served as a false bottom (see Fig. 1). Before placing the cores in the tanks, the sediment inside was carefully extruded so that it was flush with the upper lip of the cores and thus, the sediment surface would be flush with the false bottom once positioned in the tanks. Sediments (and associated infauna) were acclimated to laboratory conditions for 24 h prior to the initiation of the experiments.

Male crabs of 60 to 80 mm carapace width (adolescent and small adult males) were collected in regular sampling of Bonne Bay as described above. Crabs were acclimated for at least 24 h before 1 individual was added to each tank. Different crabs were used for each experiment. Crabs had access to 3 of the cores (predator treatments), whereas the other 3 cores were protected from crabs with a $\sim 0.6 \times 0.6$ cm plastic mesh (exclusion treatment). Predator and exclusion cores were randomly distributed within each tank (see data analysis for details on sources of variation and degrees of freedom). Experiments lasted for 96 h, after which the crab from each tank was removed, tanks were carefully drained, and sediment cores were collected and processed as described below. Identical procedures were used to test the effects of snow crab, rock crab, and toad crab (1 crab per tank; 3 independent experiments). For 2 additional experiments, densities of snow crab and rock crab were doubled to 2 individuals per tank; these experiments were included to reflect the higher density of these species in comparison with toad crab in Small Cove as well as other areas of the bay (Quijón & Snelgrove in press). For each experiment, fresh sediments were collected from the same site.

Sample processing and analysis. Cores of sediments from field and laboratory experiments were sieved through a 500 μm mesh, fixed in a 10% formalin-seawater mixture, and then stored in 70% ethanol with Rose Bengal. Benthic organisms were counted and identified to species level. Samples of sediment ($n = 4$ per treatment) were used to describe the bottom of the study area and to evaluate potential artifact effects by comparing predator and artifact treatments. Those samples were analyzed as follow: a sub-sample was separated in >350 , >250 , >177 , >125 , >88 , >62.5 , >53 , >44 , >37 , >31 , >15 , >7.8 , >3.9 , >2.0 , >0.98 , >0.49 μm fractions (see details in Ramey & Snelgrove 2003). Each fraction was expressed as percentage of total dry weight, and pooled into medium sand (>250 μm), fine and very fine sand (>62.5 μm), silt (>3.9 μm), and clay (<3.9 μm) based on the Wentworth scale (Folk 1980). A second sub-sample of sediment was processed with a CHN analyzer (Perkin Elmer Model 2400) to estimate C and N as a function of sediment dry weight and to determine C:N ratios (an estimator of food quality for deposit feeders; Blackburn et al. 1996).

Data analysis. For the field experiment and each laboratory experiment, benthic community structure was analyzed using Chord Normalized Expected Species Shared (CNESS). This similarity index estimates the number of species shared between 2 samples based on a random draw of m individuals (Trueblood et al. 1994). A random draw of $m = 10$ was used for all data sets except the experiment using 1 rock crab ($m = 5$; overall density of most samples exposed to rock crabs was <10 ind. per core, necessitating a smaller size for m). The CNESS dissimilarity sample \times species matrix was also used to cluster samples based on unweighted pair-group mean average sorting. The program COMPAH 90 (E. D. Gallagher, University of Massachusetts, Boston) was used for this analysis. The CNESS sample \times species matrix was then transformed to a normalized hypergeometric probability matrix (H), and used in a Principal Components Analysis (hereafter called PCA-H) to produce a 2-dimensional metric scaling of CNESS distances among samples. This approach produced a very similar representation as multidimensional scaling (P. A. Quijón & P. V. R. Snelgrove unpubl. data), but the CNESS plots have the added advantage that they can be overlaid with Gabriel Euclidean Distance Biplots (Gabriel 1971) that identify species particularly important in determining CNESS variability among samples, and thus, driving community composition.

Total density (N) and number of species (S) per sample (77 cm^2 in the field experiment; 38.5 cm^2 in the laboratory) were also calculated. For the field experiment, statistical comparisons were carried out with a 2-factor 'before-after, control-impact' (BACI) design. In this factorial design, the evidence for an impact (predator exclusion in this case) appears as a significant time \times treatment interaction term (Green 1979). As a significant interaction term does not necessarily imply predator-related causal effects (cf. Underwood 1996), results of these analyses were examined with caution and contrasted with results from the corresponding PCA-H analyses. The model of the ANOVA was $y = \mu + \text{time} + \text{treatment} + (\text{time} \times \text{treatment}) + \epsilon$, where y refers to each response variable, μ is a mean constant, *time* refers to before-after (0 to 4 wk or 0 to 8 wk), *treatment* refers to control-impact (predator versus exclusion), and ϵ refers to the error term. Although the BACI design is powerful, more recent versions include nested terms (observation [time]) that require at least 2 observations 'before' and 'after' (cf. Stewart-Oaten & Bence 2001), which we do not have. Nonetheless, our approach is more powerful than separate predator/exclusion contrasts for 4 and 8 wk. An additional ANOVA model excluding time and interactions factors was used to compare artifact and predator treatments in the 8th

week. All the factors associated with the field experiment were considered fixed (Sokal & Rohlf 1994).

Statistical comparisons between predator and exclusion treatments in the laboratory experiments were carried out with a randomized block design. The model for these comparisons was $y = \mu + tank + treatment + \epsilon$, where *tank* refers to replicate tanks (1 to 3), *treatment* refers to predator versus exclusion treatments, and ϵ refers to the error term. Tank and treatment were considered random and fixed factors, respectively. Assumptions of normality and homogeneity of residuals were examined in each analysis (the latter with the Levene test), and in cases where data did not fit these assumptions, data were $\log_e(x)$ transformed (Sokal & Rohlf 1994).

RESULTS

Field experiment and community structure

The first 2 principal components of the PCA-H explained 35% of the variation in species density and composition (Fig. 2). Exclusion cages were clearly separated from predator (ambient) and artifact treatments, indicating a change in species composition and density in response to predator exclusion. The biplots identified *Pholoe tecta* and *Macoma calcarea* as the species that characterized exclusion sediments, and 3 polychaetes (*Tharyx acutus*, *Mediomastus ambiseta*, and *Aricidea nolani*) characterized predator (ambient) and artifact treatments. Densities of the most abundant species in the area (Fig. 3, upper panel) were not significantly different between treatments ($p > 0.05$). In contrast, densities of the 3 species identified by the biplots (*P. tecta*, *M. calcarea*, and *T. acutus*) were significantly higher in the corresponding treatments ($p < 0.05$; Fig. 3, lower panels).

