

Impact of predation-disturbance by large epifauna on sediment-dwelling harpacticoid copepods: field experiments in a subtidal seagrass bed*

D. G. Webb and T. R. Parsons (1991)

Department of Oceanography, University of British Columbia, Vancouver, British Columbia, Canada V6T 1W5

Date of final manuscript acceptance: February 8, 1991. Communicated by R. O'Dor, Halifax

Abstract. The hypothesis was tested that predation-disturbance by epibenthic macrofauna affects the abundance of sediment-dwelling harpacticoid copepods. The copepods inhabited a subtidal seagrass (*Zostera marina* L.) bed in British Columbia, Canada. The response of the harpacticoid community was observed in controlled field experiments in which epibenthic predators-disturbers were excluded from portions of the seagrass bed. Controlled, exclusion-cage (0.8 m² area, 7-mm mesh) experiments were conducted within the seagrass bed from late March/early April to mid-June in both 1986 and 1987. Sampling was conducted biweekly. Exclusion of large epibenthic predators-disturbers had little effect on sediment-dwelling harpacticoid copepod density. Total harpacticoid numbers and abundances of dominant species generally did not increase in the exclusion treatment relative to the control. Shifts in species composition of the harpacticoid community did not occur. The treatment control was adequate in simulating the exclusion cage structure. It appears that large epibenthic predators-disturbers have little impact on the abundance of harpacticoid copepod populations at this study site.

Introduction

Marine harpacticoid copepods are a significant food source for juvenile fishes (e.g. Alheit and Scheibel 1982, Hicks 1984, Gee 1989) and other large epibenthic predators (e.g. mysids, Johnston and Lasenby 1982; and shrimp, Jensen and Jensen 1985). Attempts have been made to assess the importance of predation (or associated disturbance during foraging) in affecting copepod density, using experiments manipulating potential predator numbers in the field. A conclusion of significant predator

impact has been reached in some studies (Bell 1980, Bell and Woodin 1984, Fleeger 1985, Gee et al. 1985, Hunt et al. 1987, Ellis and Coull 1989), but not in others (Fleeger et al. 1982, Fitzhugh and Fleeger 1985). However, with the exception of the studies by Fleeger et al. (1982), Bell and Woodin (1984), Hunt et al. (1987) and Ellis and Coull (1989), all have problems with experimental design and/or subsequent statistical analysis. Pseudoreplication (Hurlbert 1984) has led to the use of inappropriate error terms in the statistical analyses (see Bell 1980, Fitzhugh and Fleeger 1985, Fleeger 1985, Gee et al. 1985). While the results of these studies may still have ecological significance, statistical interpretation is difficult. Therefore, accurate knowledge of the impact of epibenthic predators on harpacticoid copepods, gained from field experiments, is limited.

Both potentially predatory macroinfauna and macroepifauna generally have higher densities within seagrass beds than in adjacent unvegetated areas (see Summerson and Peterson 1984). It appears that the high level of structure present in seagrass beds may provide these animals with a refuge from predation (Orth et al. 1984). Leber (1985) observed, in predator (shrimp) inclusion experiments, that seagrass structure decreases predation rates on some epifauna by inhibiting predator effectiveness. Further studies also have indicated that the presence of seagrasses increases survival (Peterson 1986, Wilson et al. 1987). However, there is evidence to suggest that high animal densities in seagrass beds may simply be a function of active habitat preference (Bell and Westoby 1986) or passive deposition of planktonic larval stages as a result of decreased current speeds within the beds (Eckman 1987). Whatever the mechanism, seagrass beds contain extremely high densities of epifauna (e.g. crabs, juvenile fishes), potentially predatory on sediment-dwelling harpacticoid copepods. Therefore, manipulation of epifauna density in seagrass habitats and monitoring of the harpacticoid community's response should provide a powerful test of the significance of predator effects. No previous studies of this type concerning meiofauna have been performed in seagrass beds.

