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Predation regulation of sedimentary faunal structure: potential effects of a fishery-induced switch in predators in a Newfoundland sub-Arctic fjord

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Abstract The collapse of the cod fishery in Newfoundland has coincided with marked increases in abundances of snow crab, pandalid shrimp, and other crustaceans that prey on sedimentary infauna. A 3-year sampling program in Bonne Bay, Newfoundland indicates differences in composition and number of these predators in the two main arms of the fjord that coincide with strong differences in benthic community structure. To test whether predation pressure contributes to the observed patterns in sedimentary fauna, exclusion field experiments with full and partial cages were deployed in both arms at 30-m depth and sampled along with ambient sediments at 0-, 4-, and 8-week periods. Predation significantly influenced species composition, abundance and, in some cases, diversity. The most striking changes included increases in the polychaetes Phöloe tecta and Ophelina cylindricaudata in exclusions relative to controls, and concurrent declines in the polychaete Paradoneis lyra and the cumacean Lamphros fuscata. In laboratory experiments, fresh non-disturbed sediment cores from each experimental area were either protected or exposed to snow crab, the most abundant predator in the bay. A snow crab inclusion experiment was also carried out in the field, using cages similar to those used for exclusions. Despite differences in sedimentary faunas in the two arms, both types of experiments detected a predator effect that was very similar to that documented in exclusion experiments. Thus, despite differences in the scales associated with each type of manipulation, our

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P. V. R. Snelgrove Canada Research Chair in Boreal and Cold Ocean Systems results suggest that crab predation is a significant structuring force in Newfoundland sedimentary communities. Given the historical changes that have occurred in predator composition as a result of cod overfishing, we hypothesize that broad-scale community changes may be taking place in North Atlantic benthic ecosystems.

Keywords Predation · Fishery · Sedimentary benthos · Sub-Arctic fjord

Introduction

Among the most pervasive effects of fisheries is the alteration of food webs through removal or alteration of top predators (e.g. Botsford et al. 1997; Pauly et al. 1998: Jackson et al. 2001), and the potential establishment of alternate states that favor different predator fields. In coastal Newfoundland, overfishing led to a complete collapse of all cod stocks (Hutchings 1996; Myers et al. 1996), with an associated increase in primarily benthic predators such as snow crab and shrimp (Koeller 2000; Worm and Myers 2003). The collapse of cod, a natural predator of snow crab and shrimp, may represent a predator release that has resulted in increased numbers of both crustacean species (Lilly et al. 2000; Bundy 2001). This switch in top predators is expected to have significant ramifications for benthic infauna, given that snow crab and shrimp, in contrast with adult cod, are primarily benthic feeders (Brêthes et al. 1984; Bergström 2000). Few studies have examined cascading effects of ecosystem alteration in the marine realm, but there is evidence that top-down effects may be more important than bottom-up effects (Jennings and Kaiser 1998; Micheli 1999). Thus, the rapid increase in shrimp and crab in coastal Newfoundland over the last decade may have cascading effects in sedimentary systems.

Numerous benthic predators including blue crab reach their northern distribution limit near Cape Cod (Williams 1984), and it has been suggested that predation plays a lesser role in benthic communities located further north in the western Atlantic (Woodin 1976). Nonetheless, increasingly large numbers of northernnative species (rock crab, Jonah crab, snow crab, pandalid shrimp, mud shrimp) and invasive species (e.g. green crab in Nova Scotia) suggest otherwise (Hudon and Lamarche 1989; Jamieson 2002). Predation is thought to play a key role in marine sedimentary systems, in part, because of the lack of clear evidence for competitive exclusion (Peterson 1979; Wilson 1991; Woodin 1999). Although some effects of predation have been demonstrated (see Ólafsson et al. 1994; Lenihan and Micheli 2001), numerous experimental studies have found no consistent regulatory role (Thrush 1999). Explanations for the absence of a clear effect include prey mobility and exchange that mask predation losses (Frid 1989; Englund 1997; Cooper et al. 1990), prev recruitment outpacing post-settlement consumption (Thrush 1999), and indirect interactions counterbalancing negative effects of epibenthic predators (Commito and Ambrose 1985; Kneib 1991). Variation in predator density, mobility, and feeding rates also hinder our capacity to detect predation effects (Clark et al. 1999; Seitz et al. 2001).