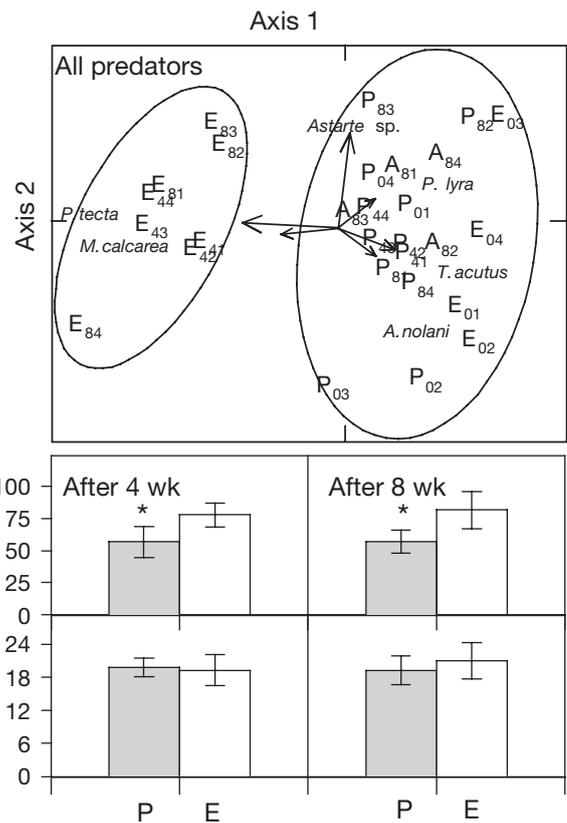


Fig. 2. Field experiment: Upper panel: Major clusters and metric scaling plots of samples based on PCA-H of CNESS similarity for exclusion (E), predator (P), and artifact (A) treatments. Subscripts denote duration (0, 4 or 8 wk) and replicate (1 to 4). Arrows are Gabriel biplots, which identify species that contribute the most to between-sample differences. Bottom panels: Average and 95% confidence intervals of density (N) and species richness (S) per 77 cm². For simplicity, only predator and exclusions after 4 and 8 wk are plotted (see text). *: $p < 0.05$

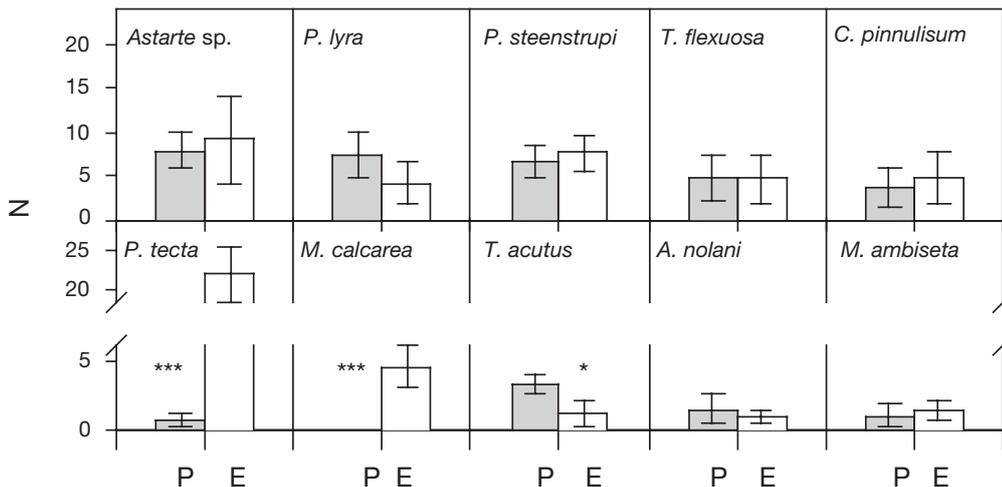


Fig. 3. Field experiment: Average and 95% confidence intervals of density (N) per 77 cm² of the most abundant species in the area (top panels), and those identified by Gabriel biplots (lower panels; see Fig. 2). P denotes predator-exposed treatments and E denotes exclusion treatments. Given that no differences were detected between 4 and 8 wk, the values presented correspond to averages of both sampling periods. *: $p < 0.05$; ***: $p < 0.001$

Table 1. Field experiment. Sum of square (SS) values from factorial ANOVA comparisons of total density (N) and species richness (S) per sample. Factors include time (before-after, i.e. 0 to 4 and 0 to 8 wk), treatment (predator versus exclusion) and their interaction. **: $p < 0.01$

Source	df	N		S	
		0 to 4 wk	0 to 8 wk	0 to 4 wk	0 to 8 wk
Time	1	885.06**	1139.06**	2.25	7.56
Treatment	1	95.06	175.56	0.25	7.56
Time × Treatment	1	1040.06**	1278.06**	2.25	0.56
Error	12	946.25	1147.75	65.00	86.25

Table 2. Field experiment. Sum of square (SS) values from ANOVAs comparing artifact and predation (ambient) treatments. Response variables include density (N), species richness (S), percentages of medium sand (m-sand), fine + very fine sand (f-sand), silt, clay, and C:N ratio. All significance values are > 0.05

	df	N	S	m-sand	f-sand	silt	clay	C:N
Treatment	1	0.50	0.13	63.80	3.59	20.58	28.57	0.04
Error	6	687.00	40.75	672.80	124.98	392.69	87.40	12.49

Predator-exclusion effects on total density were detected after 4 and 8 wk as shown by significant time × treatment interaction terms in both ANOVAs (Table 1). A comparison of predator versus exclusion treatment at both times (4 and 8 wk) indicates that total densities increased with the exclusion of predators (Fig. 2, lower panels) but no significant effects on species numbers were detected ($p > 0.05$; Table 1, Fig. 2). These results were interpreted to be unrelated to caging artifacts, given the absence of a significant difference between predator and artifact treatments when faunal variables were compared ($p = 0.897$ to 0.949 ; Table 2). The same applies to results obtained from the comparison of sedimentary characteristics: none of the sedimentary variables measured in the artifact treatment was significantly different from those measured in the predator treatment ($p = 0.211$ to 0.893 ; Table 2).

Laboratory experiments

The influence of the 2 densities of snow crab is summarized in Fig. 4. Together, the 2 first principal components of each analysis explained 50% (1 snow crab per tank) and 47% (2 snow crab), of the overall variation in community structure. At both snow crab densities, sediments protected from predation (exclusion treatments) were clustered and segregated from sediments exposed to predators along the first axis. Gabriel biplots identified the polychaete *Pholoe tecta* as the main species characterizing exclusion treatments. Two other polychaetes (*Euchone papillosa* and *Mediomastus ambiseta*) and a small amphipod (*Phoxocephalus holbolli*) were most important in open (predator) sediments in experiments using 1 and 2 snow crab, respectively (Fig. 4, top panels). Between-treatment differences in the density of the main species characterizing exclusion and

predator sediments (*P. tecta* and *E. papillosa*) were significant ($p < 0.001$; see below). Overall, the exclusion of snow crab resulted in total density and species richness up to 30 and 27% higher, respectively. However, these changes were significant in only 2 of the 4 comparisons (Table 3, Fig. 4, lower panels).