* Please address all correspondence to Dr. Webb at Department of Oceanography, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1

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This paper reports the results of predator exclusion experiments conducted in 1986 and 1987 in a *Zostera marina* L. bed in British Columbia, Canada. The response of the sediment harpacticoid community to macroepifauna exclusion was monitored over time in both years. The goal was to exclude macroepifauna from portions of the seagrass bed and, using appropriate experimental design and statistical analysis, to provide a test of the impact of exclusion on sediment-dwelling harpacticoid copepod abundance.

Materials and methods

The study was conducted on Roberts Bank, British Columbia, Canada (49° N, 123° W), near Stn H (Fig. 1). Stn H was located between the Westshore Terminals Ltd. causeway and the Tsawwassen Ferry Terminal causeway. The area is vegetated with the seagrasses *Zostera marina* L. seaward and *Zostera japonica* Aschers. and Graebn along its landward extent [see Harrison (1987) for a detailed description of vegetation patterns]. Stn H was located within the main body of the *Z. marina* bed and was in a shallow, effectively subtidal area. Although Stn H is ca. 1.6 m above chart datum (D'Amours 1987), approximately 5 cm of water covers the sediment surface at low tide, trapped by the *Z. marina* shoots (D'Amours 1987; Harrison 1987). Thus, although by definition intertidal, Stn H is covered by water at all times. Maximum water depth at high tide is ca. 3.2 m. Sediments are fine sands (Swinbanks and Luternauer 1987).

Predator exclusion experiments were conducted from 31 March to 10 June 1986 and 2 April to 11 June 1987. April to June spans the time of major recruitment of potential harpacticoid predators, such as juvenile fishes (e.g. salmonids, sculpins) and macroinvertebrates (e.g. Dungeness crab), to the Roberts Bank seagrass beds (Gordon and Levings 1984). Both fishes and crabs are known to prey extensively on sediment-dwelling harpacticoid copepods (Harrison 1981; Gee et al. 1985; D'Amours 1987; Webb 1989).

Circular aluminium cages (1 m diameter, 0.5 m high, 7-mm square mesh; 0.8 m² enclosed area) were placed within the seagrass

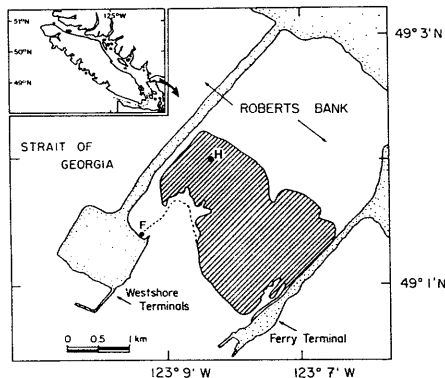


Fig. 1. Station location on Roberts Bank, British Columbia, Canada. Stn H is the location of the experimental cages. Hatched area indicates extent of *Zostera marina* bed (after Harrison 1987); dotted line shows seaward limit of shallow flat. Stn F is site of a separate investigation

bed 4 m southeast of Stn H. Cages were designed to minimize potential artifacts of cage introduction. The circular design was selected to permit drift algae (e.g. *Ulva* spp.) in the study area to roll around the cages rather than block the mesh (after Leber 1985). The large diameter of the cages was chosen to allow the enclosure of a large number (>75) of whole *Zostera marina* shoots and to allow them to lie normally within the shallow water present at low tide, which was confirmed upon observation during repeated sampling. The extended height of the cages allowed for typical upright posture of the seagrass shoots during high tide. Repeated observations by divers indicated that normal behaviour of the shoots within cages was observed at high tide (e.g. upright, swaying in wave surge). The large mesh size employed (7 mm) was determined to be sufficiently small for excluding large epibenthic predators (e.g. juvenile crabs and fishes) but large enough to allow water flow through the cages when fouled. Observations made during sampling indicated that although fouling was observed, the majority of the intermesh space was unblocked. Coupled with the fact that flow within seagrass beds is turbulent due to the leaves acting as a "mesh" (Nowell and Jumars 1984), artifacts within the cages due to impeded flow (e.g. siltation; Virnstein 1978; Hulberg and Oliver 1980) should be small.