Detection of predation is challenging. Field manipulations have significant limitations (Hulberg and Oliver 1980; Peterson and Black 1994) but remain the best tool for testing predator effects (Hall et al. 1990). Nonetheless, cage experiments alone may not suffice if they are restricted to a single site (Fernandes et al. 1999) or are not combined with surveys and/or other types of manipulations (Thrush et al. 1997 and references therein). Combined field and laboratory experiments have proven to be among the most informative experimental approach because they examine different scales, have different strengths, and may potentially complement each other (Wiens 2001). We used this combined approach to study the role of predation in Bonne Bay, a Newfoundland sub-Arctic fjord in the northwest Atlantic. Preliminary observations from inner and outer areas of the bay indicated strong differences in benthic community structure, and in the number and composition of epibenthic predators (Wieczorek and Hooper 1995). The fact that infaunal organisms constitute the main part of crab and shrimp diets (Squires and Dawe 2003; Scarrat and Lowe 1972; Bergström 2000) suggests that increased predation pressure from these species may play a key regulatory role for benthic community structure.

We tested this hypothesis by deploying cage exclusion experiments and an inclusion experiment in the two main arms of the fjord, and by using sediments (with intact infauna) from these sites to carry out parallel laboratory predation experiments. Bonne Bay also offers a unique opportunity to study these interactions because an abundant guild of crabs and shrimps, which typically occur at greater depths, congregate in sedimentary habitats that are accessible by divers during the springsummer season (Hooper 1996; Ennis et al. 1990). Additional studies have focused on predator life histories in the bay (snow crab: Comeau et al. 1998, 1999; Conan et al. 1996), and in the Gulf of St. Lawrence (snow crab: Brêthes et al. 1987; Sainte-Marie and Gilbert 1998; pandalid shrimp: Ouellet and Lefaibre 1994; Ouellet et al. 1995; Simard et al. 1990; Rock crab: Hudon and Lamarche 1989). Based on these preliminary observations, we hypothesize that there are strong epifaunal predatory influences on infaunal abundance, diversity and dominance.

Materials and methods

Study area

Bonne Bay fjord is located in Western Newfoundland (Fig. 1) and is comprised of two main arms. East Arm is a deep (up to 230 m) inner basin that is partly separated from the outer bay by a shallow sill (\sim 12-deep), whereas South Arm is a shallower basin (up to 55-m deep) that is fully open to the adjacent Gulf of St. Lawrence. Study sites for crab abundance estimates and experiments were established in each of these main



Fig. 1 Map of Bonne Bay, with the location of a South and b East Arms where predator sampling and manipulative experiments were conducted. *Lower panels* indicate mean summer abundances $(\pm 95\%$ confidence intervals) of the most abundant epibenthic predators measured in baited traps during 1999–2001. *SN* Snow crab, *SH* Shrimp, *TO* Toad crab, *RO* Rock crab

arms. Currents and circulation in some areas of the bay have been described by Gilbert and Pettigrew (1993). Detailed studies of benthic communities are lacking except for lists of invertebrates (Rivard and Bowen 1971; Hooper 1975), and selected communities (Wiecsorek and Hooper 1995).

Predator distribution

Relative abundances of epibenthic predators were estimated with traps (~40×30×60 cm, ~5×15 cm opening, ~ 1 cm net) that were baited with mackerel and deployed during the summer seasons of 1999-2001. Traps were deployed at 35- to 50-m depth, separated by \sim 50–80 m and kept at the bottom for 1–2 days (data standardized as crab $trap^{-1} day^{-1}$) every 2-3 weeks. Direct comparison of catch numbers and frequencies was not possible because deployments were not simultaneous and catch rates were highly variable (within and among traps, sites, and summers). Instead, summer averages were calculated by using average standardized daily catches per sampling period as replicates. Baited traps do not provide absolute density estimates, and this approach yields only relative density comparisons between the two sites.

Field-exclusion experiments

Two exclusion experiments were deployed at \sim 30-m depth in South and East Arms (Fig. 1). Each experiment included three treatments and four replicates that were haphazardly interspersed; treatments included full cages or "exclusions", partial cages or "artifact treatments", and ambient undisturbed sediments or "controls". Cages (1-m diameter \times 15 cm high, pushed 3 cm into sediments) were circular in shape to minimize erosion/ deposition of sediments in different areas of the cages. Cages were anchored to the bottom by four ~4-cm-long "legs" extended from the main frame into the sediment. Plastic 1 cm×1 cm mesh covered partial (50% of top and side) and full cages. Infaunal organisms were sampled with tube cores (7-cm diameter; 10-cm deep; two cores per sample) that were collected by scuba divers. Initial sampling (two groups of four samples at each of the two study locales) took place on 25th June 1999, immediately prior to deployment of full and partial cages. These samples were used for comparison with ambient sediments and cages sampled after 4 and 8 weeks (see BACI design below). Sampling was never repeated within a given caged or ambient location, because cages were removed immediately after sampling. This approach minimized potential disturbance effects and created statistical independence in evaluating predation after 4 and 8 weeks. Coincident with the 8-week samples, additional sediment cores were collected from all treatments in order to study grain size distribution and CHN content. These analyses allowed us to evaluate potential sediment-related artifacts associated with caging treatments. Logistical constraints precluded sediment sampling after 4 weeks, although any artifact effects would be expected to be much stronger after 8 weeks than after 4 weeks.

