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Effects of epibenthic macropredators on community structure in an eutrophicated shallow water area, with special reference to food consumption by the common goby *Pomatoschistus microps*

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Abstract

Field manipulative cage experiments were performed on an unvegetated shallow water mudflat in the eutrophicated inner Oslo fjord. Enclosure and enclosure cages each covering an area of 0.6 m², were maintained on the mudflat to protect infauna from epibenthic macropredators in general and for exposing the infauna to different densities of the common goby, *Pomatoschistus microps*, a common predator in the area. Predation effects were determined by comparing faunal composition and abundance inside and outside the cages after 2 1/2 months. Irrespective of the number of gobies in the cages only minor differences in faunal composition and abundance were found between cage and control. It is therefore concluded that epibenthic macropredators in general and *P. microps* in particular do not crop infauna to an extent sufficient to alter faunal composition and to reduce abundance discernibly.

Introduction

Marine ecologists have become more and more interested in the possible importance of biological interactions as a factor structuring communities. Studies on biological interactions often involve field experiments with cages to manipulate the abundance of predators or competitors.

Most experiments of this type have so far been made on rocky shores where competition for space often leads to the exclusion of inferior competitors with the result that the substrate will be locally monopolised by one or a few species (usually bivalves) (PAINE 1966, 1974). Disturbances either by predation or physical factors like wave action may, however, prevent competitive exclusion by removing competitive dominant species.

Experiments involving the exclusion of epibenthic macropredators with cages on unvegetated intertidal mud-flats will not result in a few species monopolising the substrate but rather in an increase in infaunal density (PETERSON 1979). This was first reported as far back as 1927 by BLEGVAD, and similar results were found by REISE (1978, 1979). Investigations by BERGE (1980) indicate that predation by epibenthic macropredators is of minor importance in structuring communities on the subtidal mudflats in the eutrophicated Oslo fjord, Norway, and a series of recent experiments seems to confirm this assumption.

Some bottom-feeding fish are found to be important macropredators in shallow soft-bottom areas (VIRNSTEIN 1977). COMMITO (1976), however, found little support for a

hypothesis that fish (and crabs) control the structure of two soft-bottom intertidal communities in the Newport Estuary, N.C., U.S.A.

The effect of predation by epibenthic macropredators on structuring marine softbottom communities thus remains a controversial question. PETERSON (1979), when reviewing publications on predator exclusion experiments, thus pointed out that a serious bias may exist as unsuccessful experiments (e.g. no predation effect) are not likely to be published.

In shallow water of the Oslo fjord gobies are the most frequent group of bottom-feeding fish. Consequently, they should be regarded as potentially important predators.

The intention of the present study was to determine the possible effect of epibenthic macropredators, particularly the common goby, *Pomatoschistus microps*, on the community structure and infaunal densities, in a low energy shallow water eutrophicated area in the Oslo fjord. Here tidal and wind-induced currents are at a minimum, and as a result habitat modifications caused by differential sediment deposition and erosion inside and outside cages are suspected to be low.

Material and methods

The area studied was in a shallow bay in the innermost Oslo fjord (59°52'49''N, 10°43'30''E) in Norway. The site was situated 10–30 cm beneath the depth usually exposed at low tide. In the area the mean tidal range is only about 24 cm and the whole area is regarded as eutrophicated. Little macro-vegetation was found on the mud flat where the experiments were performed.

Wire-mesh cages were used either to exclude macropredators or confine gobies to a restricted area. The cages were made of stainless steel wire-mesh with square mesh-size 3.2 mm. The area inside the cages was 0.6 x 1.0 m, and the height of the cage was 0.2 m. The top of the cage was equipped with a 0.48 m² opening covered with a removable PVC net (square mesh size = 3 mm) for inspection of the cage. The side of the cages were pushed about 5 cm into the sediment. During the actual experiment the cages were randomly scattered in two groups (X-region and Y-region respectively).

The various treatments are presented in Table 1.

Sediment for animal density, determination outside and inside cages, was sampled with hand operated plexi-glass corers (inside diameter 6 cm i.e. 28.3 cm²) according to the scheme shown in Table 1. Only the topmost three cm of the sediment was used in this investigation.

The core samples were washed through a 250 µm sieve and Bengal rose added. The retained animals were sorted, identified and counted. Nematodes and protozoans were not included.

The stomach contents of the gobies was also identified.