Full-exclusion cages and cage "controls" were used in this experiment in both years. Cage controls were of the same design as the full-exclusion cages except that two opposing 50 x 50 cm segments of mesh were removed on the sides. These controls were used to mimic any effects of cage structure (e.g. shading, reduced flow) while still allowing access by potential epibenthic predators. Observations by divers at high tide indicated that cage controls did not act as "reefs" attracting large numbers of fish and macroinvertebrates.

Cages were placed within the seagrass bed at low tide 4 d before the first sampling to allow any effect of disturbance on the harpacticoid copepod community caused by emplacement to subside. After disturbance (e.g. raking the sediment), harpacticoid copepod abundance and species composition attain pre-disturbance values after a maximum of ca. 2 d (e.g. Sherman and Coull 1980; Thistle 1980; Chandler and Fleeger 1983). Three replicate cages of each treatment [exclusion cages (hereafter referred to as the exclusion treatment) and cage controls (hereafter referred to as the control)] were used. The six cages were placed 1 m apart in a line perpendicular to the incoming tidal flow. The controls were oriented so that the areas with mesh were also perpendicular to the tidal flow. The two treatments were alternated in a systematic design to ensure adequate interspersed treatments. The skirt of each cage was pushed ca. 3 cm into the sediment and each cage was anchored with nylon cable ties to three aluminium posts hammered 50 cm into the sediment. Sampling was performed through a hinged port on the top of the exclusion cages and through the holes in the sides of the controls.

To determine if sediment grain size differed between treatments, two 19.6-cm² cores were taken randomly in each cage to a depth of 1 cm at the beginning and end of each experiment. No core was closer than 5 cm to the cage edge. Cores were air-dried for 1 wk and, after drying, the sediment was divided into size fractions on a graded sieve series (595, 355, 180, 75 and 53 μ m). The amount of sediment trapped by each sieve was weighed and converted to a percentage of the total sediment weight on all the sieves. The average value of the percentage on each sieve from the two cores per cage was taken (see Hurlbert 1984). The percentages in each size class were compared between treatments using Student's *t*-test.

Sediment harpacticoid copepod sampling was conducted within the cages at approximately biweekly intervals, from 31 March to 10 June 1986 and 2 April to 11 June 1987. Three 5.31-cm² cores were taken for harpacticoid copepods randomly in each cage on each sampling date. No core was closer than 5 cm to the cage edge. Core samples for harpacticoids were taken to a depth of 1 cm, as >80% of the copepods occupy this depth stratum at Stn H (Webb 1989). The top centimeter of each core was extruded and preserved in 4% formaldehyde. At the conclusion of sampling on each date, the exterior of the cages was brushed free of fouling organisms. The choice of number of cages of each treatment (3) and number of cores per cage (3) was made on the basis of processing time of individual core samples.

In the laboratory, filtered seawater was added, the samples were decanted, the sediment allowed to settle for 5 s and the supernatant decanted through a 63 μ m sieve. The procedure was repeated five times and recovered >99% of the copepods from the 0- to 1-cm depth fraction (Webb 1989). All harpacticoid copepodites (juveniles and adults) were enumerated and the first 50 individuals encountered were removed and identified to species. Abundance of each species in the sample was then estimated as a proportion of the total number of copepods. Nauplii were not enumerated. Averages of the three cores per cage were obtained, thus giving one value for each cage (see Hurlbert 1984). Harpacticoid densities, normalized to per cm² sediment area, were compared between the two treatments on each sampling date using Student's *t*-test.