Laboratory experiments

Two laboratory experiments were conducted in June 2000 to evaluate the potential impact of snow crab predation on benthic organisms under controlled conditions. A series of flow-through tanks $(1-2^{\circ}C)$ at the Bonne Bay Field Station were supplied with cold water pumped from depths where cores were collected. Within these tanks, freshly collected sediment cores with intact infauna were exposed to snow crab feeding. Sediment cores (7-cm diameter) were obtained from each experimental site (South and East Arms) by divers who gently pushed corers into the sediment to avoid physical disturbance, sealed them with rubber corks, and brought them to the surface where they were transported to the laboratory in coolers to minimize disturbance of infauna. This protocol maximized the likelihood that initial core communities would be representative of nature. Six sediment cores were placed in each tank and a plastic plate was used to create a false bottom so that the plastic core tube was flush with the plate. Sediment inside the cores was gently extruded so that it was also flush with the acrylic plate, creating a smooth transition between sediments, core tube, and plastic plate. Sediments (and infauna) were acclimated to these conditions for 24 h prior to initiation of experiments. Male snow crabs of 60-75 mm CW, a range including immature, adolescent, and small adult snow crab (cf. Sainte-Marie et al. 1995) were considered representative of the size structure reported for the depth and location of the study area (P.A. Quijón and P.V.R. Snelgrove, unpublished; Hooper 1996; Comeau et al. 1998). One of these snow crabs was added to each tank and offered open access to three randomly selected cores (controls). The other three cores in the tank were protected with horizontal plastic mesh, thus excluding the predators. Experiments lasted for 96 h, after which the snow crabs were removed, tanks were carefully drained, and sediment cores were collected and processed (see below).

Inclusion experiment

In order to provide a linkage between field-exclusion experiments and laboratory manipulations, full cages similar to those used for exclusion experiments were used to confine snow crabs (one crab per cage; same CW range reported above) for 96 h. Crabs were then released and samples were collected from cages and ambient sediments as described above for exclusion experiments. Inclusion experiments were initiated in both arms of the bay during June 1999, but weather constraints made recovery of samples from South Arm impossible. Thus, only results from East Arm are reported.

Sample processing and analysis

Cores of sediments from field and laboratory experiments were processed through a 500-µm sieve and preserved in a 10% sea water-formalin solution, prior to transfer to 70% ethanol with Rose Bengal to facilitate sorting and identification. Macrofaunal organisms were enumerated and identified to the lowest taxonomic level possible, which was usually species. Samples for grain size analysis were pre-treated with a 1:1 water:peroxide solution and heated to 300°C to remove organic matter. They were then disaggregated by re-suspension with 0.1% Calgon solution, and passed through sieves to separate fractions of > 350, > 250, > 177, > 125, > 88, and $> 62.5 \mu m$ by wet sieving. Finer fractions were subsampled (50 ml) and analyzed with a Sedigraph 5100 Particle Size Analyzer. Based on grain settling velocity, the Sedigraph separated >53, >44, >37, >31, >15, >7.8, >3.9, >2.0, >0.98, and $>0.49 \mu m$ fractions. Each fraction was then expressed as percentage of total dry weight, and pooled into categories based on the Wentworth scale (Folk 1980): fine + very fine sand $(>62.5 \ \mu m)$, silt $(>3.9 \ \mu m)$, and clay $(<3.9 \ \mu m)$. Additional sediment samples were processed with a CHN analyzer (Perkin Elmer Model 2400) to estimate C and N as a function of sediment dry weight. C:N ratios (an estimator of food quality for deposit feeders; Blackburn et al. 1996) were also calculated.

Data analysis

Patterns in benthic community structure were studied using Chord Normalized Expected Species Shared (CNESS). This similarity index estimates the number of species shared between two samples based on a random draw of m = 10 individuals (cf. Trueblood et al. 1994) that makes the index sensitive enough to detect the contribution of rare as well as abundant species (Grassle and Smith 1976). The CNESS dissimilarity sample × species matrix was also used to cluster samples based on un-weighted pair-group mean average sorting. The program COMPAH 90 (E.D. Gallagher, U. Massachusetts, Boston) was used for this analysis. The CNESS sample by species matrix was then transformed to a normalized hypergeometric probability matrix (H), which was used in a principal components analysis of hypergeometric probabilities (hereafter called PCA-H) to produce a two-dimensional metric scaling of CNESS distances among samples. Gabriel Euclidean Distance Biplots (Gabriel 1971) identified the species that were most important for among-sample variation, and thus, driving community composition differences.

