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Effect of predation by juvenile Pacific salmon on marine harpacticoid copepods. II. Predator density manipulation experiments

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ABSTRACT: The impact of predation by juvenile chum *Oncorhynchus keta* (Walbaum) and pink *O. gorbuscha* (Walbaum) salmon on harpacticoid copepods inhabiting a shallow subtidal seagrass *Zostera marina* L. bed on Roberts Bank, British Columbia, Canada, was examined. Previous studies of the impact of juvenile salmonid predation on harpacticoid communities have yielded contradictory results and have been based on indirect and weak evidence. The influence of predation by large epibenthos (such as salmon) in controlling the dynamics of 3 harpacticoid species (*Harpacticus uniremis, Tisbe* cf. *furcata* and *Zaus aurelii*) was determined. The response of these 3 species was observed in controlled field experiments in which epibenthic predators were excluded from portions of the seagrass bed. Controlled, exclusion-cage (7 mm mesh) experiments were conducted from late March-early April to mid June in both 1986 and 1987. Sampling was conducted every 2 wk. Exclusion of large epibenthic predators had little effect on the density of the 3 harpacticoid species. Total numbers and abundances of juvenile copepodites, adult males and adult females of all 3 species generally did not increase in the exclusion treatment relative to the control. The treatment control was adequate in simulating the environment of the exclusion cages. It appears that juvenile salmonids have little impact on the dynamics of harpacticoid copepod populations at this study site.

INTRODUCTION

Juvenile Pacific salmon *Oncorhynchus* spp. are known to consume large numbers of marine harpacticoid copepods when feeding nearshore (e.g. Feller & Kaczynski 1975, Healey 1979, Godin 1981). The effect of this predation on the dynamics of harpacticoid communities has been estimated by Healey (1979) and Cordell (1986). Healey (1979) determined that juvenile chum salmon *Oncorhynchus keta* (Walbaum) in the Nanaimo River estuary, British Columbia, Canada, had a significant impact on the density of *Harpacticus uniremis* Kröyer, their favoured harpacticoid prey. However, it is unclear in this study whether samples for estimation of copepod density were taken in areas where the fish were foraging. Therefore, the conclusion of significant predatory impact on this one copepod species may be erroneous. The study by Cordell (1986), conversely, suggested that predation by juvenile chum and pink *O. gorbuscha* (Walbaum) salmon on harpacticoid copepods in Alaska had little impact on copepod population dynamics. His conclusion was simply based on peaks in copepod population density at times when salmon gut contents had maximal densities of harpacticoids. No estimates of salmonid density or changes in feeding rate were attempted. Cordell's conclusion may be as erroneous as that of Healey's (1979). It is still unclear, therefore, whether juvenile salmon predation on harpacticoid copepods has a significant impact on copepod populations.

In the companion paper reporting on studies conducted in a subtidal seagrass *Zostera marina* L. bed on Roberts Bank, British Columbia (Webb 1991), patterns of consumption of harpacticoid copepods by juvenile pink and chum salmon were shown to bear little relationship to patterns of mortality in the most heavily consumed copepod species. The absence of such a relationship suggests a lack of predatory control of harpacticoid densities by juvenile salmon feeding. Although appearing valid, it was impossible to assign a statistical significance to the observed results. This

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paper reports the results of predator exclusion experiments conducted concurrently with the population dynamics study (Webb 1991). The response of the 3 harpacticoid species most heavily consumed by juvenile salmonids (*Harpacticus uniremis, Tisbe* cf. *furcata* (Baird) and *Zaus aurelii* Poppe; Webb 1991) to predator exclusion was monitored over time, in both the seagrass-leaf and sediment habitats. The primary goal was to corroborate the conclusion regarding the impact of salmonid predation reached by Webb (1991).

MATERIALS AND METHODS

Predator exclusion experiments were conducted from March 31 to June 10 in 1986 and April 2 to June 11 in 1987, near Stn H on Roberts Bank, British Columbia (see Webb 1991 for a detailed description of the study area). These periods bracketed the time of major abundance of juvenile chum and/or pink salmon in the study area in both years (Webb 1991).

Circular aluminium cages (1 m diameter, 0.5 m high, 7 mm square mesh; 0.8 m^2 enclosed area) were placed within the seagrass bed 4 m southeast of Stn H. The large diameter of the cages was chosen to allow the enclosure of a large number (> 75) of entire *Zostera marina* shoots and to allow them to lie normally in shallow water at low tide. The height of the cages allowed the typical upright posture of the seagrass shoots during high tide. Repeated observations indicated normal behaviour of the shoots within the cages. The mesh size employed (7 mm) excluded large epibenthic predators (e.g. juvenile salmon) but was large enough to allow water flow through the cages when fouled. Although some fouling was observed during sampling, the majority of the intermesh space remained unblocked. Because flow within seagrass beds is turbulent due to the leaves acting as a 'mesh' (Novell & Jumars 1984), artifacts within the cages due to impeded laminar flow (e.g. siltation (Virnstein 1978, Hulberg & Oliver 1980) should be small. Control cages were of the same design as the full exclusion cages except that 2 opposing 50 cm × 50 cm segments of mesh were removed on the sides. These controls were used to mimic any effects of the cage structure (e.g. shading, reduced flow) while still allowing access by potential epibenthic predators. Observations by divers at high tide indicated that neither type of cage acted as a 'reef', attracting higher than normal numbers of fish and macroinvertebrates.

Cages were placed within the seagrass bed at low tide 4 d before they were first sampled 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 predisturbance values after a maximum of about 2 d (e.g. Sherman & Coull 1980, Thistle 1980, Chandler & Fleeger 1983). Three replicate cages of each type (exclusion and control) were used. The 6 cages were placed 1 m apart in a line perpendicular to the incoming tidal flow with the 2 treatments alternated. The controls were oriented so that the areas with mesh were also perpendicular to the tidal flow. The skirt of each cage was pushed ca 3 cm into the sediment and each cage was anchored with nylon cable ties to 3 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 open sides of the controls.

To determine whether sediment grain size in the cages differed between treatments, two 19.6 cm^2 cores were taken to a depth of 1 cm in each cage at the beginning and at the termination of the experiment in each year. Cores were taken randomly but no closer than 5 cm to the cage edge. The sediment was air-dried for 1 wk and then divided into size fractions on a graded sieve series (595, 355, 180, 75 and 53 µm). 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 2 cores per cage was taken (Hurlburt 1984). Percentages in each size class were compared between treatments using Student's *t*-test.