For all statistical comparisons between treatments, homogeneity of variance was assessed using Bartlett's test at the 0.05 level of significance. If heteroscedasticity was observed, the data were subjected to arcsine square-root and both log_e(x+1) and square-root transformations for sediment grain size and harpacticoid abundance, respectively. If transformation did not alleviate heteroscedasticity, the non-parametric Mann-Whitney *U*-test was used to compare values between treatments. The 0.05 level of significance was used. All statistical analyses described in this section were conducted using the MGLH and NPAR modules of SYSTAT (Wilkinson 1985) on an IBM PC/XT microcomputer.

Results

Potential artifacts of cage emplacement

From observations at each sampling date in both years of the experiment, caging seemed (qualitatively) to have little effect on the enclosed environment. Invertebrates which could travel through the mesh (e.g. amphipods) did not appear to have larger populations inside the cages than in the surrounding area. The appearance of the sediment surface inside the cages did not seem to be different from that in the general vicinity. Surficial manifestations of increased biological activity (e.g. increased number of polychaete burrows) were not evident inside the cages. One noticeable difference, however, was that leaf epiphytic growth (e.g. diatoms) seemed lower on seagrass shoots inside the cages than outside. However, this decrease appeared to be similar in both the exclusion treatment and the control.

In 1986, sediment-grain size characteristics in the cages at the start of the experiment (31 March) showed no significant difference between treatments in any size

category (Student's *t*-test, $P > 0.10$) (Table 1). On 25 June, however, both grain size categories <75 μ m were significantly higher in the exclusion treatment cages (Student's *t*-test, $P < 0.01$ in both cases) (Table 1). However, differences between treatments were small. The 53-74 μ m category consisted of a mean of 1.9% of the total sediment in the exclusion treatment compared to 1.2% in the control, while the <53 μ m size class had a mean of 4.9% of the total sediment in the exclusions and 3.4% in the control. In 1987, at the start of the experiment (2 April), the percentage of sediment in the 355-594 μ m size class was significantly higher in the control relative to the exclusion treatment (Mann-Whitney *U*-test, $P < 0.05$) and the percentage of total sediment in the 75-179 μ m size class was significantly greater in the exclusion treatment (Mann-Whitney *U*-test, $P = 0.05$) (Table 1). However, differences between treatments were again small, with the 355-594 μ m size class consisting of 0.98% of the total sediment in the control vs 0.80% in the exclusion treatment, and the 75-179 μ m size class composed of 69.5% of the sediment in the exclusion treatment compared to 66.3% in the control. At the end of the experiment (11 June), however, no significant differences were observed between treatments in any sediment-grain size class (Student's *t*-test, $P > 0.30$ in all cases) (Table 1).

Response of the harpacticoid community

Given the large number of species found in this study (55 species; Webb 1989), only total harpacticoids and individual harpacticoid species with densities at their abundance peak of $\geq 10\%$ of the total harpacticoid numbers on a given sampling date, in either year, are considered further. Five species met this cutoff criterion: *Amphiascus undosus* Lang, *Ectinosoma melaniceps* Boeck, *Daniellsonia typica* Boeck, *Halectinosoma* sp. 1, and *Pseudobrydya lanceta* Coull. Only these species met the cutoff criterion in either treatment in either year. These groups were tested for differences in abundance between the exclusion treatment and control on each sampling date in each year of the experiment. The overall conclusion of the analysis of harpacticoid densities was that no difference in abundance was observed between the exclusion treatment and control on each sampling date, in both years.