Four community response variables were calculated: total density and number of species per sample (77 cm^2) , Shannon–Wiener Diversity $(H' = -\sum_{i=1}^{n} p_i \log_e(p_i))$; with p_i density of *i* species/total density), and Evenness (J' = H')H'max; with H'max = log_eS). Selection of indices was based on their widespread use in the literature (H'), sensitivity to rare species and independence from species richness (J'), and discriminant ability (H') (Magurran 1988; Smith and Wilson 1996). Statistical comparisons were all carried out with ANOVAs in SPSS (version 10). For the field-exclusion experiments, a "before-after, control-impact" (BACI) design was used. In this factorial design, the evidence for an impact (predation effect) appears as a significant time by treatment interaction (Green 1979). The model for this ANOVA was $y = \mu$ + time + treatment + time × treatment + ϵ , where y refers to each response variable, μ is a mean constant, time refers to the "before-after" comparison (0-4 week or 0-8 week), treatment refers to the "impact" comparison (control versus predator exclusion), and ϵ refers to the error term. Because artifact treatments were available only for the 8-week period, artifact data were analyzed separately using the model $y = \mu +$ site + treatment + site \times treatment + ϵ . In this model, site is South or East Arm, treatment is control or artifact, and ϵ is the error term. The model for the laboratory experiments was $v = \mu + \tanh + \text{treatment} + \epsilon$, where tank refers to replicate tanks 1-3, and treatment refers to control (exposed to crab predation) versus exclusion, with no interaction term. The model for the inclusion experiment was $v = \mu$ + treatment + ϵ , where treatment refers to crab inclusion versus ambient sediments. All variables, with the exception of "tank" (laboratory experiments) were treated as fixed factors. Assumptions of normality and heterogeneity were tested in each analysis by plotting residual histograms and applying Levene's test, respectively. Application of log_e transformation proved sufficient to homogenize variances in those instances where data transformation was necessary (Sokal and Rohlf 1994).

Results

Predator abundance

Four species of decapods dominated average summer abundances of epibenthic predators (Fig. 1). Snow crabs (*Chionoecetes opilio*, South Arm mean = 0.96 crabs trap⁻¹ day⁻¹) and pandalid shrimp (*Pandalus montagui*, East Arm mean = 0.85 shrimp trap⁻¹ day⁻¹) dominated the two study sites respectively. Snow crabs were almost one-fifth as abundant in East Arm (0.21 crab trap⁻¹ day⁻¹), whereas shrimp were absent from South Arm. Toad crabs (*Hyas* sp.) were less abundant but similar in density between sites (0.15 and 0.10 crabs trap⁻¹ day⁻¹). Rock crabs (*Cancer irroratus*) abundances were 0.08 and 0.30 crab trap⁻¹ day⁻¹ at South and East Arms, respectively. Ambient communities and predator exclusion experiments

Overall, abundances of benthic invertebrates in ambient sediments from South Arm were significantly higher than in East Arm (P < 0.05; Fig. 2). The three most abundant species from South Arm (the clam Astarte sp. and the polychaetes Paradoneis lyra and Prionospio steenstrupii) were all significantly more abundant than in East Arm (P < 0.05) for each time period. The cumacean Lamphros fuscata was consistently more abundant at East Arm than in South Arm (P < 0.05); however, the two next most abundant species from East Arm (the bivalve Thyasira flexuosa and the amphipod Bathymedon obstusifrons) were generally not significantly different from corresponding densities in South Arm (Fig. 2).

Exclusion experiments carried out in both arms of the bay are summarized in Fig. 3. Together, the first two principal components of the analysis explained 44% of the data variation. As was apparent in the clustering analysis, the PCA-*H* clearly separated South from East Arm communities (PCA1), and predator exclusions from ambient and partial cages treatments (PCA2). At both sites, sampling period (4th vs. 8th week) had no clear effect on patterns in the PCA-*H* plot. Gabriel biplots identified two polychaetes, *Phöloe tecta* and *Prionospio steenstrupi*, as particularly important in exclusion sediments in South Arm (Fig. 3). Three other polychaetes, *Ophelina cylindricaudata*, *Euchone papillosa*, and *Praxillella praetermissa*, were important in exclusion treatments in East Arm. The polychaete *Paradoneis lyra* was important in describing ambient and control sediments in South Arm, whereas the cumacean, *Lamphros fuscata*, and the amphipod *Bathymedon obtusifrons* were important in ambient sediments and partial cages in East Arm. Comparisons of species densities (Fig. 4) were consistent with the interpretation based on biplots (Fig. 3). For example, *P. tecta* was abundant in exclusion treatments, whereas *L. fuscata* was more abundant in controls (P < 0.001). Densities of *O. cylindricaudata* and *P. lyra* were also consistent with the biplots, though differences were not significant.