Harpacticoid copepod sampling was conducted within the cages at ca 2 wk intervals. Four leaf samples and 3 cores were taken in each cage on each sampling date. Both leaf and core samples were taken randomly but no closer than 5 cm to the cage edge. The oldest leaf on the shoot present at the picked location was sampled. This was done instead of sampling the longest leaf and estimating abundance using intrashoot distributions (Webb 1989, 1990) because this sampling technique would entail lifting the shoot from the water to calculate relative leaf age. This disturbance to the shoots within cages might have influenced copepod numbers in following samples. Leaves were sampled using the tube sampler in an identical manner to that described in Webb (1991). Core samples for harpacticoids were taken to a depth of 1 cm as > 80 % of copepods were found to be in this stratum at Stn H (Webb 1989). Core sampler size and sample collection were identical to the methodology described in Webb (1991). At the conclusion of sampling on each date, the exterior of the cages was brushed free of fouling organisms.

Leaf and core sample processing in the laboratory was similar to that described in Webb (1991) except that the 50 copepodites of *Harpacticus uniremis, Tisbe*

cf. *furcata* and *Zaus aurelii* were only identified to gross developmental stage (juvenile, adult male and adult female). Since intrashoot distributions to estimate abundance were not used, densities were expressed as number cm^{-2} leaf area. Since samples were all taken from the oldest leaves on shoots, the data can better be viewed as an index of abundance for comparison between treatments, rather than absolute values. Both the 4 leaf samples and 3 cores per cage were averaged to obtain mean values per cage (Hurlburt 1984). Leaf and core harpacticoid densities on each sampling date were compared between the 2 treatments using Student's *t*-test.

For all statistical comparisons between treatments, homogeneity of variance was assessed using Bartlett's test. If heteroscedasticity was observed, the sediment grain size data were subjected to arcsine square root transformation and harpacticoid abundance data to $\log_e(x + 1)$ and square root transformations. If transformation did not alleviate heteroscedasticity, the nonparametric Mann-Whitney *U*-test was used to compare values between treatments. The 0.05 level of significance was used for all tests. 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

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, small shrimp) 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 appear to be different from that in the general vicinity. Evidence of increased biological activity (e.g increased number of polychaete burrows) was not present inside the cages. Epiphytic growth on leaves (e.g. diatoms) seemed to be 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 (March 31) showed no significant difference between treatments in any size category (Student's *t*-test, $p > 0.10$) (Table 1). On June 25, both grain size categories < 75 µm 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 µm category composed a mean of 1.9 % of the total sediment in the exclusion treatment compared to 1.2 % in the control while the < 53 µm 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 (April 2), the percentage of sediment in the 355–594 µm 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 µm size class was significantly greater in the exclusion treatment (Mann-Whitney *U*-test, $p = 0.05$) (Table 1). Differences between treatments were again small with the 355–594 µm size class consisting of 0.98 % of the total sediment in the control versus 0.80 % in the exclusion treatment and the 75–179 µm 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 (June 11), 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).

In 1986, *Harpacticus uniremis* densities on leaves were not different between treatments on any date for

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 means ± 1 SE, n = 3

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

total numbers, juveniles and females (Fig. 1). Numbers of males were significantly higher in the control on March 31 (Student's *t*-test, $p < 0.05$) (Fig. 1c). In the sediment, in 1986, total numbers were significantly higher in the control on May 12 (Student's *t*-test, $p < 0.05$) and in the exclusion treatment on June 10 (Student's *t*-test, $p < 0.05$) (Fig. 2a). The increase in total numbers in the controls on May 12 was mainly due to a significant increase in female abundance (Student's *t*-test, $p < 0.05$) (Fig. 2d). The increase in the exclusion treatment on June 10 appeared to be general since, individually, juvenile, male and female densities were not significantly higher.

In 1987, *Harpacticus uniremis* total numbers on the leaves were higher in the exclusion treatment on April 2 (Student's *t*-test, $p < 0.05$) and in the control on May 14 (Student's *t*-test, $p < 0.05$) (Fig. 3a). Individually juveniles, males and females were not higher in the exclusion treatment on April 2 but all 3 groups were significantly more abundant in the control on May 14 (Student's *t*-test, $p < 0.05$ in all cases) (Fig. 3b, c, d). Sediment densities were not different between treatments for total numbers and juvenile or female abundance (Fig. 4). Males were not found in sediment samples in 1987.

Tisbe cf. *furcata* total numbers on leaves in either year were not different between treatments (Figs. 5a & 7a). In 1986, juvenile and male densities were not different between treatments on any date but female numbers were significantly larger on leaves in the exclusion treatment on April 28 (Student's *t*-test, $p = 0.05$) and May 26 (Mann-Whitney *U*-test, $p < 0.05$) (Fig. 5d). No groups were different between treatments in 1987 (Fig. 7b, c, d). Total numbers and juvenile, male or female densities were not different between treatments in the sediment on any date in either year (Figs. 6 & 8).

Zaus aurelii total numbers and juvenile, male or female abundance did not differ between treatments on any date on leaves in 1986 (Fig. 9) and 1987 (Fig. 11) or in the sediment in 1986 (Fig. 10). This species was not found in sediment samples in 1987.

DISCUSSION

The caging experiments were adequate in design and tested for an effect of epibenthic predation on the target harpacticoid copepod species. General qualitative observational data indicated that conditions inside