The experiments started in August and lasted 2 1/2 months. However, a problem turned up as three of our six cages were destroyed due to vandalism or human curiosity. Nevertheless one complete replicate (three cages) was still intact at the end of the experiment and forms the basis of this report. The material from this experiment is summed up in Table 1.

Results

Table 1 shows that the number of fish in cages with fish had decreased in the course of the experiments. The common gobies, which are normally partly buried in the

Table 1

Summary of autumn experiments 1979. In the uncaged area 6 samples were taken in each region at start of experiment and 4 samples at end of experiments. Numbers in paranthesis show number of gobies recaptured at the end of the experiment.

Treatment	Symbol	At start, 31. August		At end, 19. November	
		No. of core samples	No. of fish in cage	No. of core samples	No. of fish observed in cage
Uncaged area	X	6	—	4	—
Uncaged area	Y	6	—	4	—
Empty cage	C-0		0	4	0
Cage with gobies, "normal" density	C-3		3	4	1 (1)
Cage with gobies, "high" density	C-10		10	4	3 (2)

sediment, may have been overlooked, but a certain natural mortality over 2 1/2 months period cannot be ruled out. We feel confident that no gobies had escaped the cages. We do not know for how long the predation pressure inside the cages was of the planned size, but inside the cage with the original "high" density (C-10) the number of fish at least equalled a "normal" density for the whole period of the experiment.

Of the three fish collected at the end of the experiment, one had recently died, but all appeared well fed. The total lengths were 52, 57 and 58 mm respectively and compared with the average length (48.4 mm) and range of lengths (47 – 53 mm) at the start of the experiments, it seems that the three specimens had grown and consequently must have been feeding.

The food items found in the stomach of *P. microps* collected at the start of the experiment, reflected the composition of the fauna in the area. It is thus clear that *P. microps* is a predator on the fauna we have been studying.

The faunal groups recognized in the experiments are seen in Table 2. Ranking the different taxonomic groups at start and end of experiment according to abundance and testing for the existence of a correlation (Spearman's r_s ; SIEGEL 1956) gives a good agreement between the two ranks ($r=0.82$). This indicates that the relative composition of the fauna in the experimental area had not changed dramatically during the experimental period. However, the mean density per corer decreased from 897 to 656.

Some significant differences in infaunal densities between the two sampling regions (X and Y) were found (Table 3), but the community structure was comparable ($r_s = 0.84$). We have therefore performed tests for significant differences between treatments and control with samples from X and Y pooled and separated (Table 3).

The faunal abundance of the identified taxa in cages and controls are shown in Fig. 1B for the X-region, in Fig. 1A for the Y-region and in Fig. 2 for the lumped cages and

Table 2

Mean number of animals in topmost 3 cm of corers from control samples in X and Y region and in combined controls (X + Y). The animals are ranked according to decreasing abundance in combined controls. Mean number of individuals = N. Standard deviation = SD. Confidence limit (95 %) as percentage of mean = % CL.

Rank	X			Y			X + Y		
	N	SD	%CL	N	SD	%CL	N	SD	%CL
A Total fauna	498	83	19	775	102	13	656	171	19
B Oligochaeta I	196	27	15	330	31	10	272	76	21
C Benthic copepods	156	84	61	201	27	13	182	58	23
D Ostracods	29	18	70	84	34	40	60	39	27
E <i>Polydora</i> sp.	16	10	70	55	53	94	38	43	84
F <i>Mya arenaria</i> (L.)	37	4	10	25	3	10	31	7	15
G Oligochaeta II	24	8	38	20	6	29	20	5	18
H <i>Cerastoderma edule</i> (L.)	16	5	31	9	3	27	12	5	30
I <i>Manayunkia aestuarina</i> (Bourne)	13	5	40	10	5	49	11	5	30
J <i>Corophium volutator</i> (Pallas)	5	5	116	16	12	73	11	11	71
K <i>Mytilus edulis</i> L.	2	0.8	46	13	9	65	8	9	77
L Gammarids (– <i>C. volutator</i>)	3	3	113	8	5	70	6	5	64
M <i>Nereis diversicolor</i> (O.F. Müller)	2.5	1.3	59	4	1.8	44	3.3	1.7	42
N Other taxa	2	1.7	98	1.5	0.6	39	1.7	1.1	48

Table 3

Test (Student t-test, log n + 1 transformed data) for the existence of faunal differences ($p = 0.05$) between treatments. Significant differences between treatments detected = +. No significant differences detected = –. Significant difference detected with cage densities higher than in control = ⊕.