Rock crab also influenced community composition (PCA 1 and 2 explained 36 and 38% of variation for 1 and 2 rock crab, respectively); exclusion treatments (E) were clustered and separated from predator (P) treatments along the first principal component of both PCA-H plots (Fig. 5, top panels). The most important species in exclusion treatments of both experiments were the polychaete *Pholoe tecta* and the bivalve *Macoma calcareea*. The polychaetes *Aricidea nolani* and *Phyllodoce mucosa* were particularly important in sediments exposed to predation by 1 rock crab (see

Table 3. Laboratory experiments. Sum of square (SS) values from ANOVA comparisons of density (N) and species richness (S) per sample. Factors include tank and treatment, where treatment refers to predator versus exclusion. *: $p < 0.05$; ***: $p < 0.001$

Variable	Source	df	Snow crab		Rock crab		Toad crab 1 ind. tank ⁻¹
			1 ind. tank ⁻¹	2 ind. tank ⁻¹	1 ind. tank ⁻¹	2 ind. tank ⁻¹	
Density	Tank	2	784.3	146.8	625.3	134.3	600.4
	Treatment	1	1512.5*	470.2	11450.9***	7360.9***	2112.5
	Error	14	3563.7	1786.1	3373.8	2228.8	11314.0
Species richness	Tank	2	0.444	7.444	29.78	23.1	0.11
	Treatment	1	2.722	20.056*	338.0***	117.6***	5.55
	Error	14	10.778	53.444	104.0	84.4	53.44

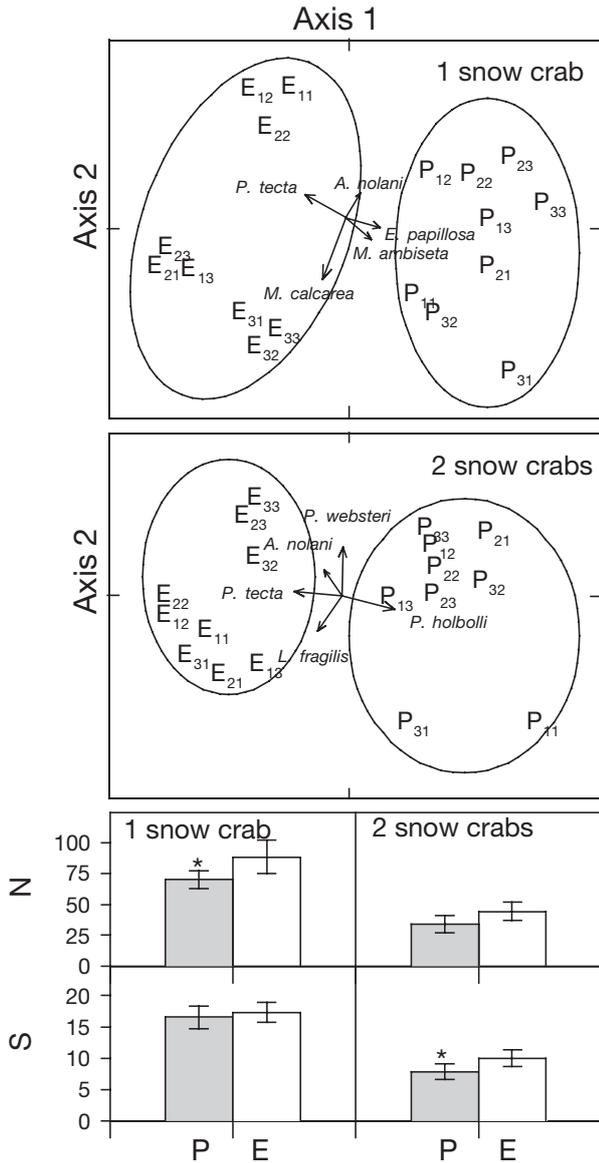


Fig. 4. Laboratory predation experiments using 1 and 2 snow crabs. Top panels: Major clusters and metric scaling plot of samples based on PCA-H of CNESS similarity. Letters indicate treatments: P: predator, with snow crab; E: exclusion. Subscripts denote tank and replicate, respectively. Bottom panels: Average and 95% confidence intervals of density (N) and species richness (S) per 38.5 cm² from predator (P: with crab) and exclusion (E) treatments. *:p < 0.05

species density comparisons below). The amphipod *Phoxocephalus holbolli* the polychaete, *Laonice cirrata*, and an unidentified juvenile clam were the most important in exposed sediments in experiments with the higher density of rock crabs. The exclusion of rock crab resulted in total infaunal densities that were 2 times greater than in sediments exposed to predators, and species richness was elevated more than 50% (p < 0.05 in all comparisons) (Table 3; Fig. 5, lower panels).

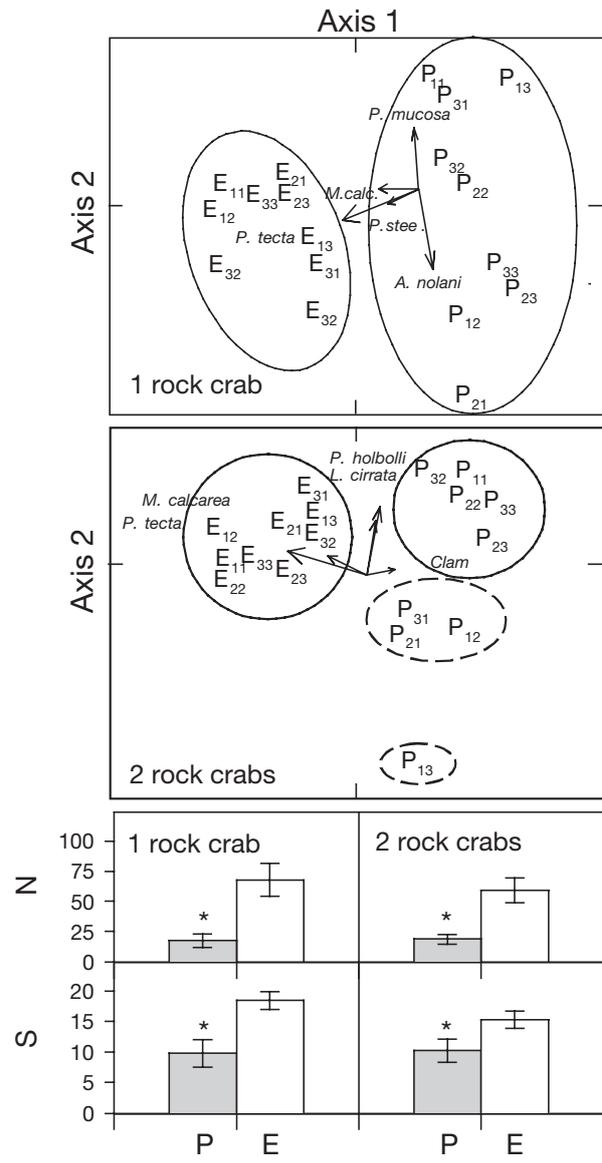


Fig. 5. Laboratory predation experiments using 1 and 2 rock crabs. Top panels: Major clusters and metric scaling plots of samples based on PCA-H of CNESS similarity. Bottom panels: Density (N) and species richness (S) per 38.5 cm². Letters and subscripts as in Fig. 4 (*M. calc.* = *Macoma calcarea*; *P. stee.* = *Prionospio steenstrupi*). *:p < 0.05