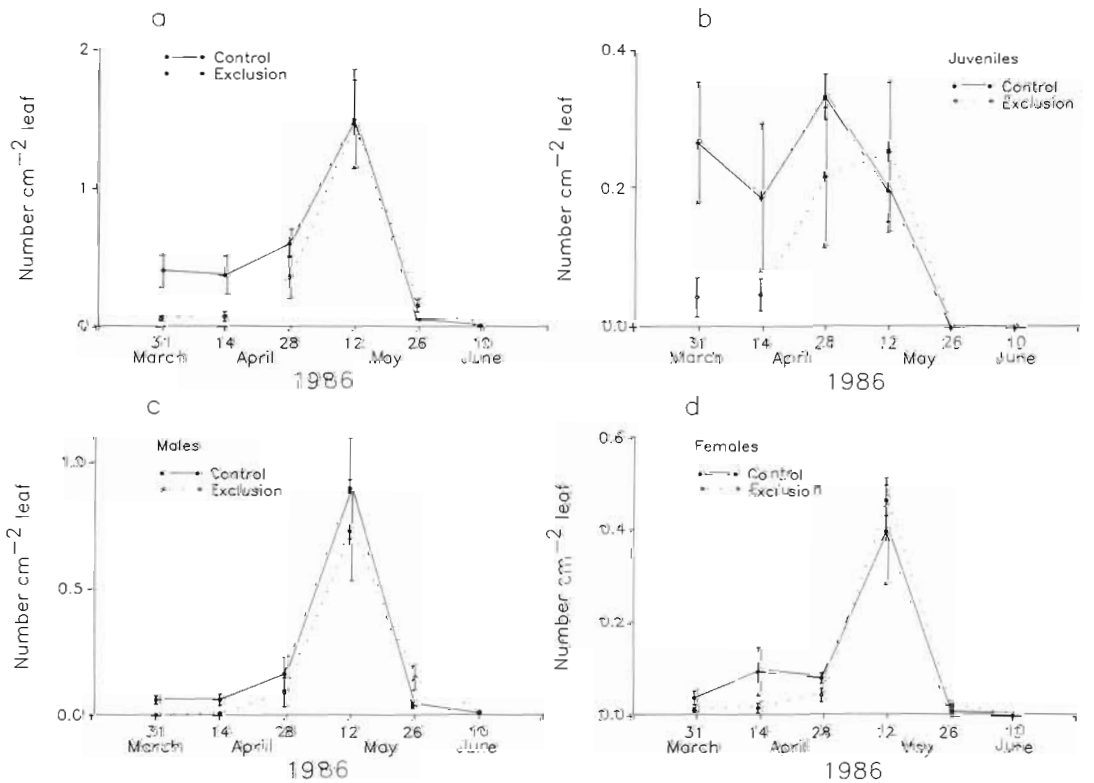

Fig. 1. *Harpacticus uniremis*. (a) Total abundance, and (b) juvenile copepodite, (c) adult male and (d) adult female abundance on *Zostera marina* leaves (number cm^{-2} leaf) in the Control and Exclusion treatments in 1986. Values are means ± 1 standard error, n = 3

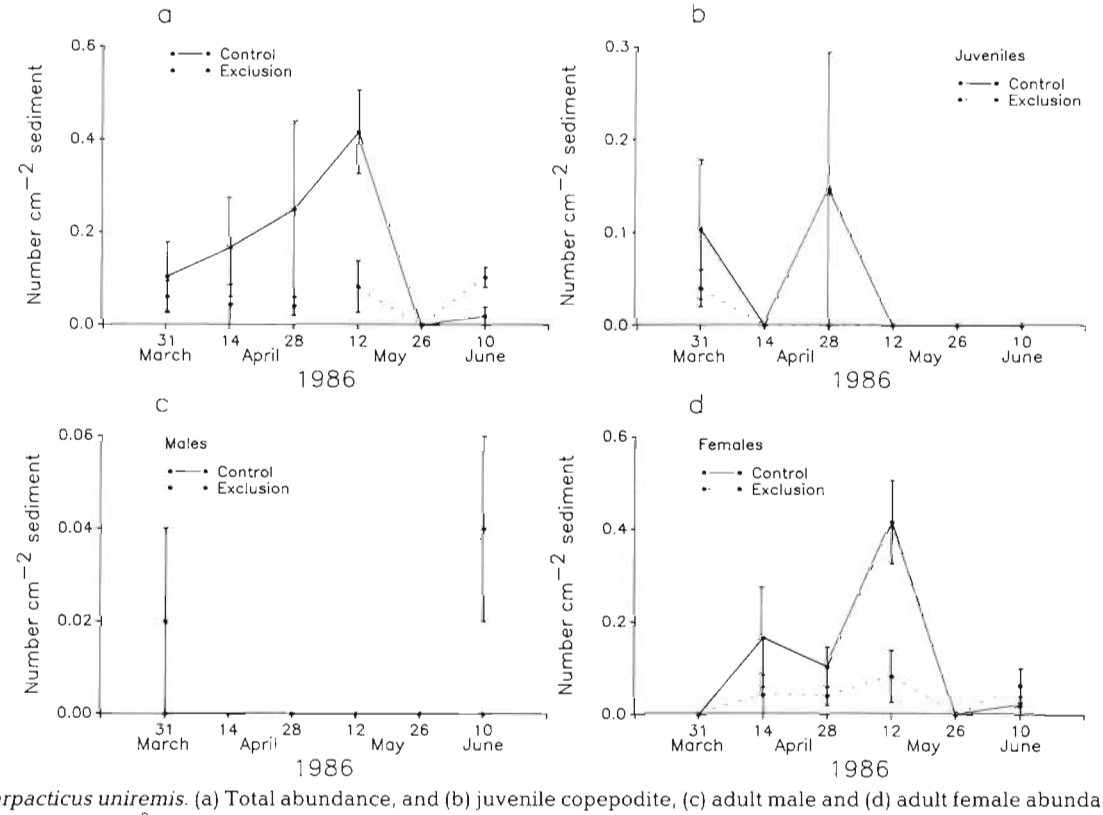

Fig. 2. *Harpacticus uniremis*. (a) Total abundance, and (b) juvenile copepodite, (c) adult male and (d) adult female abundance in the sediment (number cm^{-2} sediment) in the Control and Exclusion treatments in 1986. Values are means ± 1 standard error, n = 3