Treatments tested	X Y	C-10 X	C-3 Y	C-0 Y	C-0 X + Y	C-3 X + Y	C-10 X + Y	All cages X + Y	C-3 C-0
Total fauna	+	–	–	–	–	–	–	–	–
Oligochaeta I	–	–	–	–	–	–	–	–	–
Benthic copepods	–	–	–	–	–	–	–	–	–
Ostracods	+	–	⊕	⊕	⊕	⊕	–	⊕	–
<i>Polydora</i> sp.	–	⊕	–	–	–	⊕	–	–	+
<i>M. arenaria</i>	+	–	⊕	–	–	–	–	–	–
Oligochaeta II	–	–	–	–	–	–	–	–	–
<i>C. edule</i>	+	–	–	–	–	–	–	–	–
<i>M. aestuarina</i>	–	–	–	–	–	–	–	–	–
<i>C. volutator</i>	–	–	–	–	–	–	–	–	+
<i>M. edulis</i>	+	–	–	+	–	–	–	–	+
Gammarids (– <i>Cor.</i>)	–	–	⊕	–	–	⊕	–	⊕	+
<i>N. diversicolor</i>	–	–	–	–	–	–	–	–	–
Other taxa	–	–	⊕	–	+	⊕	–	–	+

controls. When comparing rank numbers for the different faunal groups, good correlation was found between all treatments and their representative control ($r_r = 0.86-0.93$).