The exclusion of toad crab did not result in changes in composition, total density, or species richness (p > 0.05) (Table 3, Fig. 6). The first 2 components of the PCA-H explained 40% of the observed variation, but samples from predator and exclusion treatments were all interspersed and mixed in the PCA-H plot (Fig. 6). Gabriel biplots identified *Macoma calcarea* and 4 species of polychaetes as the most important taxa in describing variability among cores: *Tharyx acutus*, *Eteone heteropoda*, *Syllides japonicus*, and

DISCUSSION

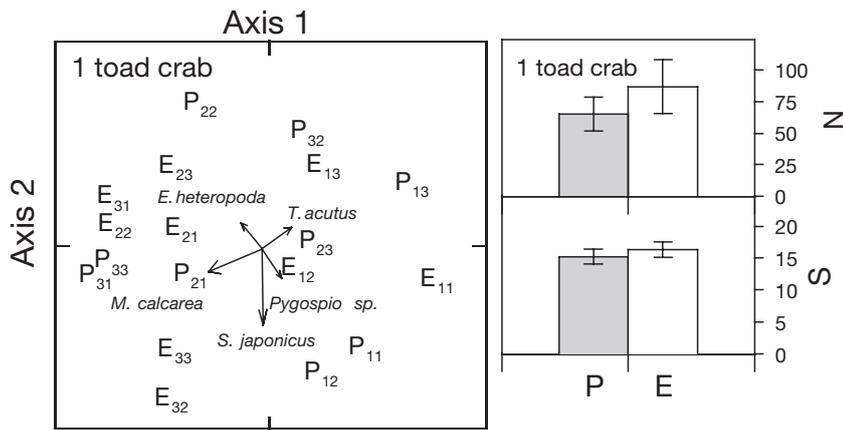


Fig. 6. Laboratory predation experiments using 1 toad crab. Left panel: Major clusters and metric scaling plots of samples based on PCA-H of CNESS similarity. Right panels: Density (N) and species richness (S) per 38.5 cm². Letters and subscripts as in Fig. 4

Our results indicate that the influence of the exclusion of predators is not simply a function of the number of epibenthic predators in a given area (Quijón & Snelgrove in press), but also depends on their composition. Irrespective of the densities used here, snow crab and rock crab, which are 2 species that are relatively common in Bonne Bay (A. Quijón & P. V. R. Snelgrove unpubl. data), displayed a strong influence over 1 or more community variables, so that exclusion treatments were quite distinct from sediments exposed to predators.

Influence on species composition

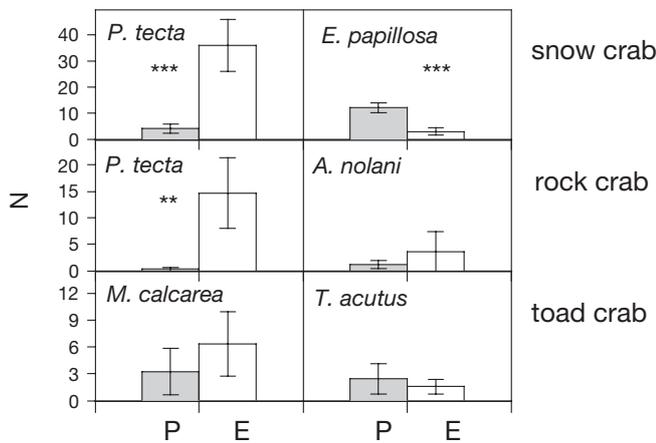


Fig. 7. Average and 95% confidence intervals of density (N) per 38.5 cm² of the most important species contributing to the differences between exclusion (E) and predator (P) treatments in the laboratory experiments. For simplicity, only data from experiments using 1 crab per tank are plotted. **: p < 0.01; ***: p < 0.001

Pygospio sp. Nonetheless, variation in infaunal composition was apparently unrelated to the exclusion of toad crab.

A comparison of the density of the main species characterizing exclusion and predator treatments in the 3 experiments using 1 crab is summarized in Fig. 7. The density of *Pholoe tecta*, the species most strongly associated with snow crab and rock crab exclusion treatments, was significantly more abundant in exclusion sediments (p < 0.01). The most abundant species in ambient sediments varied in density but did not exhibit consistent between-treatment differences.

Gabriel biplots generally identified a similar species response to the exclusion of snow crab and rock crab: *Pholoe tecta* and *Macoma calcarea* were key species in describing infauna in exclusion treatments. *P. tecta* is a mobile predatory polychaete (Fauchald & Jumars 1979), and its high abundance in the exclusion sediments in comparison with predator treatments suggests that (1) this species actively escapes predation by moving into 'refuge' habitats, and (2) that more than 2 trophic levels may be involved in the effects detected in community structure (Ambrose 1984, Commito & Ambrose 1985). Ambrose (1984) argued against the classical idea of 2 trophic levels represented by epibenthic predators (e.g. crabs, shrimps, fishes) and infaunal prey, and instead proposed an additional 'predatory infauna' level that mediates the interactions between top epibenthic and non-predatory infauna. Wilson (1986) questioned this view, arguing that in order to verify the existence of such trophic complexity in soft sediments, top (epibenthic) predators should display strong preference for predatory infaunal species. Our design was not intended to resolve this debate, but using Wilson's arguments, our results clearly support the view of Ambrose (1984): *P. tecta* was several times more abundant in exclusion than in predator treatments, both in field and in laboratory experiments. Further studies are required to clarify the interactions between *P. tecta* and non-predatory infaunal species such as *Tharyx acutus*, a cirratulid polychaete that occurred in higher numbers in sediments exposed to predators relative to sediments that excluded top (epibenthic) predators (cf. Kneib 1991 and Posey & Hines 1991).

The higher density of *Macoma calcarea* in exclusion treatments may be the result of increased mortality in

exposed sediments, and active immigration into predator exclusion treatments. Both possibilities are consistent with studies indicating that species of *Macoma* are an important dietary component of snow crab (Wieczoreck & Hooper 1995), and have the capacity for secondary (adult) dispersal following disturbance or predation (Armonies 1992). Intriguingly, *Pholoe tecta* has not been reported from stomach contents of any of those predators. However, similar polychaetes classified as 'Sigalionidae', 'Polynoidae', and 'scale worms' have been listed amongst the most frequent prey of snow crab (Lefevre & Brêthes 1991). This overlap may not be a coincidence given the taxonomic affinity between these 3 groups and Pholoidae (originally part of Sigalionidae, Rouse & Pleijel 2001), and their potentially problematic identification in partially digested specimens. The importance of *M. calcaria* and potentially *P. tecta* in the diet of snow crab and other crustaceans in the area, suggests that the results of the laboratory exclusions are causally related to the foraging and not just to the presence of predators. However, further studies are required to evaluate potential responses of infaunal species to predator chemo (odor)-tactical signals, as demonstrated, for example, in clam and crab species (e.g. Finelli et al. 2000, Salierno et al. 2003).