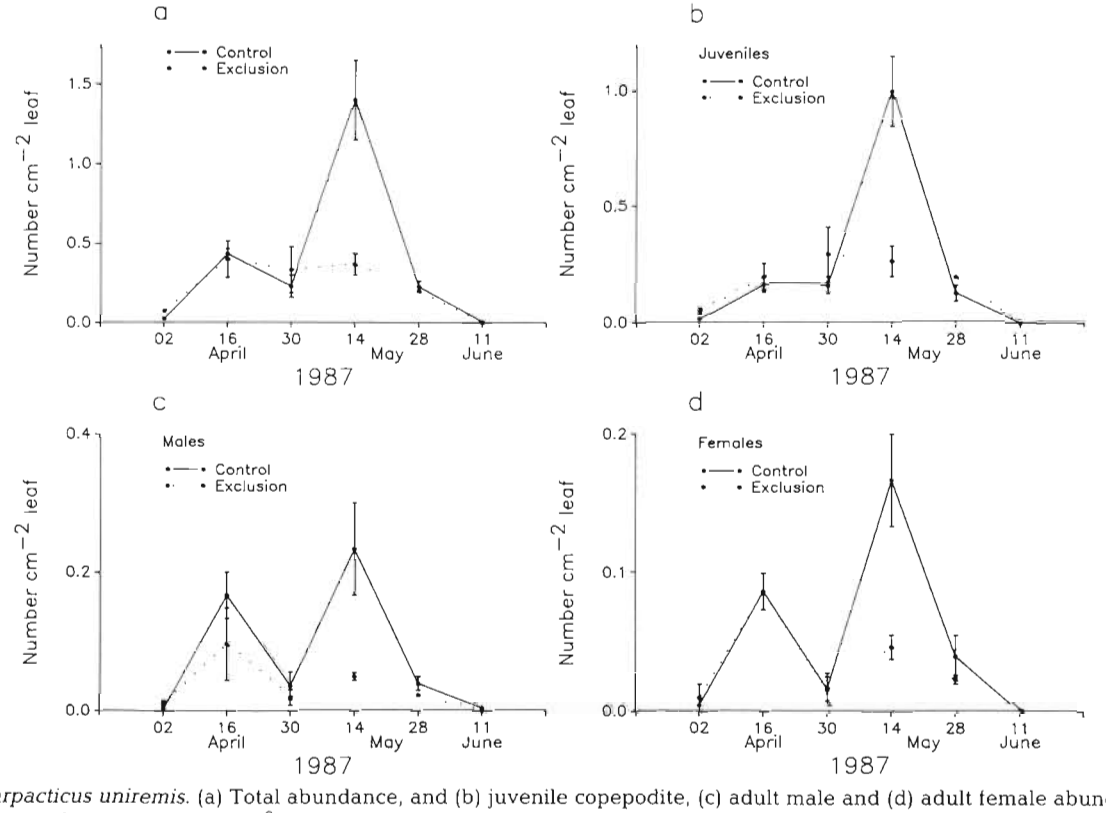

Fig. 3. *Harpacticus uniremis*. (a) Total abundance, and (b) juvenile copepodite, (c) adult male and (d) adult female abundance on *Zostera marina* leaves (number cm^{-2} leaf) in the Control and Exclusion treatments in 1987. Values are means ± 1 standard error, n = 3

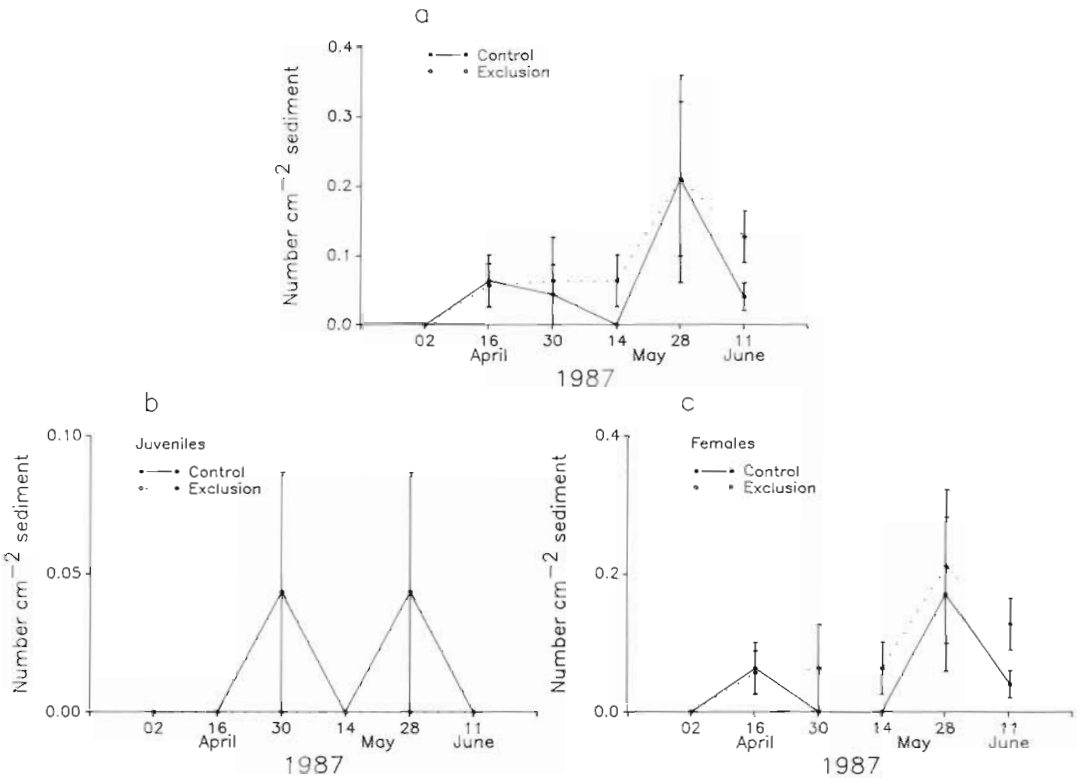

Fig. 4. *Harpacticus uniremis*. (a) Total abundance, and (b) juvenile copepodite and (c) adult female abundance in the sediment (number cm^{-2} sediment) in the Control and Exclusion treatments in 1987. Values are means ± 1 standard error, n = 3