Table 1. Amounts of sediment (% of total) in various grain size categories at the beginning and end of the experiment in both 1986 and 1987. B: beginning; E: end; C: control; X: exclusion. Values are mean \pm 1 SE, $n = 3$

Year	Time	Treatment	Grain size					
			$\geq 595 \mu\text{m}$	355-594 μm	180-354 μm	75-179 μm	53-74 μm	<53 μm
1986	B	C	0.64 \pm 0.07	0.96 \pm 0.04	35.5 \pm 1.3	56.9 \pm 0.94	1.9 \pm 0.09	4.1 \pm 0.37
	B	X	0.48 \pm 0.08	0.83 \pm 0.09	32.2 \pm 1.1	60.6 \pm 1.5	2.0 \pm 0.03	3.9 \pm 0.25
	E	C	0.30 \pm 0.06	1.3 \pm 0.07	40.6 \pm 1.1	53.2 \pm 1.3	1.2 \pm 0.07	3.4 \pm 0.25
	E	X	0.79 \pm 0.31	1.6 \pm 0.22	38.1 \pm 2.0	52.7 \pm 2.1	1.9 \pm 0.12	4.9 \pm 0.05
1987	B	C	0.66 \pm 0.02	0.98 \pm 0.16	26.5 \pm 0.79	66.3 \pm 0.85	1.8 \pm 0.12	3.8 \pm 0.03
	B	X	0.54 \pm 0.02	0.80 \pm 0.01	23.6 \pm 0.67	69.5 \pm 0.08	1.9 \pm 0.25	3.7 \pm 0.44
	E	C	1.4 \pm 0.30	1.3 \pm 0.15	27.1 \pm 0.90	64.3 \pm 1.5	1.8 \pm 0.14	4.1 \pm 0.29
	E	X	1.1 \pm 0.22	1.3 \pm 0.30	26.1 \pm 0.28	65.9 \pm 1.2	1.8 \pm 0.22	3.8 \pm 0.64

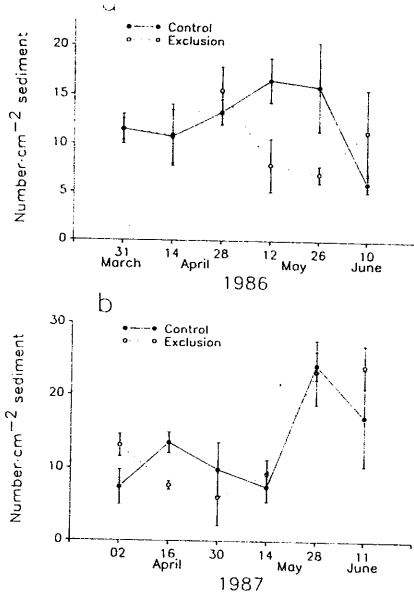


Fig. 2. Abundance of total harpacticoid copepods in the sediment (no. of individuals per cm^2) in the control and exclusion treatments in (a) 1986 and (b) 1987. Values are mean \pm 1 SE, $n=3$

Total harpacticoid densities were not different between treatments on any date in 1986 (Fig. 2a). In 1987 (Fig. 2b), total copepod density was significantly higher in the control treatment on 16 April (Student's t -test, $P < 0.05$). *Amphiascus undosus* densities were not different between treatments during the 1986 experiment (Fig. 3a), but this species was significantly more abundant in the exclusion treatment on 14 May 1987 (Mann-Whitney U -test, $P < 0.05$) (Fig. 3b). *Danielssenia typica* abundances did not differ between treatments during the 1986 experiment (Fig. 4a). However, in 1987, densities were significantly higher in the control on 16 April (Student's t -test, $P < 0.05$) (Fig. 4b). Densities of *Ectinosoma melaniceps*, *Hallectinosoma* sp. 1 and *Pseudobradya lanceata* did not differ between treatments on any date in either year and therefore these data are not presented.