As expected, a different set of species was associated with sediments exposed to snow crab or rock crab. In the experiments using toad crab, however, samples did not segregate as a function of treatment, suggesting little influence of this species on benthic composition. Toad crabs were observed feeding on exposed sediment cores and generating some degree of sediment disturbance. Therefore, the absence of stronger effects may result from some degree of re-colonization of exposed cores by fauna moving from cores protected from predation (cf. Zajac et al. 1998). Re-colonization was presumed to occur in all of the other laboratory experiments (using snow crab and rock crab), but only for toad crab feeding did re-colonization by mobile infauna obliterate any predation effect. The mesh used to exclude predators and the distance among cores inside each tank were intended to allow migration and interchange of infauna. Two arguments justified such a decision. First, adult or juvenile dispersal and re-colonization have been demonstrated in the literature (eg. Comito et al. 1995), particularly at small spatial scales (Norkko et al. 2001). Second, this is an escape opportunity available only to those species without strict sedentary habitats at the adult stage (cf. Günther 1992). The lack of laboratory evidence for toad crab-mediated changes in composition suggests that this species plays a minor role in the regulation of these benthic communities.

Influence on density and species richness

Beyond their similar influence on species composition, snow crab and rock crab did play different roles with respect to overall density and species richness. As expected from active predators (Moody & Steneck 1993, Yamada & Boulding 1996), the exclusion of both species enhanced density and species richness. However, snow crab effects were not always significant. In contrast, the exclusion of rock crab produced a stronger and more consistent increase in density and richness. Differences among predator effects are likely a result of their different feeding rates and the degree to which they disturb the sediment while feeding or searching for prey (Thrush 1986, Palomo et al. 2003). Rock crab feeding rates are far higher than those measured in snow crab (cf. Elner & Jamieson 1979, Thompson & Hawryluk 1989, Barbeau & Scheibling 1994a,b). We did not quantify predator-related sediment disturbance, but during the experiments we observed that, rock crab consistently disturbed the upper centimetres of sediment while feeding. In contrast, disturbance by snow crab was restricted to a more careful digging and scraping of sediment while feeding, a behavior already reported from field observations in the area (Wieczoreck & Hooper 1995).

Given the influence of snow crab and rock crab as individual predators, we expected similar (density-independent predation) or more intense (additive effects when adding a second crab to each tank (cf. Real 1979, Weissberger 1999)). Overall, different predator numbers resulted in similar effects on benthic abundance and species richness. Whether these results reflect density-independent predation or simply the existence of some degree of agonistic response that restricts predation is uncertain. These relationships are usually measured in terms of predation (feeding) rates on individual species rather than as generalized predation effects on species assemblages (cf. Stephen & Krebs 1986, Seitz et al. 2001). However, observations carried out during the experiments suggest that agonistic behaviors may be the main factor, at least for rock crab. This behavior explains the apparent contradiction between the voracious feeding activity of individual crabs and the absence of an additive effect when more than 1 crab was added, particularly at such a small scale.

From the laboratory to the field

Results of the field experiment were remarkably similar to those detected in the feeding experiments using snow crab and rock crab. This similarity suggests that even when there is a variety of other invertebrate and

vertebrate predators in the area, that decapod crustaceans, and these 2 species in particular, are likely to be the major players in structuring benthic communities. The same species (*Pholoe tecta* and *Macoma calcarea*) were associated with exclusion treatments, and similar clustering and segregation of these treatments from predator and artifact treatments was detected. The clustering of ambient (with predators) and artifact treatments is also consistent with the lack of apparent artifact effects, as indicated by the non-significant differences between predator and artifact treatments in ANOVAs using an array of faunistic and sedimentary variables (cf. Table 2). Both results suggest that the observed changes are causally related to the exclusion of predators and not to hydrodynamic interference created by the deployment of cages (cf. Hulberg & Oliver 1980, Hall et al. 1990, Steele 1996).

A more variable set of species dominated sediments exposed to predation. As discussed above, *Tharyx acutus* was significantly more abundant in exposed than in exclusion sediments (cf. Fig. 3). We did not identify a specific mechanism to explain this pattern with certainty, but potential negative interactions between this species and those most favored by the exclusion of epibenthic predators (e.g. *Pholoe tecta*) are likely. The length and timing (June to August) of the field experiment suggest that some degree of settlement or recruitment could have taken place during the course of the experiment. However, (1) the lack of artifact effects resulting from the deployment of cages, and (2) the similarity between species composition after 4 and 8 wk, as shown by the PCA-H plots, suggest that cumulative recruitment effects were not a significant factor contributing to our results.

Similarities between field and laboratory experiments suggest that predator foraging, and not just predator presence, is an important, if not the main, mechanism contributing to community structure at the local (metres to 100s of metres) scale (Seitz & Lipcius 2001). Extrapolation beyond this scale, however, requires caution. Processes acting at larger spatial scales may change in intensity (Fauchald & Erikstad 2002) or may simply be different (Schneider et al. 1997, Pace 2001). Overall, these results suggest that experimental manipulations involving habitats with contrasting numbers of snow crab and rock crab will likely result in different outcomes. This hypothesis is consistent with the view that design of predator-exclusion experiments should always incorporate an explicit spatial component (Fernandes et al. 1999). Otherwise, natural

Table 4. Relative abundances of snow crab, rock crab, and toad crab during the summers of 1999 to 2001. Sites compared are Small Cove (experimental site) and Mike's Cove (both located in South Arm), and South East Arm (located in East Arm, see Fig. 1). Values correspond to means ($\pm 95\%$ confidence intervals) of crabs trap⁻¹ d⁻¹ estimated from multiple deployments of traps

Sites (Main Arm)	N	Snow crab	Rock crab	Toad crab
Small Cove – South Arm	16	0.96 (0.59)	0.08 (0.06)	0.15 (0.09)
Mike's Cove – South Arm	14	0.24 (0.18)	0.44 (0.28)	0.03 (0.04)
South-East Arm – East Arm	15	0.21 (0.16)	0.30 (0.20)	0.10 (0.07)

variability in predator numbers (and not just prey numbers) cannot be properly incorporated in models of benthic regulation.