Predation effects (i.e. significant time × treatment interactions) on density and evenness were detected after 4 and 8 weeks in South Arm (Table 1). Similar effects were detected on density, number of species, and diversity after 4 week at East Arm, but these effects did not persist to the 8th week (Table 1). A control-exclusion comparison at each sampling date (Fig. 5) indicates that the exclusion of predators increased the density and reduced evenness (South Arm), whereas species richness and Shannon diversity were not significantly affected. In East Arm, exclusion of predators for 4 weeks significantly increased the density, species richness and Shannon diversity but did not affect evenness (Fig. 5). Sedimentary and faunal response variables were used to test for potential artifacts (Table 2). In all cases, site was the only significant factor, indicating no measurable caging artifacts on sediment composition or community structure. These results coincide with diver observations



Fig. 2 Mean total densities and most abundant infaunal taxa $(\pm 95\%)$ confidence intervals) in ambient (control) sediments from South (*open bars*) and East Arms (*shaded bars*) at **a** 0-week, **b** 4-week, and **c** 8-week periods in the field experiments. Asta Astarte sp., Para Paradoneis lyra, Prio Prionospio steenstrupi, Thya Thyasira flexuosa, Lamp Lamphros fuscata, Bath Bathymedon obstusifrons. Asterisks indicate significant difference between South and East Arms (*P < 0.05, **P < 0.01, ***P < 0.001)



Fig. 3 Cluster and metric scaling plot of treatments and ambient samples using PCA-*H* of CNESS similarities (NESSm = 10). South Arm (*upper case*) and East Arm (*lower case*) treatments are indicated as follows: *C*, *c* control, *E*, *e* exclusion, *A*, *a* artifact. *Numbers* indicate sampling periods (0, 4, or 8 weeks) and *subscript numbers* denote replicates (1–4). *Vectors* represent Gabriel biplots that identify species that explain for the most variability among samples. *Dashed circles* indicate samples forming subgroups into the groups represented by *solid lines*



Fig. 4 Mean densities ($\pm 95\%$ confidence intervals) of four species that explain most of the between-sample variation between controls (ambient) (*open bars*) and exclusion treatments (*shaded bars*) in Fig. 3. **a** *P. tecta*, **b** *O. cylindricaudata*, **c** *P. lyra*, and **d** *L. fuscata*. *Asterisks* indicate significant differences between treatments (***P < 0.001)

at the study sites, which indicated that predators did enter the partial cages.

Laboratory and inclusion experiments

The use of snow crab as a predator in laboratory experiments yielded similar results to those observed in the field experiments (Fig. 6). The first two principal components of the laboratory experiments explained 50% and 45% of the variation in South and East Arm, respectively. Irrespective of the source of the sediments (South or East Arms), cores exposed to predators were distinct from predator-exclusion treatments (Fig. 6, top and middle panels). The polychaete *P. tecta* and the bivalve *Macoma calcarea* were important in describing exclusion treatments for South Arm, whereas the poly-

Table 1 Predation effects on community response variables



Fig. 5 Mean values ($\pm 95\%$ confidence intervals) for density (**a**, **b**), species richness (**c**, **d**), diversity or H' (**e**, **f**), and evenness or J' (**g**, **h**) estimated from control (*open bars*) and exclusion (*shaded bars*) treatments. Mean values are based on four replicates except at the beginning of the experiments (week 0; n=8) when two groups of four samples were averaged and plotted as a *single open bar*. Asterisks indicate significant differences between treatments at each period. *P < 0.05; **P < 0.01

chaetes O. cylindricaudata and E. papillosa were important in exclusions for East Arm. Mediomastus ambiseta and E. papillosa (South Arm) and Aricidea nolani (East Arm) were important to control treatments. In the fieldinclusion experiment (Fig. 6, bottom panel), the first two

	Source	df	Ν	S	H'	J'
South Arm	Time	1	885.06**	2.25	0.0728	0.0133**
0–4 week	Treatment	1	95.06	0.25	0.0169	0.0026
	Interaction	1	1040.06**	2.25	0.0748	0.0048*
	Error	12	946.25	65.00	0.2842	0.0088
South Arm	Time	1	1139.06**	7.56	0.1561	0.0302**
0–8 week	Treatment	1	175.56	7.56	0.0184	0.0074*
	Interaction	1	1278.06**	0.56	0.0779	0.0108*
	Error	12	1147.75	86.25	0.4970	0.0165
East Arm	Time	1	10.56	203.06***	2.9451***	0.1036***
0–4 week	Treatment	1	126.56	14.06	0.0092	0.0008
	Interaction	1	351.56**	45.56**	0.2424**	0.0015
	Error	12	444.25	48.25	0.2659	0.0235
East Arm	Time	1	162.56	156.25***	2.3846***	0.0853***
0–8 week	Treatment	1	0.56	1.00	0.0305	0.0015
	Interaction	1	45.56	4.00	0.0491	0.0007
	Error	12	738.75	64.50	0.2093	0.0175

Values are sum of squares (SS) from two-way ANOVAs (BACI design, see text). Factors include time (before–after; 0–4 and 0–8 week), treatment (control–exclusion) and their interaction. *Asterisks* indicate significance associated with each SS.

