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Field Experiments on the Role of Epibenthic Predators in Determining Prey Densities in an Estuarine Mudflat

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A series of caging experiments was performed on an estuarine mudflat at three seasons of the year, in which *Carcinus maenas* L. and *Pomatoschistus microps* (Kroyer) were either excluded from, or allowed to prey upon, the benthos in order to determine to what extent infaunal abundance and mortality was a result of predation by epibenthic predators.

The difficulties of conducting and interpreting the results of such experiments are recognized. The benthic macrofauna of this mudflat is dominated numerically by small annelids and there is evidence that adult *C. maenas* can cause significant increases in the oligochaete component of this assemblage, probably as a result of disturbance caused by its burrowing activity. Juvenile *C. maenas* on the other hand significantly reduced the abundance of small annelids, particularly the dominant polychaete *Manayunkia aestuarina* (Bourne) and could be responsible for year-to-year variations in abundance of this species. The role of fish predators (in this case *P. microps*) is more problematical but it is suggested that in the densities at which they occur naturally on the mudflat they have little direct effect on the abundance of prey species. There is no evidence that seasonal mortality of small annelids is reduced in the absence of predation and this is taken to indicate that not all mortality is due to epibenthic predation. Certain changes in relative abundance of the component species of the harpacticoid copepod community were discerned but it is suggested that the plasticity of their reproductive potential is such that the effect of predation on the group as a whole is usually masked.

Introduction

Over the past decade, much of the work on the benthos in the River Lynher estuary in Cornwall has been concerned with quantifying the production dynamics of the benthic community of an intertidal mudflat (Warwick & Price, 1975, 1979; Teare & Price, 1979; Price and Warwick, 1980*a*, *b*). These studies culminated in the construction of a steady state energy budget and a dynamic simulation model of the flow of energy through this ecosystem (Warwick *et al.*, 1979). The model follows the assumption, often made in the literature (e.g. Arntz & Brunswig, 1975) that all production is utilized as food for carnivores and almost all mortality is due to predation (Peer, 1970). This implies that predation is a major factor controlling the abundance and productivity of species in the community and therefore also the community structure itself.

That this is so was first demonstrated experimentally in rocky shore communities by using cages to control the levels of predation. Connell (1961) showed that in the absence of predation, intense competition for space (a two-dimensional, limiting resource in

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these habitats) results in the exclusion of inferior species by competitively dominant species, resulting in a decrease in the diversity of the community and its virtual domination by one successful species. Connell (1970), Dayton (1971) and Paine (1974) showed that predation and physical disturbance play a major role in maintaining the community species diversity by reducing the abundance of the dominant species to a level at which competition for space is less intense and by making available free space for colonization by newly settled larvae. Peterson (1979), in reviewing recent similar work in unvegetated soft sediments, has shown that in this habitat the above model of community organization does not apply. In the absence of predators there appears to be no tendency towards competitive exclusion and there is an increase in both the abundance and richness of the species in the community (Blegvad, 1928; Nagvi, 1968; Young *et al.* 1976; Reise, 1977, 1978; Virnstein, 1977, 1979), the largest increases occurring in rapid growing, shallow living, opportunistic species with planktonic larvae. Peterson (1979) suggests that the mobility and three-dimensional nature of the sediments; the intense negative interactions between densely established adults and potentially colonizing larvae; and the relatively low energy requirements of benthic infauna, make interference competition a less effective or more long-term mechanism determining community structure. However, predation and disturbance (Vanblaricom, 1979) by epibenthic predators are thought to retain an important organizing role, although some recent authors have found little evidence for this (Berge & Hesthagen, 1981).

The objectives of the present study were to determine: (1) to what extent the benthic community structure and abundance on the Lynher River mudflat is a function of the presence of predators and (2) whether, in fact, all mortality of the benthic fauna is due to predation. In pursuance of the first of these objectives some long-term (one year), small mesh (1 mm) predator exclusion experiments were conducted on the mudflat. These experiments, however, were unsuccessful because of problems caused by fouling, erosion and sedimentation altering the physical and biological characteristics of the environment (Arntz, 1977, 1981; Hulbert & Oliver, 1980). In order to overcome these problems the approach was switched to short-term (one month) predator enclosure experiments using higher than natural densities of predators for maximum impact. The disadvantage of this approach is that the time span of the experiments is too short to detect any changes in the structure of the species assemblage (species richness), at least in groups other than the meiofauna. However, effects on species abundance and mortality should still be detectable.