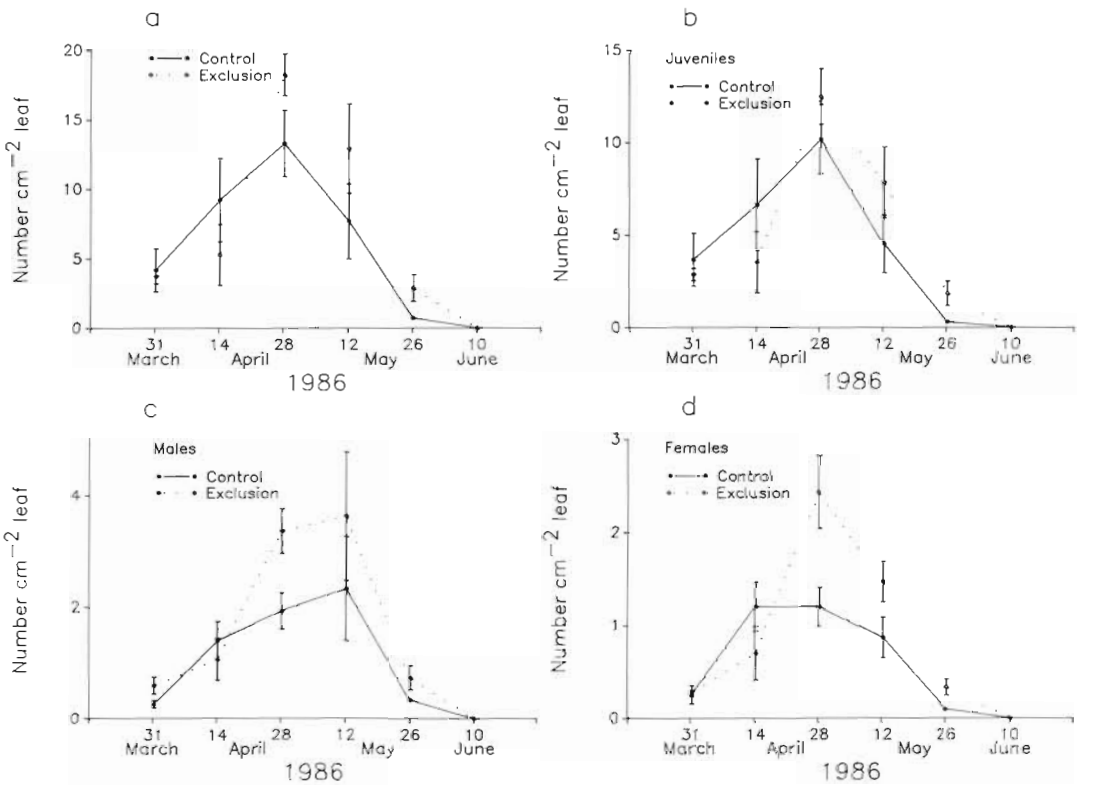

Fig. 5. *Tisbe* cf. *furcata*. (a) Total abundance and (b) juvenile copepodite, (c) adult male and (d) adult female abundance on *Zostera marina* leaves (number cm^{-2} leaf) in the Control and Exclusion treatments in 1986. Values are means ± 1 standard error, n = 3

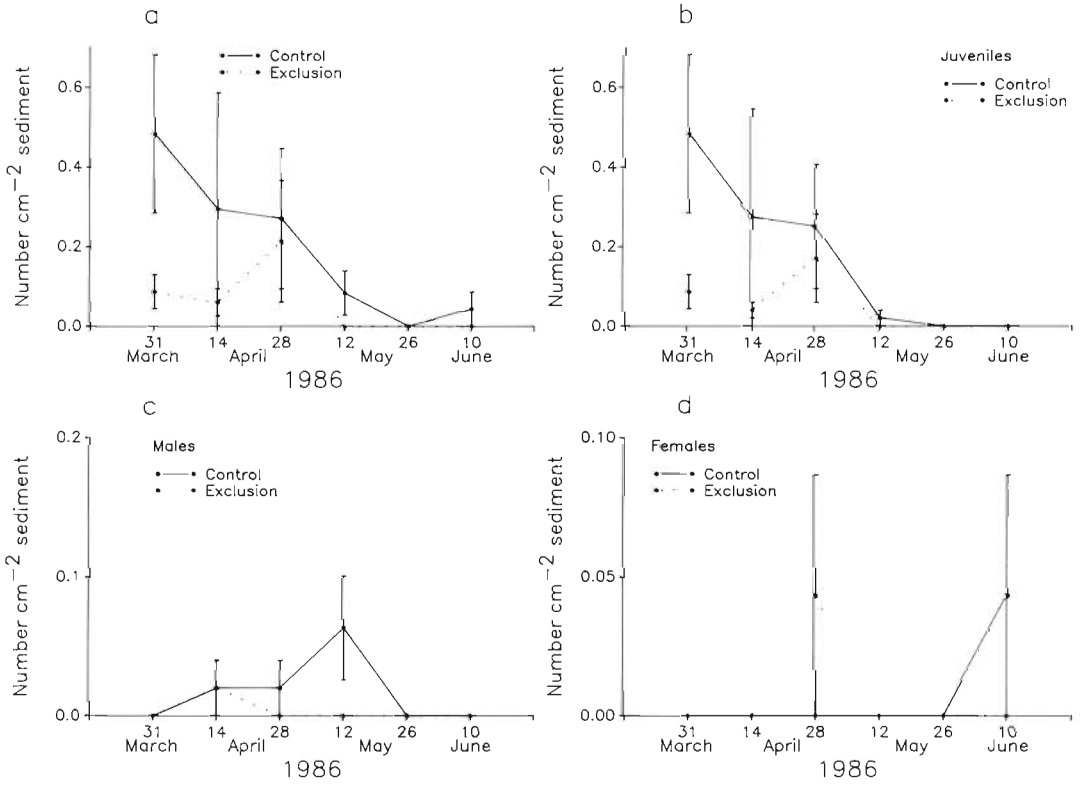

Fig. 6. *Tisbe* cf. *furcata*. (a) Total abundance, and (b) juvenile copepodite, (c) adult male and (d) adult female abundance in the sediment (number cm^{-2} sediment) in the Control and Exclusion treatments in 1986. Values are means ± 1 standard error, n = 3