*P < 0.05, **P < 0.01,

Table 2 Artifact effects on sedimentary and community response variables

Sedimentary variables	df	Fine sand	Silt	Clay	C:N
Site	1	406.51***	350.43*	302.71*	84.08*
Treatment	1	2.73	116.97	9.89	0.84
Site × treatment	1	1.06	19.35	19.48	1.44
Error	12	142.3	471.24	99.83	18.32
Community variables	df	Ν	S	Н	J'
Site	1	1444.0**	5.06	0.008	0.007^{**}
Treatment	1	1.0	7.56	0.074	0.002
Site × treatment	1	4.0	10.56	0.014	~ 0.000
Error	12	1,376	158.75	0.445	0.005

Values are sums of squares (SS) from two-way ANOVAs. Factors include site (South vs. East), treatment (Control vs. Artifact), and their interaction.

*P < 0.05, **P < 0.01; ***P < 0.001

components explained 54% of the variation, and clearly separated inclusion from ambient sediments. *E. papill*osa, Yoldia sp., and Tharyx acutus were important species in the inclusion treatment, whereas Lamphros fuscata was the most important species in ambient sediments. In general, densities of most of the representative species identified in Fig. 6 were significantly different between treatments (Fig. 7).

In terms of community variables, results from the laboratory and the inclusion experiments were similar to those in exclusion experiments. In general, site (South or East Arm) explained most of the significant differences in variables (P < 0.05 for all variables, Table 3); however, treatment (predator exclusion vs. exposed) also had significant effects on density and evenness (P < 0.05). Because site effects were significant, data were re-analyzed separately for each site. For South Arm, snow crabs significantly reduced density (N), and increased evenness (J') (P < 0.05), but did not affect species richness or Shannon diversity. For East Arm, snow crabs reduced total density and increased species richness and Shannon diversity (H') (P < 0.05), but had no effect on evenness (P > 0.05) (Fig. 8). The results of the inclusion experiment were very similar to the laboratory experiment: confined snow crabs reduced significantly the number of species and diversity (P < 0.05), but did not significantly reduce the total density, or modify evenness (P > 0.05).

Discussion

Overall, our results indicate that predation significantly contributes to patterns of infaunal composition and abundance in Bonne Bay. This conclusion is based on laboratory and field experiments that were consistent in their findings despite their obvious differences in scale (Kemp et al. 2001; Wiens 2001). Among-site differences reflect spatial variation that cannot be fully understood with manipulative experiments that are limited to a single site (Fernandes et al. 1999) and exemplify the need for including more than one spatial/temporal scale in our experiments (Thrush et al. 1997; Schneider 2001).

Predator abundance

Though noisy, our baited trap data suggest differences in epifaunal predator abundance between East and South Arm. Predator numbers may differ because of productivity differences; South Arm is considered to be more productive than East Arm (R. Hooper, Memorial University Personal Communication) Recruitment may also play a role. The sill that limits exchange with East Arm also limits larval transport, which may contribute to fewer snow crab and more shrimp recruiting in East Arm (P.A. Quijón, P.V.R. Snelgrove, submitted).

Predation effects on composition

Two groups of species were expected to benefit most from the exclusion of predators: sedentary polychaetes or clams unable to escape by emigration or burial (Roberts et al. 1989), and infaunal predatory species (Commito and Ambrose 1985). In our experiments, sedentary polychaetes such as the maldanid P. praetermissa, the sabellid Euchone papillosa, and the ampheretid Lyssipe labiata, were nearly twice as abundant in exclusion treatments than in ambient sediments in East Arm. Similarly, Mediomastus ambiseta was twice as abundant in exclusion than in ambient sediments in South Arm. The clams Yoldia sp. and Macoma calcarea also benefited from the refuge created by exclusion treatments. Yoldia sp. was two times and M. calcarea five times more abundant in East and South Arm exclusion treatments, respectively. These results are consistent with previous studies on predator diet. Stomach content analyses have shown that clams and sedentary polychaetes are important dietary components of snow crab populations from Bonne Bay (Wieczorek and Hooper 1995), Gulf of St. Lawrence (Powles 1968), and Eastern Newfoundland (Squires and Dawe 2003).