Reise (1978) suggested that small epibenthic predators were the major determinants of the dynamic species abundance pattern in lower tidal flats and studies of the fish and crustacea inhabiting the Lynher mudflat at high water suggested that the goby *Pomatoschistus microps* (Kroyer) and the shore crab *Carcinus maenas* L. were the two most common predators feeding on the benthos during late spring to late autumn. These therefore were the predators investigated in this series of experiments. It has also been shown that numbers and size frequency of these predator populations fluctuate markedly throughout the year and that the gobies at least tend to switch their diet at certain times of the year. Any predator impact is therefore likely to vary seasonally, a fact not often taken into account in previous enclosure studies, and so comparable experiments were carried out at different times of the year.

Methods

Three experiments were performed, each lasting approximately 30 days and starting

in June 1980, September 1980 and April 1981. They were all conducted in a specially designated area, described in detail by Warwick and Price (1975), around mean tide level on a mudflat near Anthony in the estuary of the River Lynher, Cornwall. The cages, used in all experiments and figured in Warwick *et al.* (1982), each consisted of a solid sided, square base, 300 mm high, onto which was clipped a detachable, 250-mm high, wooden frame covered with 2-mm mesh nylon netting. The cage bases were pushed into the mud leaving 50 mm above the mud surface.

Each experiment used 0·2-m^2 blocks of mudflat sediment which were either left uncovered (uncaged controls) or covered with cages. These either excluded predators (caged controls) or enclosed a known number of gobies or crabs. All blocks were replicated (Table 1). In the first two experiments the cages were set out in three rows (parallel

TABLE 1. Details of treatments, layout and sampling of the benthos in the experimental series

	Exp. 1 Summer	Exp. 2 Autumn	Exp. 3 Spring
Dates (begin/terminate)	9.6.80–11.7.80	18.9.80–22.10.80	31.3.81–1.5.81
Treatments (number of cages/number of predators per cage)			
Control cage	3/0	3/0	4/0
Adult goby cages	3/10	3/10	4/10
Juvenile goby cages	0/0	3/10	
Adult crab cages	3/1	0/0	0/0
Juvenile crab cages	3/15	3/15	4/17
Uncaged control blocks	1/0	1/0	4/0
Treatment arrangement	Columns	Columns	Latin square
Benthos sampling (Number of samples per cage at beginning/10 days/20 days/termination)			
Meiofauna and small annelids	+/3/3/3	0/3/3/3	3/3/3/3
Macrofauna	+/0/0/1	0/0/0/+	0/0/0/0
Epifauna	+/0/0/1	0/0/0/1	0/0/0/1

+, denotes only the outside control sampled.

to the incoming tide) of four columns (at right angles to the tide), all 2 m apart. The cage treatments were arranged so that one occurred in each row but in only one column. The uncaged controls were randomly chosen outside the area immediately occupied by the cages. In the April 1981 experiment all the blocks were arranged in a 4×4 latin square array with one treatment in each row and column.

P. microps were caught on site, using a 5 mm bunt mesh sand eel seine net, during the high tide immediately prior to the start of an experiment. Those to be used in the experiment (10 per goby treatment cage) were transferred to holding tanks of clean seawater before being placed in the cage. The remainder of the catch was anaesthetized in MS 222, killed and fixed in 10% formalin. The characteristics of the experimental fish at the start were taken to be the same as those of a similar size in the remainder of the catch. Adult gobies were approximately 35–42 mm SL and juveniles 25–32 mm SL. *C. maenas* were collected from the shore as it was being uncovered by the tide and transferred to the cages at the same time as the gobies. At the start of the experiment the carapace width of *C. maenas* juveniles was approximately 10–15 mm and that of adults about 50 mm.

During the course of the experiment, any dead predators were removed but not replaced. At termination the surviving predators were removed, anaesthetized and fixed.

On a high tide, as near the end of the experiment as possible, another field sample of gobies was netted and preserved, for comparison with the caged fish. In the laboratory the *P. microps* were sexed, measured, weighed and the gut contents identified either to species or some higher taxonomic category. The contribution of each category to the diet was measured numerically and volumetrically by the subjective points method of Hynes (1950).

The benthic infauna samples in this study are referred to in three categories, based on different sampling and extraction techniques for different size fractions of the community.