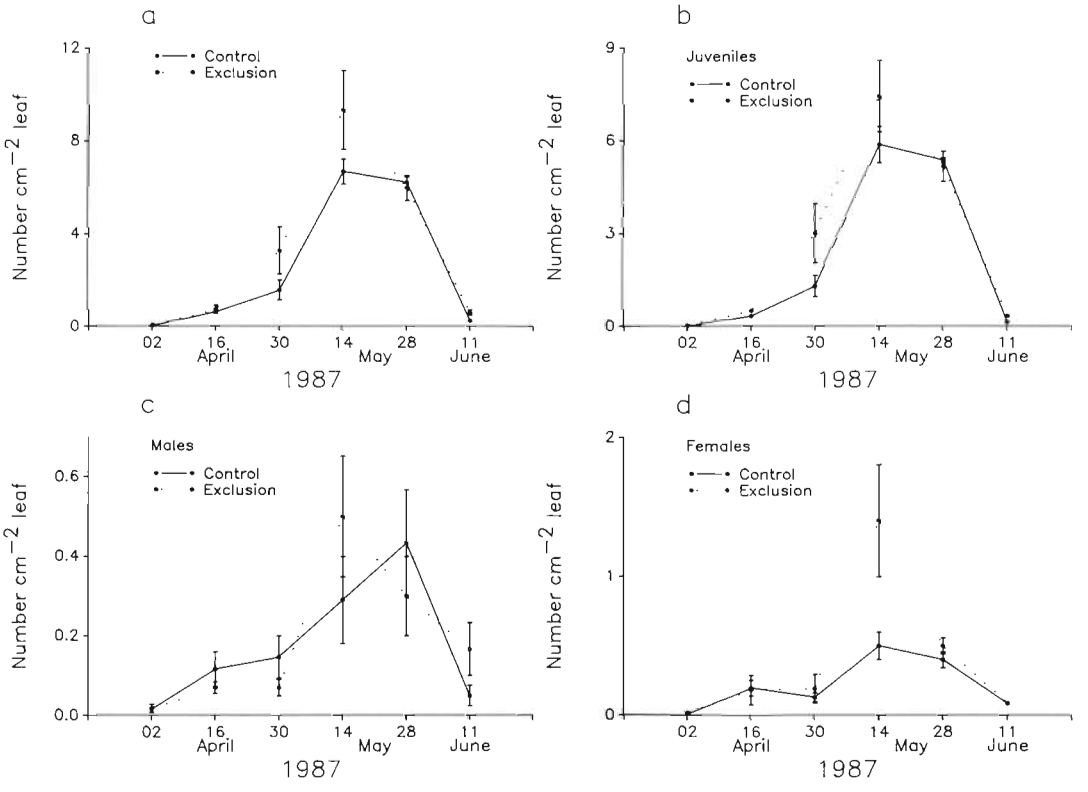

Fig. 7. *Tisbe* cf. *furcata*. (a) Total abundance, and (b) juvenile copepodite, (c) adult male and (d) adult female abundance on *Zostera marina* leaves (number cm^{-2} leaf) in the Control and Exclusion treatments in 1987. Values are means ± 1 standard error, n = 3

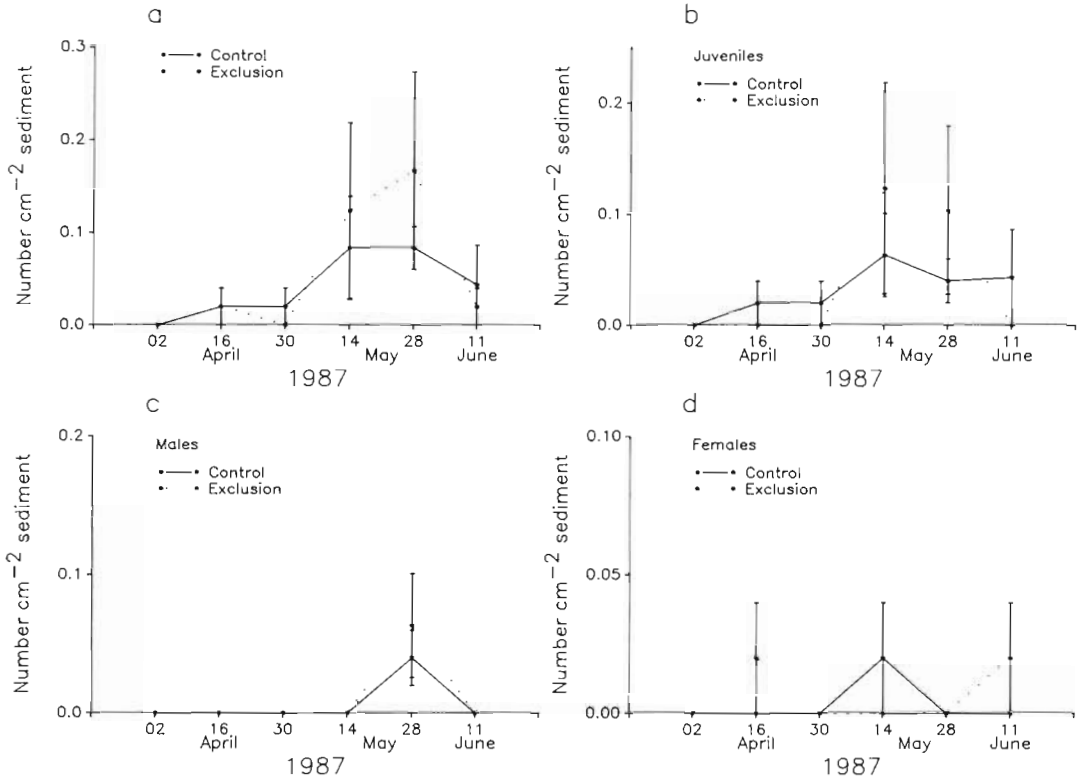

Fig. 8. *Tisbe* cf. *furcata*. (a) Total abundance, and (b) juvenile copepodite, (c) adult male and (d) adult female abundance in the sediment (number cm^{-2} sediment) in the Control and Exclusion treatments in 1987. Values are means ± 1 standard error, n = 3