Discussion

The caging experiments conducted in both 1986 and 1987 were adequate in design and appropriately tested for an effect of epibenthic predators on the harpacticoid copepod community near Stn H. General observational data indicated that conditions inside the cages were similar to

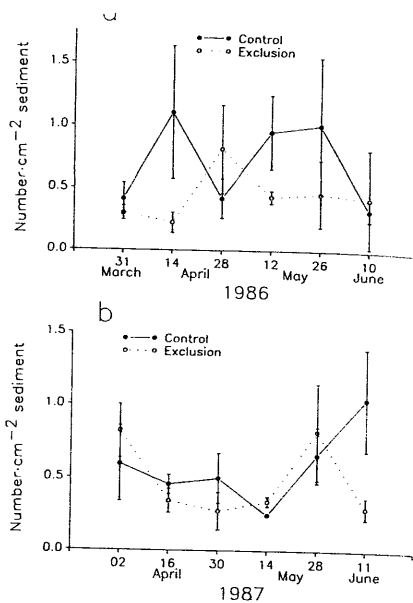


Fig. 3. *Amphiascus undosus*. Abundance in the sediment (no. of individuals per cm^2) in the control and exclusion treatments in (a) 1986 and (b) 1987. Values are mean \pm 1 SE, $n=3$

those in the surrounding area (e.g. surficial sediment structure) and those that were not (e.g. seagrass epiphytic growth) were mimicked by the control cage treatment. Comparison of sediment grain sizes between treatments at the end of the experiments indicated a significant increase in the $< 75 \mu\text{m}$ fraction in the exclusion treatment in 1986 and no difference in 1987. However, the increase in this size class was only a mean of 2.2% (total sediment weight) higher than the control. This is a small change in comparison to the minimum 19% increase in silt-clay ($\leq 62 \mu\text{m}$) content compared to surrounding sediment observed by Virnstein (1977) in 12-mm mesh cages in Chesapeake Bay. Therefore, artifacts introduced by caging seem to be minor and the control treatment seems to be adequate in design, and so comparison between the exclusion treatment and the control should provide a valid test of the effect of large epibenthic predators on harpacticoid abundance at the study site.

Exclusion of large epibenthic predators (e.g. juvenile salmonids, crabs) seems to have had little effect on densities of harpacticoid copepods living in the sediment in either year. Overall, species abundances were either not different between treatments or were higher in the controls. Species abundances generally did not increase in the exclusion treatment, as would be expected if consump-

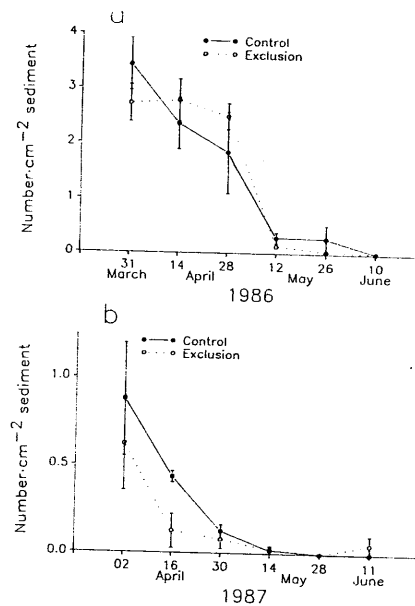


Fig. 4. *Danielssenia typica*. Abundance in the sediment (no. of individuals per cm^2) in the control and exclusion treatments in (a) 1986 and (b) 1987. Values are mean \pm 1 SE, $n=3$

tion by large epibenthic predators were causing declines in population densities. Of the five dominant harpacticoid species, only *Amphiascus undosus* exhibited any significant increase in the exclusion treatment. However, this was only on one date and the increase was not maintained subsequently. Changes in species dominance (see Gee et al. 1985) also did not occur, since the abundant species were the same in both treatments. The sediment harpacticoid copepod community was mainly composed in both years of the family Ectinosomatidae, especially the species *Hallectinosoma* sp. 1. Community dominance by members of this family is not uncommon in shallow, soft-sediment habitats (see Hicks and Coull 1983).