(a) *Macrofauna*: the species which, during the major part of their productive life are retained by a 500-μm sieve. These are the molluscan and large polychaete species listed in Warwick and Price (1975). They were only sampled at the end of the June 1980 experiment by removing and sieving 0·1 m^2 of sediment from the cages after all other samples had been taken. The sieved samples were fixed, stained with Rose Bengal and the animals sorted from the retained detritus by hand.

(b) *Small annelids:* most of these pass through a 500-μm sieve but the adults are retained by a 125-μm sieve. This is the assemblage of oligochaete and polychaete species, some of which [e.g. *Manayunkia aestuarina* (Bourne)] are usually considered part of the meiofauna and some [e.g. *Streblospio shrubsolii* (Buchanan)] part of the macrofauna. These animals were recovered from 4·4 cm^2 sediment samples by staining and sieving the sample and extracting the animals from the retained fraction by differential floatation as described by Jonge and Bouwman (1977) using colloidal silica (Ludox-TM) diluted to S.G. 1·15.

(c) *Meiofauna:* all the other animals which are retained on a 63-μm sieve, the most abundant of which are nematodes and harpacticoid copepods. These animals were recovered from 0·5-cm^2 sediment samples by staining and sieving the samples and centrifuging the retained fraction with kaolin and colloidal silica (as above).

The small annelids and meiofauna samples were taken from the same core, obtained using a plastic core tube of cross-sectional area 4·9 cm^2. The site was visited at 10-day intervals and three replicate cores were obtained from each treatment block at each visit (Table 1). The position of the cores was fixed using a specially constructed grid of 10×10 squares which just covered the 0·2-m^2 block. Core position was predetermined on a random number basis with the proviso that no two samples were taken from the same or contagious squares or from the row of squares adjacent to the block sides.

At the end of each experiment any epifauna present in the cages was sampled by repeatedly sweeping the cage bottom with a close fitting, 2-mm mesh, hand net until nothing was caught.

The individual core counts of small annelids and meiofauna at termination of an experiment were subjected to two-way ANOVA which analysed the variance of core counts in each block both within and between treatments (the treatments being: no cages; cages with no predators; cages with gobies; cages with crabs). If there was a significant difference between core counts from each block within a treatment this was regarded as a block effect and in subsequent analyses the mean core count from each block was used as a treatment replicate. Where no such block effect was detected individual core counts were used as treatment replicates. These were then examined for significance on a multi-comparison basis by one-way ANOVA and the Tukey T-test (Scheffe, 1959). Counts of

the macrofauna and eipfauna were examined for significance using the non-parametric Mann-Whitney test in which each treatment was compared with the control (Siegel, 1956).

Results

Predators

For the results of these studies to reflect natural processes in the community the predators should be feeding, growing and surviving as normally as possible. A preliminary experiment on the effect of caging and stocking density on the survival and condition index (a measure of the increase or decrease in weight at a given length) of *P. microps* indicated that neither were significantly reduced in relation to wild fish at densities of 5–10 per cage (Table 2).

TABLE 2. Size, condition, mortality and gut fullness of predators in each experiment. Gut fullness index is assessed on a points scale from 0 (empty) to 16 (fully distended)

	Exp. 1: Adult			*Exp. 2: Adult*			*Exp. 2: Juv.*			*Exp. 3: Adult*		
	Caged		Wild	Caged		Wild	Caged		Wild	Caged		Wild
P. microps	Start	End	End	Start	End	End	Start	End	End	Start	End	End
Number in cages	30	28	—	30	25	—	30	12	—	40	18	—
Mean length (mm)	36	36	38	40	38	40	30	27	30	34	32	36
Mean wt. (gm)	0·61	0·67	0·95	0·89	0·83	0·99	0·37	0·30	0·41	0·63	0·53	0·81
Sex ratio (M : F)	1:1·0	1:0·3	1:2·3	1:0·7	1:0·9	1:0·7	1:0·8	1:1·0	1:1·0	?	1:0·2	1:2·0
% mortality in cages		7			17			40			55	
Mean somatic CI	1·03	1·28	1·35	1·26	1·36	1·42	1·19	1·25	1·34	1·38	1·44	?
% with food in gut	73	100	95	100	100	100	80	100	95	100	83	97
Mean gut fullness index	2·9	4·3	6·6	5·9	4·4	4·4	6·1	8·3	4·4	5·5	2·7	6·1