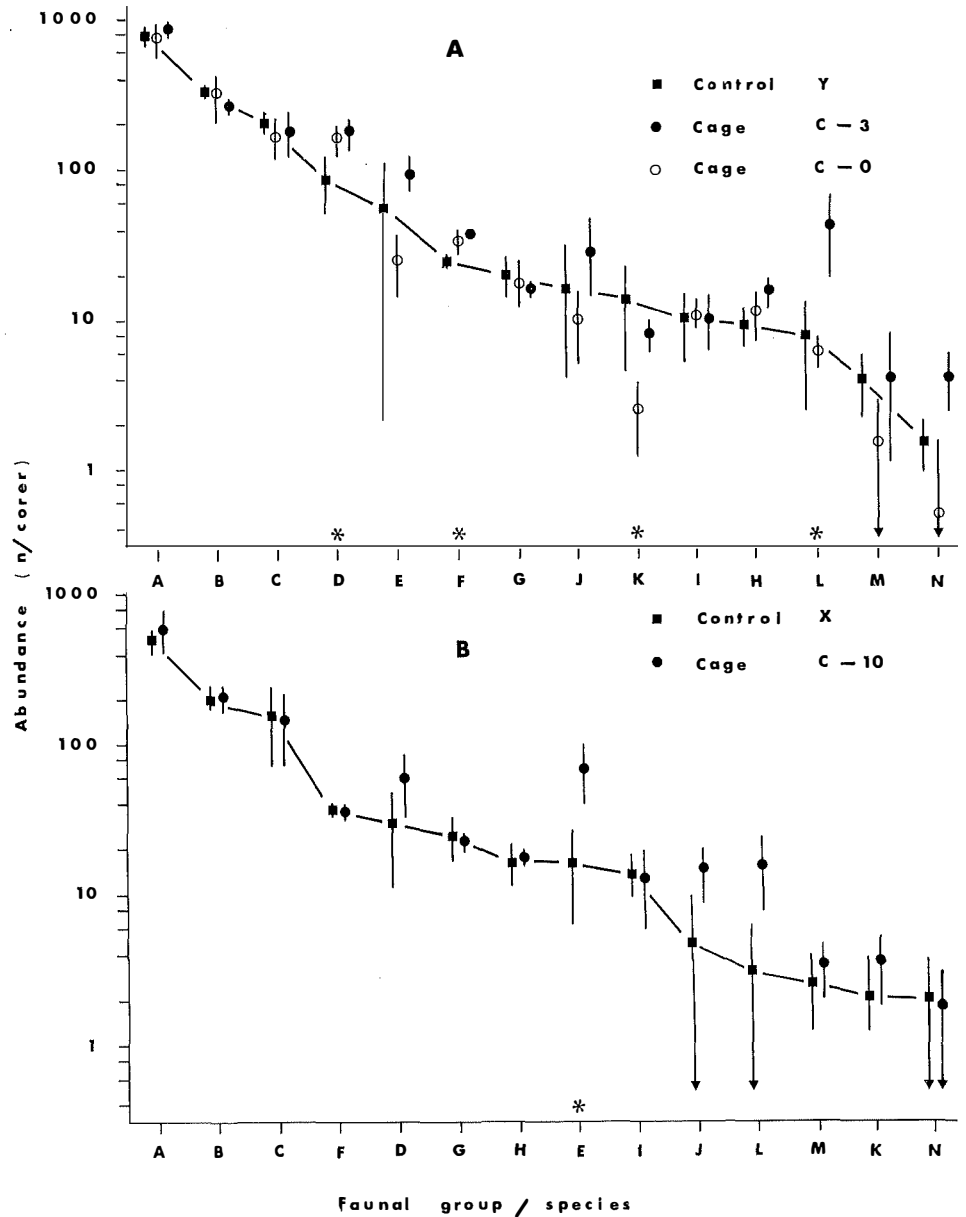


Figure 1

Abundance of animals in cage and control as a function of rank in control. Vertical lines indicate 1 SD. A star indicates that significant ($p=0.05$) difference is found. Symbols on the abscissa are explained in Table 2.

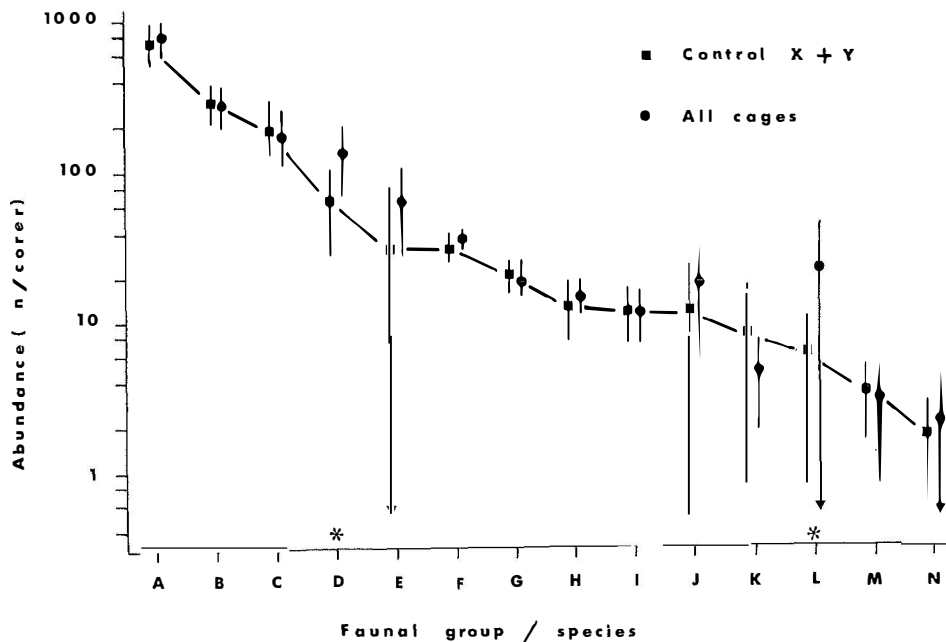


Figure 2

Abundance of animals in cage and control as a function of rank in control. Vertical lines indicate 1 SD. A star indicates that significant ($p = 0.05$) difference is found. Symbols on the abscissa are explained in Table 2.

No significant differences were found for total number of individuals for any of the treatments except between the controls in the X and Y region (Table 3). Lumping the samples from all cages and comparing mean densities in these with the lumped controls reveals that gammarids and ostracods were significantly more abundant in the cages (Fig. 2).

Comparing each cage with the lumped controls (X + Y) gives no significant difference for C-10 (Table 3). Comparing C-3 with X + Y reveals that *Polydora* sp., gammarids (–*Corophium*), ostracods and “others” were significantly more abundant in C-3 than in X + Y. Finally the ostracods were significantly more abundant in C-0 than in X + Y.

Inspection of Table 3 reveals that of 98 tests on density differences between a cage and a control, significant differences were only detected in 16. In two of these the densities in the control were higher than in the cage and in 14 the opposite was found.

Table 2 indicates the precision of our data showing the confidence limit (95 %) which allows detection of a significantly higher abundance in the cage than in the control assuming that the variance does not change following the density increase. For the total number of individuals the mean density must increase by 19 % in the X region and 13 % in the Y region. The individual taxonomic groups must, however, increase by a higher percentage in order to be able to detect a significant increase.

No significant difference in species richness between cages and controls was detected.