Phöloe tecta is a member of a predatory guild that is believed to generate trophic complexity in soft-sediment communities (Ambrose 1984; Commito and Ambrose 1985; Posey and Hines 1991). Predatory infauna are expected to aggregate in exclusion treatments to take advantage not only of the refuge from top predators but also the enhanced infaunal prey beneath cages (Kneib 1988, 1991). In South Arm *P. tecta* was five times more abundant in exclusion treatments than in ambient sediments. Similarly, *Phyllodoce mucosa*, the only other abundant predatory species (>1% of total) was ~twice more abundant in exclusion treatments than in ambient sediments. Species that were able to escape crab predation were expected to dominate ambient sediments. The



Fig. 6 Cluster and metric scaling plot of samples collected in laboratory snow crab feeding experiments carried out with sediments (communities) from **a** South and **b** East Arms, and from a **c** field-inclusion experiment carried out in East Arm (see text). NESSm = 10 except in the B (NESSm = 5). Vectors represent Gabriel biplots that identify species that explain the most variability among samples. Treatments are represented by *letters* (see Fig. 3; with the addition of i = crab inclusion), whereas *numbers* refer to tanks (1–3) and *subscript numbers* to replicates (1–3)

cumacean *Lamphros fuscata*, the amphipod *Bathymedon* obtusifrons, and the polychaete *Paradoneis lyra*, are all highly mobile species that were indeed more abundant in ambient sediments than in exclusion treatments. Two notable exceptions were the clam *Astarte* sp., which is characterized by a very robust shell, and the polychaete *Ophelina cylindricaudata*; neither species differed significantly between ambient and exclusion treatments. However, there is also no evidence to indicate that these species are important in the diets of snow crab (Lefebvre and Brêthes 1991), rock crab (Hudon and Lamarche 1989), pandalid shrimp (Bergström 2000), or toad crab (Squires 1996).

Predation effects on community variables

The exclusion of predators produced an increase in total abundance in both sites over 4 weeks but the increase persisted through 8 weeks only in South Arm. Predation effects are "strong" when a 100% density increase is detected in exclusion versus ambient sediments (Ólafsson et al. 1994). This strong an effect is clearly not the case in Bonne Bay, where field and laboratory experiments show that the predation influence is moderate and varies among sites. Spatial differences in predation influence and persistence may be related to predator foraging rates (Micheli 1997; Seitz et al. 2001) and predator composition (Quijón and Snelgrove 2005). On the one hand, snow crabs were nearly five times more abundant in South Arm, suggesting that their foraging in this area may be much more frequent than in East Arm. On the other hand, predation effects on species richness that were detected only in East Arm may be related to higher density of rock crabs relative to South Arm. In laboratory con-



Fig. 7 Mean densities (\pm 95% confidence intervals) of **a** *P. tecta*, **b** *O. cylindricaudata*, **c** *L. fuscata*, **d** *E. papillosa*, **e** *A. nolani*, and **f** *E. papillosa*. These species are among the ones that explained most of the between-sample variation between treatments with ("pres" = present) and without ("abs" = absent) crabs in laboratory and field-inclusion experiments (see Fig. 6)

ditions, rock crabs were at least four times more effective than snow crabs in reducing species richness (Quijón and Snelgrove 2005). These differences are consistent with feeding rates reported for both species (Himmelman and Steele 1971; Drummond-Davis et al. 1982; Thompson and Hawryluk 1989) and with laboratory observations that suggest higher rates of sediment alteration by rock crab. Thus, although snow crab had significant effects in both sites, the effects on individual species reflected differences between communities, which in turn may reflect the complex influence of multiple epifaunal predators that vary between sites.

The influence of rock crab on species richness also explains differences in diversity (H'), but not necessarily in evenness and dominance. Predation may indirectly increase the evenness when predators are non-selective foragers, i.e., when they primarily target the most abundant prey (Schneider 1978). This seems to be the case in South Arm, where the reduction in density by predation tends to equalize numbers per species (both in the field and in the laboratory). Moreover, disturbance per se, in addition to predation, can have significant consequences for sedimentary infauna (Virnstein 1977) through non-selective mortality. Most of the literature suggests that our four predators are primarily generalists (Squires and Dawe 2003; Bergström 2000; Scarrat and Lowe 1972), despite some degree of prey selectivity by snow crab (Wiecsorek and Hooper 1995). In East Arm, the reduction of density by predation (in field and laboratory experiments) resulted in the loss of species without changes in evenness. This pattern may suggest that equalization of individuals among species (Schneider 1978) is more likely in communities where abundance and species richness are comparatively high as is the case in South Arm.