	Exp. 1: Adult		*Exp. 1: Juv.*		*Exp. 2: Juv.*		*Exp. 3: Juv.*	
C. maenas	Start	End	Start	End	Start	End	Start	End
Number in cages	3	3	45	31	45	17	68	44
% mortality		0		31		62		35
Mean carapace width (mm)	50	53	13	20	11	16	?	16

Mortality of adult predators was reasonably low (Table 2) except in April 1981 when there was a week of unseasonably harsh weather conditions during the course of the experiment. Changes in the sex ratios of gobies during experiments suggested that mortality was higher in females than in males. Mortality in juveniles was high, small gobies probably being more susceptible to handling damage and small crabs to cannibalism. The condition index of caged *P. microps* was always lower than in uncaged fish by the end of an experiment but not significantly so. In respect of food intake, Table 3 shows that caged fish, in contrast to uncaged fish, were not feeding on macrofauna.

TABLE 3. Summary of gut content analysis of wild and caged gobies at the end of each experiment

	Mean number of items per fish with food						% by volume of food present					
	Wild fish			Caged fish			Wild fish			Caged fish		
	Exp. 1	Exp. 2	Exp. 3	Exp. 1	Exp. 2	Exp. 3	Exp. 1	Exp. 2	Exp. 3	Exp. 1	Exp. 2	Exp. 3
Number in sample	32	20	31	28	25	18						
Number with food	30	20	31	28	25	15						
Mean gut fullness index							6·57	4·44	6·01	4·28	4·43	2·75
Macrofauna (principally siphon tips)	2·5	0·2	1·9	0·1	0·1	+	48·1	9·7	27·0	11·2	2·0	1·1
Small annelids (principally *Manayunkia*)	10·0	20·9	47·7	9·6	7·1	33·7	11·4	31·5	40·8	17·3	11·1	49·5
Meiofauna (principally harpacticoid copepods)	5·2	9·8	12·1	25·5	2·6	9·1	1·5	5·4	1·7	11·0	0·9	3·6
Epifauna (principally planktonic copepods, mysids, gammarids)	1·2	0·9	2·2	*n*	*n*	*n*	26·9	34·5	9·2	24·1	80·8	21·8
Detritus	—	—	—	—	—	—	12·5	18·9	21·5	36·4	5·2	24·0

+, mean $<0{\cdot}1$; *n*, items of plankton too numerous to count.

TABLE 4. Experiment 1. Mean number (±SE) of animals in each treatment at termination and F values and significance levels

Species	Treatments					F values and significance (ANOVA)
	Uncaged control	Caged control	Adult goby cages	Adult crab cages	Juvenile crab cages	
No. 0·5 cm^{-2}						
Nematodes	377·0±11·8	290·0±18·1	354·0±17·6	320±16·3	350·0±17·9	4·14*
Harpacticoids	7·8±1·3	14·0±2·9	14·5±1·7	17·1±3·5	7·3±1·1	2·49
Protohydra	7·2±1·1	14·3±1·5	6·3±0·6	19·8±2·9	3·3±0·6	17·09***
No. 4·4 cm^{-2}						
Manayunkia	274·0±21·1	552·0±40·3	111·0±24·0	709·0±45·4	29·8±8·6	41·67***
Fabricia	7·6±2·3	24·7±5·3	12·5±2·0	28·0±4·7	3·7±1·9	9·03***
Streblospio	48·7±11·1	81·7±24·1	19·7±5·3	113·0±19·0	18·0±3·7	3·50*
Pygospio	9·2±4·4	8·5±1·7	0	15·6±6·3	1·2±1·2	3·20*
Peloscolex	5·7±1·2	8·5±3·6	2·0±0·9	18·5±5·0	4·5±1·5	4·82**
Oligochaetes	55·2±12·5	102·0±11·5	128·0±12·8	196·0±17·0	36·0±7·8	25·08***
No. 0·1 m^{-2}						Mann-Whitney
Nephtys	15·0±0·6	15·3±4·4	13·0±0·6	12·3±0·3	15·6±1·5	NS
Ampharete	0·3	3·7	0·3	1·7	0·3	NS
Melinna	0·7	0·3	1·0	1·0	0·7	NS
Macoma	5·7	1·7	3·7	3·7	1·3	NS
Cardium	0·3	2·7	1·7	0·7	0	NS
No. 0·2 m^{-2}						
Crangon		7·3	0·6	0·7	3·6	NS
Palaemon		11·6±8·3	0·6±0·3	32·0±6·9	7·3±2·9	NS
Amphipods		0·6	4·0	3·3	0·6	NS
Neomysis		3·3	0·3	0·3	0	NS
Carcinus		13·0±2·3	3·6±1·6	[1+] 6·6±1·2	[10·5±0·3]	
P. microps		2·3	[9·3±0·7]	1·3	1·3	
Biomass 0·2 m^2						
Carcinus		0·39	0·11	[34·0]	[12·6]	
P. microps		0·25	[6·3]	0·14	0·14	