In comparison to harpacticoid densities in sediment cores collected at Stn H concurrently with the experimental sampling, a consistent effect of caging was not observed (Webb 1989). Total sediment harpacticoid abundance in the control treatment was ca. 80% of that at Stn H in both years, with a similar temporal pattern. Densities of *Amphiascus undosus*, *Danielssenia typica*, *Ectinosoma melaniceps*, *Hallectinosoma* sp. 1 and *Pseudobradya lanceata* were similar in both years at Stn H to abundance in the control treatment, with identical temporal patterns (Webb 1989). Therefore, a cage effect in the control treatment is not evident and any differences

(or lack thereof) between treatments cannot be attributed to depressed copepod densities in the control.

A possible limitation of this experiment is that although the cage mesh size was sufficient to exclude the target predator populations, the harpacticoid copepods were not enclosed and therefore dilution of any increases in the exclusion treatment could occur, leading to no significant increases being detected between treatments. Considering that harpacticoids are commonly found to enter the water column (e.g. Walters 1988), dilution of cage populations could occur solely through transport within the water column at high tide. However, D'Amours (1987), based on a sled sampler study conducted at high tide at the study site in 1985 and 1986, observed very few individuals of the sediment-dwelling harpacticoids discussed here in the water column. Water-column entry was mainly confined to species epiphytic on the seagrass leaves (D'Amours 1987, Webb 1989).

Exclusion of large (those that cannot enter a 7-mm square mesh) epibenthic predators had no obvious effect on harpacticoid copepods in the sediment near Stn H. Predation and/or disturbance by these animals appears to have had little negative impact on harpacticoid copepods at this study site. Considering the large numbers of epibenthic macrofauna known to be resident in seagrass beds, this result suggests a negligible role of these animals in regulating sediment-dwelling harpacticoid copepod abundance in these habitats.

Although the densities of potential macroepifaunal predators-disturbers of harpacticoid copepods in seagrass beds are large compared to unvegetated habitats (Summerson and Peterson 1984), the absence of an effect of exclusion of these animals on harpacticoid abundance is consistent with the results of experiments on the response of macrofauna to predators in seagrass beds. The vegetation appears to provide protection for macroinfauna (Peterson 1982, Summerson and Peterson 1984, Leber 1985), perhaps because of decreases in the foraging efficiency of predators with increasing seagrass biomass (Nelson 1979, Stoner 1982) and increased habitat complexity (Coen et al. 1981). It seems that meiobenthic harpacticoid copepods may benefit in a similar fashion.

Of all the properly replicated and analyzed harpacticoid-predator manipulation experiments performed in the field, the present study and that of Fleeger et al. (1982) are the only ones to demonstrate no effect of the manipulation of predator numbers on the abundance of harpacticoids. Both were predator exclusion experiments. Conversely, of the three experiments where a significant effect was observed on the copepod community (Bell and Woodin 1984, Hunt et al. 1987, Ellis and Coull 1989), two were predator inclusion experiments (Hunt et al. 1987, Ellis and Coull 1989). The exclusion experiments presented here and in Fleeger et al. (1982) were valid in design with adequate controls. The conclusions reached in these studies are strong, suggesting that some mechanisms inherent in harpacticoid predator inclusion experiments in the field may influence the strength of the observed effect. The observed significance of the predators' impact on the prey community in inclusion experiments may be affected by behavioural alterations in the

predator due to confinement, or perhaps an inappropriate choice of container size (see Lafontaine and Leggett 1987). Although allowing manipulation of predator densities at intermediate levels, predator inclusion experiments may be no more preferable than exclusion studies when dealing with the sediment-dwelling harpacticoid copepod community.

Acknowledgements. We thank A. Metaxas, D. D'Amours, M. St. John, M. Gollner and W. P. Cochlan for their contributions at various stages of this study. Logistical support for this study was provided by NSERC Operating Grants to T. R. Parsons. Personal support to the senior author was provided by a NSERC Postgraduate Scholarship. Fonds FCAC (Quebec), the Kit Malkin Scholarship, a Summer University of British Columbia Graduate Fellowship and the Capt. T. H. Byrne Scholarship and NSERC Operating Grants to T. R. Parsons.

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