Artifact effects

Cage artifacts are a recurrent concern in predation studies (Olafsson et al. 1994; McGuinness 1997). It is impossible to completely eliminate cage influences on sediments, prey, or predators, but it is possible to



Fig. 8 Mean values $(\pm 95\%$ confidence intervals) for density, species richness, diversity (H'), and evenness (J') for treatments with ("pres" = present) and without ("abs" = absent) crabs in laboratory and field-inclusion experiments (see Fig. 6). Asterisks indicate significant differences between treatments in two way ANOVAs (**P* < 0.05)

evaluate and minimize caging effects. The round shape of the cages effectively eliminated variable deposition within the cage interior because no visual evidence of sediment erosion or deposition was detected, nor were significant changes in sediment parameters observed. Although separate analysis of East Arm data indicated an increase in silt content in the cages, this effect was probably not meaningful for overall sediment quality; no other grain size fraction changed significantly, nor

Table 3 Snow crab predation effects on community response variables in the laboratory and in the inclusion experiment

	Source	df	N	S	H	J
Laboratory	Site	1	41,877***	1080.21***	3.218***	0.192***
	Tank	2	399	1.47	0.255	0.021
	Treatment	1	1,039*	15.05	0.004	0.031**
	Error	30	4,577	124.61	2.065	0.099
Field inclusion	Treatment	1	84.5	24.5*	0.141*	~ 0.000
	Error	6	147.5	15.5	0.146	0.008

Values are sums of squares (SS) from three-way and one-way ANOVAs, respectively. In the laboratory experiments, factors include site (South and East), tank, and treatment (exposed to crab vs. exclusion). In the inclusion experiment treatment refers to inclusion (crab) versus ambient sediments.

Asterisks indicate significant effects associated with each SS.

P* < 0.05; *P* < 0.01; ****P* < 0.001

did the C:N ratio, our closest surrogate of food quality for deposit feeders (Blackburn et al. 1996) in the absence of chlorophyll data. More importantly, no community responses to partial cages were detected. We were unable to test for artifact effects during the first half of the experiment (0–4 weeks), but caging effects tend to be cumulative over time (Hindell et al. 2001) and, if present, should therefore have been apparent in partial cages after 8 weeks.

Implications for marine conservation

The collapse of cod and other major predators on large decapods, that were once extraordinarily abundant in coastal Newfoundland, has contributed to an explosion in shrimp, snow crab (Worm and Myers 2003) and presumably, other crustaceans. Previous studies have documented spatial differences in predation pressure on epifaunal taxa in the Gulf of Maine, and historical declines in cod abundance were hypothesized to have resulted in long-term changes in predation impact (Witman and Sebens 1992). Given that adult cod are not primarily an infaunal predator, and instead, adolescent and adult snow crabs display clear effects on benthic infauna, it is reasonable to expect that the structure of Newfoundland infaunal communities may have changed in the last few decades with the replacement of cod by a trophic guild that feeds primarily on infauna. Admittedly, in the absence of historical data on infaunal composition and structure, we must infer that the predator-mediated changes we observe in short-term experiments are reflective of long-term changes related to increased crab effects. We believe this inference is reasonable given that the recent increases in snow crab abundance in Newfoundland waters are well documented (Worm and Myers 2000) and the results of our different experiments are consistent and unambiguous. Small crabs manipulated here are representative of the study area and the region for depths and the spring-summer season (Comeau et al. 1998) but may not necessarily represent those populations living in deeper waters. Therefore, the extrapolation of our experiments should be done with caution until similar manipulations with larger crabs at deeper bottoms can be done.

Our results indicate that crabs modify benthic composition and abundance, and in more depauperate sedimentary habitats, also reduce diversity. As in other systems affected by long-term overfishing (Goni 1998; Jackson et al. 2001), the elimination of cod may have established an alternate stable state. The existence of these states has been debated for decades (Connell and Sousa 1983; Peterson 1984; Petraitis and Latham 1999; van de Koppel et al. 2001), though rarely have they been described to persist once overfishing has halted. Alternate systems in fisheries ecosystems have often been assumed to be unstable, in that they revert back to the previous state with the cessation of the disturbance (fishery) that created them. There are exceptions (Barkai and Branch 1988), however, that may include scenarios such as the Newfoundland ecosystem where cod have failed to recover even 10 years after a fishing moratorium was declared. Irrespective of whether or not an 'alternate state' applies to the Newfoundland ecosystem, it is clear that the consequences of cod collapse have been far more severe than anticipated and, as our results indicate, may have been paralleled by a fundamental change in the structure of benthic communities.

Ironically, fishing pressure now focuses on three of the four crab predators studied here. The exploitation of rock crab (Mallet and Landsburg 1996), and at a much larger scale, snow crab (Paul et al. 2002), and pandalid shrimp (Bergström 2000), grew partly as a consequence of the cod collapse and subsequent moratorium on cod fishing (Bundy 2001; Schiermeier 2002). Our results indicate a clear influence of these predators on key aspects of the structure of benthic communities. It follows that the decimation of these predators will have indirect consequences on the bottom component of the ecosystems that they currently structure. Cascading effects, as a result of fishery exerted at the top of the trophic web (Agardi 2000), have been proposed for systems dominated by fish predators. Similar cascading effects may be playing a role in benthic communities of the North Atlantic, although this remains largely unknown to date. If overfishing leads to the collapse of crab stocks, as some data are beginning to suggest (Bundy 2001), additional shifts in sedimentary communities may be expected.

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