*$P<0·05>0·01$, **$P<0·01>0·001$, ***$P<0·001$. Boxed figures represent treatment animals.

Occasionally a small piece of *Nephtys hombergi* Audouin & M. Edwards was found in a caged fish but never any lamellibranch siphon tips which were a major constituent of the diet of uncaged fish, especially in the spring and summer. Caged fish generally contained smaller quantities of food than wild fish but the latter were sampled at high water and the former at low water and Gee (unpublished) has shown that *P. microps* has a tidal feeding rhythm, with a maximum weight of food in the gut 2–3 h after high water and a minimum at approximately the same time after low water.

Benthic fauna – Experiment 1: June–July 1980

Adult and juvenile *C. maenas* and adult *P. microps* were the predators used in this experiment (Table 4). The preliminary two-way ANOVA of appropriate core counts (Table 5)

TABLE 5. *F* values and significance levels for two-way ANOVA of cages and treatments for meiofauna and small annelid core counts at termination of experiments 1–3

	Cages			Treatments		
	Exp. 1 (d.f.10/15	Exp. 2 (d.f. 10/15)	Exp. 3 (d.f.12/16)	Exp. 1 (d.f.4/15)	Exp. 2 (d.f. 4/15)	Exp. 3 (d.f.3/16)
Nematodes	1·152	0·604	2·522*	3·780*	29·535***	2·487
Copepods	1·718	6·274***	2·364	2·607	1·943	13·771***
Protohydra	1·591	1·303	1·286	13·279***	5·189*	40·688***
Manayunkia	7·805***	10·082***	1·293	41·670***	1·954	19·430***
Fabricia	0·510	—	1·070	14·225***	—	5·752**
Streblospio	9·849***	0·608	2·743*	3·504*	6·817**	2·020
Pygospio	1·780	—	1·419	2·355	—	5·085**
Peloscolex	0·832	1·443	1·418	5·404**	2·207	0·821
Oligochaetes	1·307	—	0·627	21·551***	—	1·902

*$P<0{\cdot}05>0{\cdot}01$, **$P<0{\cdot}01>0{\cdot}001$, ***$P<0{\cdot}001$. d.f., minimum and maximum degrees of freedom.

showed a block effect in *M. aestuarina* and *S. shrubsolii* which, however, was general over all treatments including the caged and uncaged controls. This would suggest, therefore, that the block effect is more a reflection of the spatial heterogeneity in the distribution of animals over the mudflat than of variations in the cage environment or the number of predators surviving in individual cages.

The significance of the differences between treatments shown by the subsequent one-way ANOVA and the Wilcox Mann-Whitney test are given in Table 4 and their source and magnitude further analysed (by the Tukey T-test) in Fig. 1.

Control cages. When predators were excluded only the small sabellids *M. aestuarina* and *Fabricia sabella* (Ehrenberg) increased significantly in abundance compared to the uncaged controls. These two species are combined under *Manayunkia* in Fig. 1(b), from which it can be seen that their increase was linear over the time course of the experiment while in the uncaged control blocks the populations remained more or less constant.