An examination of the abundance of predators in the experimental site (Small Cove, Table 4) suggests that local changes in infaunal composition are most easily attributed to differences in snow crab abundance. This conclusion is supported by the affinity between snow crab diet and the species composition in exclusion treatments (see 'Influence on species composition'), the higher density of snow crab at the Small Cove site relative to other crab species (0.92 crab trap⁻¹ d⁻¹), and the unexpected absence of a significant reduction in species richness. Changes in species numbers are more likely related to feeding by rock crab. This was the only predator that consistently modified this variable, but rock crab was the least abundant crab species at the study site (0.08 crab trap⁻¹ d⁻¹). As is true of predators elsewhere (cf. Hines et al. 1990, Fauchald & Erikstad 2002), rock crab are likely to be more influential in areas of the bay where it aggregates in higher densities (cf. Table 4). At the scale of the bay, this prediction has been already confirmed by experiments carried out in East Arm (Quijón & Snelgrove in press), where rock crab is more abundant and the outcome of predator exclusion experiments shows significant changes in species richness. Moreover, species richness in South Arm ambient sediments, where experimental cores were collected, is significantly higher than in East Arm where rock crab are more abundant, suggesting that rock crab may play a key regulatory role.

Our results suggest that 2 species currently targeted by large- and small-scale commercial fisheries (snow crab and rock crab, respectively) play significant roles in benthic community structure. In principle, this agrees with the view that indirect interactions such as fishery-related trophic cascades are taking place in the North Atlantic (Agardi 2000, Quijón & Snelgrove in press). The individual sizes of snow crabs manipu-

lated in the laboratory and in the depth range at which the field experiments were deployed are representative of the spring-summer populations in Bonne Bay and other coastal areas in the region (Hooper 1986, Ennis et al. 1990, Comeau et al. 1998). However, they are not necessarily representative of populations living in deeper waters and characterized by larger proportions of exploitable crabs (>95 mm CW males, Sainte-Marie 1997). Given that young and adult (exploitable) snow crabs display different feeding habits (e.g. Lovrich & Sainte-Marie 1997), the extrapolation of our results to complete populations, or specifically to the exploitable fraction of the snow crab populations, should be undertaken with caution until similar experiments are done with larger crabs. Given that this species constitutes the main fishery resource in eastern Canada, the stability of its stocks (cf. Orensanz et al. 1998, Paul et al. 2001) may have important consequences for the recruitment to the sizes manipulated here, and subsequently, for processes that regulate benthic communities. If, like cod, snow crab stocks and populations collapse and the species fails to recover in the short term (cf. Sainte-Marie 1997 for a review of temporal trends and resource management), parallel changes in benthic community structure are likely to occur.

Although the intensity and spatial extent of the rock crab fishery is less than that for snow crab, caution is again needed in extrapolating our results to larger (exploitable: >102 CW) individuals. Although fishery landings are smaller than those of snow crab, the growth of the rock crab fishery in areas such as the Gulf of St. Lawrence has been substantial over the last decade (Mallet & Landsburg 1996). If that growth continues, and indirectly reduces the recruitment and subsequent abundance of the young stages manipulated here, changes in benthic communities can also be expected. These changes would not be limited to variations in density and species composition, but would also include species diversity, given the strong influence of rock crab on every aspect of the benthic community structure analyzed here.

Acknowledgements. We thank D. Schneider, R. Haedrich and 3 anonymous reviewers for comments that significantly improved earlier versions of this manuscript. R. Hooper, M. Kelly, M. Norris, M. Parsons, K. Carter and multiple students at the Bonne Bay Field Station provided field assistance. K. Gilkinson, D. Steele and P. Ramey assisted in the identification of bivalves, amphipods and polychaetes, respectively. Funding was provided by a Discovery Grant from the Natural Sciences and Engineering Council of Canada to P.V.R.S., and fellowships from the Fisheries Conservation Chair, Memorial University's School of Graduate Studies and the Canadian International Development Agency (CIDA) to P.A.Q.

LITERATURE CITED

- Agardi T (2000) Effects of fisheries on marine ecosystems: a conservationist's perspective. *ICES J Mar Sci* 57:761–765
- Ambrose WG Jr (1984) Role of predatory infauna in structuring marine soft-bottom communities. *Mar Ecol Prog Ser* 17:109–115
- Armonies W (1992) Migratory rhythms of drifting juvenile molluscs in tidal waters of the Wadden Sea. *Mar Ecol Prog Ser* 83:197–206
- Barbeau MA, Scheibling RE (1994a) Temperature effects on predation of juvenile sea scallops [*Placopecten magellanicus* (Gmelin)] by sea stars (*Asterias vulgaris* Verill) and crabs (*Cancer irroratus* Say). *J Exp Mar Biol Ecol* 182: 27–47
- Barbeau MA, Scheibling RE (1994b) Behavioral mechanisms of prey size selection by sea stars (*Asterias vulgaris* Verill) and crabs (*Cancer irroratus* Say) preying on juvenile sea scallops [*Placopecten magellanicus* (Gmelin)] *J Exp Mar Biol Ecol* 180:103–136
- Beal BF, Parker MR, Vencile KW (2001) Seasonal effects of intraspecific density and predator exclusion along a shore-level gradient on survival and growth of juveniles of the soft-shell clam, *Mya arenaria* L., in Maine USA. *J Exp Mar Biol Ecol* 264:133–169
- Blackburn TH, Hall POJ, Hulth S, Landén A (1996) Organic-N loss by efflux and burial associated with a low efflux of inorganic N and with nitrate assimilation in Arctic sediments (Svalbard, Norway) *Mar Ecol Prog Ser* 141:283–293
- Brêthes J-C, Desrosiers G, Coulombe F (1984) Aspects de l'alimentation et du comportement alimentaire du crabe-des-neiges, *Chionoecetes opilio* (O. Fabr.) dans le sud-ouest du Golfe de St-Laurent (Decapoda, Brachyura). *Crustaceana* 47:235–244
- Bundy A (2001) Fishing on ecosystems: the interplay of fishing and predation in Newfoundland-Labrador. *Can J Fish Aquat Sci* 58:1153–1167
- Colbourne EB, Dawe EG, Parsons DG, Murphy EF and 7 others (2002) A preliminary review of environmental-stock relationships for some species of marine organisms in NAFO waters of the Northwest Atlantic. NAFO SCR Doc 02/34
- Comeau M, Conan GY, Maynou F, Robichaud G, Therriault J-C, Starr M (1998) Growth, spatial distribution, and abundance of benthic stages of the snow crab (*Chionoecetes opilio*) in Bonne Bay, Newfoundland, Canada. *Can J Fish Aquat Sci* 55:262–279
- Commuto JA, Ambrose WG Jr (1985) Multiple trophic levels in soft-bottom communities. *Mar Ecol Prog Ser* 26:289–293
- Commuto JA, Currier CA, Kane LR, Reinsel KA, Ulm IM (1995). Dispersal dynamics of the bivalve *Gemma gemma* in a patchy environment. *Ecol Monogr* 65:1–20
- Davis JLD, Metcalfe WJ, Hines AH (2003) implications of a fluctuating fish predator guild on behavior, distribution, and abundance of a shared prey species: the grass shrimp *Palaemonetes pugio* *J Exp Mar Biol Ecol* 293:23–40
- Drummond-Davis NC, Mann KH, Pottle RA (1982) Some estimates of population density and feeding habits of the rock crab *Cancer irroratus*, in a kelp bed in Nova Scotia. *Can J Fish Aquat Sci* 39:636–639
- Dutil J-D, Munro J, Peloquin M (1997) Laboratory study of the influence of prey size on vulnerability to cannibalism in snow crab (*Chionoecetes opilio* O Fabricius, 1780). *J Exp Mar Biol Ecol* 212:81–94
- Elner RW, Jamieson GS (1979) Predation of sea scallops, *Placopecten magellanicus*, by the rock crab, *Cancer irroratus*, and the American lobster, *Homarus americanus*. *J Fish*