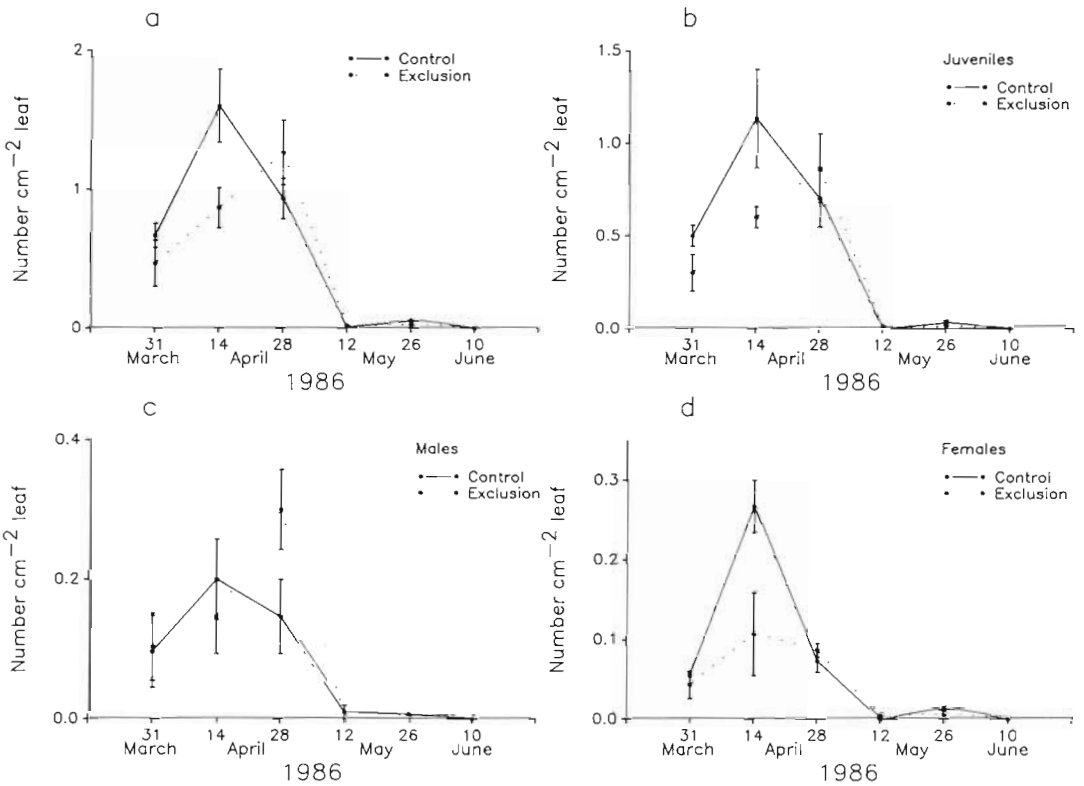

Fig. 9. *Zaus aurelii*. (a) Total abundance, and (b) juvenile copepodite, (c) adult male and (d) adult female abundance on *Zostera marina* leaves (number cm^{-2} leaf) in the Control and Exclusion treatments in 1986. Values are means ± 1 standard error, n = 3

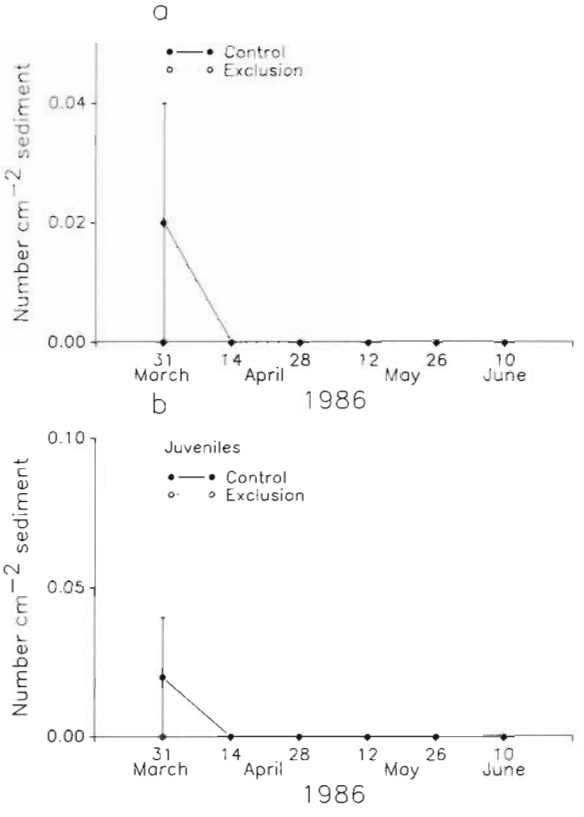

Fig. 10. *Zaus aurelii*. (a) Total abundance, and (b) juvenile copepodite abundance in the sediment (number cm^{-2} sediment) in the Control and Exclusion treatments in 1986. Values are means ± 1 standard error, n = 3

the cages were similar to those in the surrounding area (e.g. surficial sediment structure) and those that were not (e.g. seagrass epiphytic growth) also occurred in the control cage treatment. Comparison of sediment grain sizes between treatments at the end of the experiments indicated a significant increase in the < 75 µm 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% of the total sediment weight higher than the control. This is a small change in comparison to the minimum 19% increase in silt-clay (≤ 62 µm) content compared to surrounding sediment observed by Virnstein (1977) in 12 mm mesh cages in Chesapeake Bay. Artifacts introduced by caging seem to be minor and the control treatment seems to be adequate in design. Therefore, comparison between the exclusion treatment and the control should provide a test of the effect of large epibenthic predators on the densities of *Harpacticus uniremis, Tisbe* cf. *furcata* and *Zaus aurelii*.

Exclusion of large epibenthic predators (e.g. juvenile salmonids, crabs) seems to have little effect on the abundance and population structure of the 3 harpacticoid copepod species living on the seagrass or in the sediment. Overall, species abundances were either not different between treatments or densities were higher in the controls. Species abundances generally did not increase in the exclusion treatment as would be expected if consumption by large epibenthic predators was controlling population densities.

Tisbe cf. *furcata* female densities in leaf samples were higher in the exclusion treatment on 2 dates in 1986. No difference was seen in 1987. However, no sustained population of this species was observed in the exclusion treatment in 1986 and juvenile numbers did not increase relative to the control. An increase in juvenile numbers would be expected if predation on females was controlling the *T.* cf. *furcata* population through removal of reproductive individuals. The *Harpacticus uniremis* and *Zaus aurelii* populations did not increase in the exclusion treatment relative to the control in either year. It appears that exclusion of large epibenthic predators does little to halt the population declines of *H. uniremis, T.* cf. *furcata* and *Z. aurelii* in the late spring and early summer (Webb 1989) and therefore these declines, at least at this study site, are not related to predation by juvenile salmonids. This conclusion confirms the suggestion of Cordell (1986) and is contradictory to the analysis of Healey (1979).

A possible criticism of these experiments 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. This could lead to no significant increases being detected between treatments. This is possible considering that harpacticoids commonly enter the water column (e.g. Walters 1988). Therefore, dilution of cage populations could occur solely through transport within the water column at high tide. However, D'Amours (1988), based on a sled-sampler study conducted at high tide at the study site in 1986, calculated that almost no *Harpacticus uniremis, Tisbe* spp. or *Zaus aurelii* would be expected above 50 cm from the sediment. This is the height of the cages used in this study. Therefore, although lateral transport could occur throughout the seagrass bed, these copepods would not be found above the cages. Thus, any swimming activity within the cage area may not lead to a loss of copepods. Also, given that mainly adult males and late-stage female copepodites are generally found in the water column (Bell et al. 1988), adult female and total juvenile copepodite abundance should still exhibit a treatment effect if large epibenthic predators are controlling the populations of *H. uniremis, T.* cf. *furcata* and *Z. aurelii*. Sustained increases of females and juveniles in the exclusion treatment were not observed for any species. The conclusion of little effect of large