Discussion

In designing our experiment we hypothesized that epibenthic macropredators in general and *P. microps* in particular are important in regulating benthic community structure and infaunal densities. If our hypothesis was correct, the highest densities should be found in cage C-0, where all epibenthic macropredators were excluded, followed by C-3 with initially three fish confined and C-10 with initially 10 fish confined. The hypothesis should remain valid irrespective of possible habitat modifications inside the cages. The control area should have the lowest densities if predation pressure by the fish in C-10 are lower than the total predation pressure outside the cages and if habitat modifications have not influenced the results.

Few significant differences were found consistent with our hypothesis. In respect to community structure (here defined as the rank of the observed faunal groups according to abundance) no significant differences were found as a result of exclusion or inclusion of predators.

With respect to the effect of predation on densities, comparisons between C-3, C-0 and Y give a rather confusing picture of how *P. microps* influences infaunal densities. Our data do not suggest that *P. microps* crops infauna to an extent sufficient to reduce abundance significantly. The only possible exceptions were the ostracods. However, ostracod densities were higher in C-3 than in C-0. Comparisons between C-10 and X (Fig. 1B) could alone indicate that the fish in C-10 crops fauna less efficiently than the natural density of predators outside C-10. But if this is the case a more pronounced difference should have been found between C-3 and Y and an even greater one between the densities in C-0 and Y, because, no fish are confined in C-0, with the highest densities in C-0 and C-3 respectively. Table 3 and Fig. 1 show that this was not the case. Only *Polydora* sp. is more abundant in C-10 than in X and only the ostracods are significantly more abundant in C-0 than in Y. Whereas *Mya arenaria*, gammarids (– *Corophium*), ostracods and “others” were significantly more abundant in C-3 than Y and as many as five groups are significantly more abundant in C-3 than in C-0.

Thus, our results do not support the hypothesis that *P. microps* significantly crops infauna. Therefore it seems that *P. microps* neither influences community structure nor infaunal densities in the area investigated, given the variability in our data.

If *P. microps* does not significantly crop infauna the effect of epibenthic macropredators in general may be evaluated by comparing mean densities in pooled controls with cages. This comparison reveals that only ostracods and gammarids (– *Corophium*) show a significantly higher abundance in the cages (Table 3). We therefore conclude that epibenthic macropredators in general also have little effect on faunal composition and abundance, save ostracods and gammarids.

Most other comparable studies show that predators have a marked influence on faunal densities and community structure. PETERSON (1979), reviewing data on the consequences of excluding epibenthic predators from soft bottom sediments, states that usually the densities of macroinvertebrates became significantly higher inside the cages than in the control areas outside the cages. In the same review PETERSON maintains that species richness also usually increases inside cages. No such increase was found in our investigation.

We suggest that in our study habitat modifications in the cages are minimal and thereby opportunistic species (*Capitella capitata* and *Polydora*) do not increase in abundance in the cages. The production in the area may also be high or the infaunal turnover so fast that the predation by epibenthic macropredators is not sufficient to alter the community structure or faunal abundance to a detectable degree with the

precision level in our data. An exception may be for the ostracods and the gamariids (– *Corophium*), but since ostracods were not found in the stomach of *P. microps* it is possible that other predators or physical factors are responsible for this result. A high secondary production in the area was shown by HESTHAGEN (1977) who found a higher growth rate in *Pomatoschistus minutus* from the inner Oslo fjord than in populations from similar latitudes. He attributed this increased growth rate to a beneficial effect of eutrophication in the innermost Oslo fjord resulting in higher production and supply of fish food. Increase in benthic intertidal polychaete biomass has, for instance, been reported by DAUER and CONNER (1980) as a consequence of moderate sewage input.

We found no evidence of small predators being attracted to the area under the cages in great numbers as did for example ARNTZ (1977) in his experiments in Kiel Bay.

The results from our cage experiments lead us to the conclusion that community structure and abundance of the fauna studied are little affected by macrofaunal predation. Thus, our results deviate from previously published reports where large epibenthic macropredators were excluded from unvegetated soft sediment communities (PETERSON 1979). We do not believe, however, that the fauna investigated in our experiments are unimportant food items for the macropredators, only that the predation pressure exerted by these predators does not influence the community structure or infaunal densities discernably in the period we have been investigating. Different results may, however, be found at other times of the year and predators of smaller size than those excluded by our cages may also be important in regulating community parameters.

We feel that more detailed experiments both in the field and in the laboratory are needed, before more than coarse predictions can be made on how reduced predation pressure will influence a shallow water soft bottom community.

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