- Res Board Can 36:537–543
- Ennis GP, Hooper RG, Taylor DM (1990) Changes in the composition of snow crab (*Chionoecetes opilio*) participating in the annual breeding migration in Bonne Bay, Newfoundland. *Can J Fish Aquat Sci* 47:2242–2249
- Fauchald K, Jumars P (1979) The diet of worms: a study of polychaete feeding guilds. *Oceanogr Mar Biol Annu Rev* 17:193–284
- Fauchald P, Erikstad KE (2002) Scale-dependent predator-prey interactions: the aggregative response of seabirds to prey under variable prey abundance and patchiness. *Mar Ecol Prog Ser* 231:279–291
- Fernandes TF, Huxman M, Piper SR (1999) Predator caging experiments: a test of the importance of scale. *J Exp Mar Biol Ecol* 241:137–154
- Finelli CM, Pentcheff ND, Zimmer RK, Wetthey DS (2000) Physical constraints on ecological processes: a field test of odor-mediated foraging. *Ecology* 81:784–797
- Folk RL (1980) Petrology of sedimentary rocks, 2nd edn. Hemphill, Austin, TX
- Gabriel KR (1971) The biplot graphic display of matrices with application to principal component analysis. *Biometrika* 58:453–467
- Gilbert D, Pettigrew G (1993) Current-meter data from Bonne Bay, NFLD, during the summer of 1991. *Can Data Rep Hydrogr Ocean Sci* 122:1–63
- Gilbert D, Pettigrew G, Swain D, Couture M (1996) State of the Gulf of St. Lawrence: oceanographic conditions in 1994. *Can Data Rep Hydrogr Ocean Sci* 143:1–85
- Green RH (1979) Sampling design and statistical methods for environmental biologists. Wiley Interscience, New York, NY
- Günther CP (1992) Dispersal of intertidal invertebrates: a strategy to react to disturbance of different scales? *Neth J Sea Res* 30:45–56
- Hall SJ, Raffaelli D, Turrell WR (1990) Predator-caging experiments in marine systems: a re-examination of their value. *Am Nat* 136:657–672
- Hilborn R, Mangel M (1997) The ecological detective. Confronting models with data. Monographs in Population Biology 28. Princeton University Press, Princeton, NJ
- Hines AH, Haddon AM, Wiechert LA (1990) Guild structure and foraging impact of blue crabs and epibenthic fish in a subestuary of Chesapeake Bay. *Mar Ecol Prog Ser* 67: 105–126
- Hooper RG (1986) A spring breeding migration of the snow crab, *Chionoecetes opilio* (O Fabr), into shallow water in Newfoundland. *Crustaceana* 50:257–264
- Hudon C, Lamarche G (1989) Niche segregation between American lobster *Homarus americanus* and rock crab *Cancer irroratus*. *Mar Ecol Prog Ser* 52:155–168
- Hulberg LW, Oliver JS (1980) Caging manipulations in marine soft-bottom communities: importance of animal interactions or sedimentary habitat modifications. *Can J Fish Aquat Sci* 37:1130–1139
- Kneib RT (1991) Indirect effects in experimental studies of marine soft-sediment communities. *Am Zool* 31:874–885
- Lefevre L, Brêthes J-C (1991) Orientation of movements of tagged, male, snow crabs (*Chionoecetes opilio*) in the southwestern Gulf of St. Lawrence. *Can J Fish Aquat Sci* 48:1167–1175
- Lenihan HS, Micheli F (2001). Soft-sediment communities. In: Bertness MD, Gaines SD, Hay ME (eds). *Marine community ecology*. Sinauer Associates, Sunderland, MS, p 253–287
- Lovrich GA, Sainte-Marie B (1997) Cannibalism in the snow crab, *Chionoecetes opilio* (O. Fabricius) (Brachyura: Majidae), and its potential importance to recruitment. *J Exp Mar Biol Ecol* 211:225–245
- Mallet P, Landsburg M (1996) Gulf rock crab (*Cancer irroratus*). DFO Atlantic Fisheries Stock Status Report 96/98 E, Dartmouth, NS
- Moody KE, Steneck RS (1993) Mechanisms of predation among large decapod crustaceans of the Gulf of Maine coast: functional vs. phylogenetic patterns. *J Exp Mar Biol Ecol* 168:111–124
- Nadeau M, Cliche G (1998) Predation of juvenile sea scallops (*Placopecten magellanicus*) by crabs (*Cancer irroratus* and *Hyas* sp.) and starfish (*Asterias vulgaris*), *Leptasterias polaris*, and *Crossaster papposus*. *J Shellfish Res* 17: 905–910
- Norkko A, Cummings VJ, Thrush SF, Hewitt JE, Hume T (2001) Local dispersal of juvenile bivalves: implications for sandflat ecology. *Mar Ecol Prog Ser* 212:131–144
- Olafsson EB, Peterson CH, Ambrose WG Jr (1994) Does recruitment limitation structure populations and communities of macroinvertebrates in marine soft sediments: the relative significance of pre- and post-settlement processes. *Oceanogr Mar Biol Annu Rev* 32:65–109
- Orensanz JM, Armstrong J, Armstrong D, Hilborn R (1998) Crustacean resources are vulnerable to serial depletion—the multifaceted decline of crab and shrimp fisheries in the Greater Gulf of Alaska. *Rev Fish Biol Fish* 8:117–176
- Pace ML (2001) Getting it right or wrong: extrapolations across experimental scales. In: Gardner RH, Kemp WM, Kennedy VS, Petersen JE (eds). *Scaling relations in experimental ecology*. Columbia University Press, New York, p 157–178
- Palomo G, Botto F, Navarro D, Escapa M, Iribarne O (2003) Does the presence of the SW Atlantic burrowing crab *Chasmagnathus granulatus* Dana affect predator-prey interactions between shorebirds and polychaetes? *J Exp Mar Biol Ecol* 290:211–228
- Paul AJ, Dawe EG, Elnor R, Jamieson GS and 5 others (2001) Crabs in cold water regions: biology, management, and economics. *Proc Crab 2001 Symp*. Alaska Sea Grant, Anchorage, AK
- Peterson CH (1979) Predation, competitive exclusion, and diversity in the soft-sediment benthic communities of estuaries and lagoons. In: Livingston RJ (ed). *Ecological processes in coastal and marine systems*. Plenum Press, New York, p 233–264
- Posey MH, Hines AH (1991) Complex predator-prey interactions within an estuarine benthic community. *Ecology* 72: 2155–2169
- Quijón PA, Snelgrove PVR (in press) Predation regulation of sedimentary faunal structure: potential effects of a fishery-induced switch in predators in a Newfoundland sub-arctic fjord. *Oecologia*
- Ramey PA, Snelgrove PVR (2003) Spatial patterns in sedimentary macrofaunal communities on the south coast of Newfoundland in relation to surface oceanography and sediment characteristics. *Mar Ecol Prog Ser* 262:215–227
- Real L (1979) Ecological determinants of functional response. *Ecology* 60:481–485
- Robichaud DA, Elnor RW, Bailey RFJ (1991) Differential selection of crab *Chionoecetes opilio* and *Hyas* spp. as prey by sympatric cod *Gadus morhua* and thorny skate *Raja radiata*. *Fish Bull* 89:669–680
- Rouse GW, Pleijel F (2001) Polychaetes. Oxford University Press, New York
- Sainte-Marie B (1997) Comment- An improved link between industry, management and science: review of case history of the southwestern Gulf of St. Lawrence a snow crab fish-