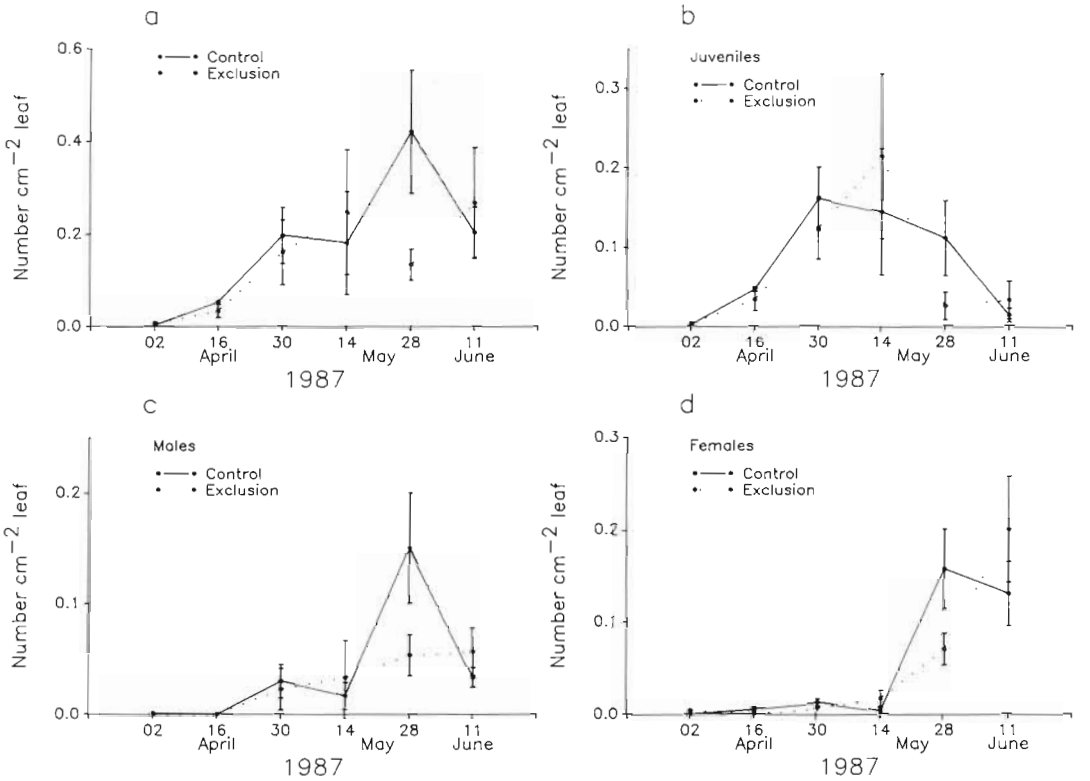

Fig. 11. *Zaus aurelii*. (a) Total abundance, and (b) juvenile copepodite, (c) adult male and (d) adult female abundance on *Zostera marina* leaves (number cm^{-2} leaf) in the Control and Exclusion treatments in 1987. Values are means ± 1 standard error, n = 3

epibenthic predators on these 3 species is, therefore, supported.

These experiments demonstrate that juvenile chum and/or pink salmon, as one predator group, exert little control on the population cycles of *Harpacticus uniremis, Tisbe* cf. *furcata* and *Zaus aurelii*. The results regarding the comparison of copepod mortality and salmonid consumption patterns presented in Webb (1991) are, therefore, supported. However, if predation by large epibenthos does not control the abundance of these 3 species, why do all 3 decline in early summer?

At this study site, seagrass-dwelling *Harpacticus uniremis, Tisbe* cf. *furcata* and *Zaus aurelii* start to increase in abundance during mid-March to mid-April and have generally disappeared by mid-June (Webb 1989). A possible explanation for this pattern is predation by animals small enough to pass in and out of the 7 mm mesh used in the exclusion experiments in this study. Small potential predators were not investigated. However, in qualitative examination, leaf samples contained only small numbers of other meiofauna (e.g. nematodes, mites). Organisms such as amphipods, juvenile polychaetes and gastropod molluscs were also uncommon in comparison to the dominant harpacticoid copepods. Amphipods are not abundant at this study site until later in the summer than sampled here (Miller 1985). Given the rapid population declines observed for the aforementioned copepod species, it is hard to ascribe a significant role to predation by other small invertebrates. An intriguing possibility, however, is the interaction of the epiphytic copepods with the structure of the primary epiphyte community (e.g. diatoms) on the seagrass leaves. The epiphytic diatom community changes in early June.

Macroalgal epiphytes on seagrass leaves were not commonly observed either during sampling or on preserved leaf samples during this study. Analysis of qualitative scrapings of seagrass leaf surfaces throughout the sampling period in both years by transmitted light and epifluorescence microscopy indicated that the primary epiphytic community was composed chiefly of bacteria and diatoms. Until early June, the diatom flora was dominated by the genera *Cocconeis* and *Isthmia* and little vertical relief was observed on the leaves. However, after this time, the diatom community was dominated by a tube-building *Navicula* sp., along with species of *Synedra* and *Rhoicosphenia*. The leaf epiphyton in June had a vertical, filamentous appearance due to the tube-building *Navicula*.

Dorso-ventrally flattened epiphytic harpacticoids, such as *Zaus* spp., have been found to be more abundant on macroalgal surfaces or seagrass leaves with

low primary epiphytism compared to surfaces with high epiphyte loads (Caine 1980, Hall & Bell 1988, Webb 1989). *Tisbe furcata* feeds raptorially by forming spherical masses from flocculant material and gleaning food from the surface while the sphere is rotated by the mouthparts (Marcotte 1977). Perhaps the decline in *T.* cf. *furcata* and *Z. aurelii* is related to a reduced feeding rate for *T.* cf. *furcata* on the more structurally complex leaf surface and for *Z. aurelii* due to the higher epiphyte loads being inhospitable. Unfortunately, no information on feeding mechanisms is available for *Harpacticus uniremis*. Interestingly, species of the genus *Heterolaophonte* appear to have an almost obligate requirement to feed off cylindrical objects (Marcotte 1977). *Heterolaophonte variabilis* Lang becomes the dominant leaf-dwelling harpacticoid as *H. uniremis, T.* cf. *furcata* and *Z. aurelii* densities are declining (Webb 1989). This increase in *H. variabilis* abundance may be linked to an appropriate habitat such as the one created by the tube-building *Navicula* sp. Changes in epiphytic architecture on seagrass leaves as a factor influencing successional patterns of epiphytic harpacticoid copepods may be a fruitful avenue for further research.

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