- ery. *Can J Fish Aquat Sci* 54:496–500
- Sainte-Marie B, Raymond S, Brêthes J-C (1995) Growth and maturation of the benthic stages of male snow crab, *Chionoecetes opilio* (Brachyura: Majidae). *Can J Fish Aquat Sci* 52:903–924
- Salierno JD, Rebach S, Christman MC (2003) The effects of interspecific competition and prey odor on foraging behavior in the rock crab, *Cancer irroratus* (Say). *J Exp Mar Biol Ecol* 287:249–260
- Scarrat DJ, Lowe R (1972) Biology of the rock crab (*Cancer irroratus*) in the Northumberland Strait. *J Fish Res Board Can* 29:161–166
- Schneider DC, Walters R, Thrush SF, Dayton PK (1997) Scale up of ecological experiments: density variation in the mobile bivalve *Macomona liliana*. *J Exp Mar Biol Ecol* 216:129–152
- Seitz RD, Lipcius RN (2001) Variation in top-down and bottom-up control of marine bivalves at differing spatial scales. *ICES J Mar Res* 58:689–699
- Seitz RD, Lipcius RN, Hines AH, Eggleston DB (2001) Density-dependent predation, habitat variation, and the persistence of marine bivalve prey. *Ecology* 82:2435–2451
- Sih A, Englund G, Wooster D (1998) Emergent impacts of multiple predators on prey. *Trends Ecol Evol* 13:350–355
- Sokal RR, Rohlf FJ (1994) *Biometry. The principles and practice of statistics in biological research*. WH Freeman, San Francisco, CA
- Squires HJ (1996) Decapod crustaceans of Newfoundland, Labrador and the Canadian Eastern Arctic. *Can Manuscr Fish Aquat Sci* 2359, St. John's, NF
- Squires HJ, Dawe EG (2003) Stomach contents of snow crab (*Chionoecetes opilio*, Decapoda, Brachyura) from the Northeast Newfoundland Shelf. *J Northw Atl Fish Sci* 32:2738
- Steele MA (1996) Effects of predators on reef fishes: separating cage artifacts from effects of predation. *J Exp Mar Biol Ecol* 198:249–267
- Stehlik LL (1993) Diet of brachyuran crabs *Cancer irroratus*, *C. borealis*, and *Ovalipes ocellatus* in the New York Bight. *J Crustac Biol* 13:723–735
- Stephen DW, Krebs JR (1986) *Foraging theory*. Princeton University Press, Princeton, NJ
- Stewart-Oaten A, Bence JR (2001) Temporal and spatial variation in environmental impact assessment. *Ecol Monogr* 71:305–339
- Thompson RJ, Hawryluk M (1989) Physiological energetics of the snow crab, *Chionoecetes opilio*. In: *Proc Int Symp King and Tanner crabs*. University of Alaska Sea Grant Report, 90–04, Fairbanks, AK, p 283–291
- Thrush SF (1986) Spatial heterogeneity in subtidal gravel generated by the pit-digging activities of *Cancer pagurus*. *Mar Ecol Prog Ser* 30:221–227
- Thrush SF (1999) Complex role of predators in structuring soft-sediment macrobenthic communities: implications of changes in spatial scale for experimental studies. *Aust J Ecol* 24:344–354
- Tremblay MJ, Eagles MD, Elnor RW (1994) Catch, effort and population structure in the snow crab fishery off eastern Cape Breton, 1978–1993: a retrospective. *Can Tech Rep Fish Aquat Sci* 2021, Halifax, NS
- Trueblood DD, Gallagher ED, Gould DM (1994) Three stages of seasonal succession on the Savin Hill Cove mudflat, Boston Harbor. *Limnol Oceanogr* 39:1440–1454
- Underwood AJ (1996) Environmental design and analysis in marine environmental sampling. *IOC Manuals and Guides No 34*. UNESCO, Paris
- Weissberger EJ (1999) Additive interactions between the moon snail *Euspira heros* and the sea star *Sterias forbesi*, two predators of the surfclam *Spisula solidissima*. *Oecologia* 119:461–466
- Wieckzoreck SK, Hooper RG (1995) Relationship between diet and food availability in the snow crab *Chionoecetes opilio* (O. Fabricius) in Bonne Bay, Newfoundland. *J Crustac Biol* 15:236–247
- Wilson WH Jr (1986) Importance of predatory infauna in marine soft-sediment communities. *Mar Ecol Prog Ser* 32:35–40
- Wilson WH Jr (1991) Competition and predation in marine soft-sediment communities. *Annu Rev Ecol Syst* 21:221–241
- Worm B, Myers RA (2003) Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. *Ecology* 84:162–173
- Yamada SB, Boulding EG (1996) The role of highly mobile crab predators in the intertidal zonation of their gastropod prey. *J Exp Mar Biol Ecol* 204:59–83
- Zajac RN, Whitlatch RB, Thrush SF (1998). Recolonization and succession in soft-sediment infaunal communities: the spatial scale of controlling factors. *Hydrobiologia* 375/376:227–240

Editorial responsibility: Otto Kinne (Editor-in-Chief), Oldendorf/Luhe, Germany

*Submitted: April 29, 2004; Accepted: August 31, 2004
Proofs received from author(s): January 8, 2005*