Adult C. maenas cages. Adult *C. maenas* clearly had no effect on the abundance of any of

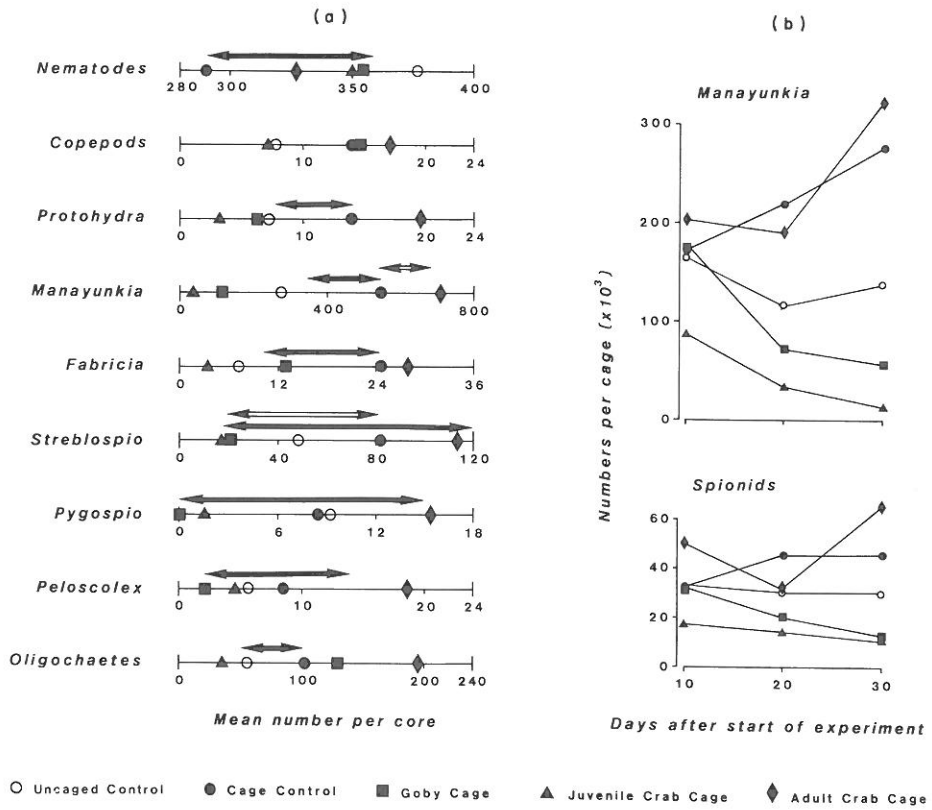

Figure 1. Experiment 1. (a) Showing the mean number per core of each species in each treatment. Bar length indicates the least significant difference between any pair of means, a solid bar when each core is a treatment replicate, an open bar when all cores from each treatment are a treatment replicate. (b) Mean numbers of *M. aestuarina* and spionids in each treatment at each sampling.

the epifaunal or larger macrofaunal species. However, much of the significance of the differences between treatments in the small annelids and meiofauna species [Fig. 1(a)] can be attributed to the consistently higher counts in this treatment compared with all other treatments, although only in the case of *Peloscolex benedeni* (Udeken) and other oligochaetes were the counts significantly higher than the controls.

Adult P. microps cages. It has been shown earlier that caged *P. microps* were not feeding on macrofauna. However, the adults of the species of macrofauna, listed in Table 4, other than *Ampharete acutifrons* (Grube), are too large to be consumed whole by *P. microps* and therefore no effect on abundance of caged macrofauna would be expected, even if *P. microps* had been feeding on them to the same extent as uncaged fish. *A. acutifrons* varies in abundance from year to year (Price & Warwick, 1980*a*) and in this year recruitment, which Warwick and Price (1975) showed as being completed by April, obviously failed as numbers were very low in all blocks. Predation of juvenile *N. hombergi* would not be expected at this time as recruitment does not take place until later in the year (Price & Warwick, 1980*a*).

Table 4 indicates that the numbers of all the small annelids (other than oligochaetes) were lower in the goby cages at termination than in the control cages, but Fig. 1(a) confirms that only in the case of *M. aestuarina* are the differences significant. Figure 1(b) illustrates the rate of decrease of the number of *M. aestuarina* and spionids over the last 22 days of this experiment. If it is assumed that the decrease in *M. aestuarina* in the goby cages is due solely to gobies consuming worms, then the daily consumption of the gobies can be calculated. The relative growth rate ($R=(\log_e N_2-\log_e N_1)/t_2-t_1$; where N_1 and N_2 are numbers in the population at times t_1 and t_2) of the control cage population of *M. aestuarina* is 0·022 day^{-1} over the 22 days. Assuming the reduction in numbers in the goby cages between measured points is linear, the number of worms in the population each day (P_n) can be estimated. The mean daily consumption per goby over each 11-day period is:

$$(E(P_{n+1}—P_n) + 0{\cdot}022\,P_n))/110$$

During the two 11-day periods shown in Fig. 1(b) the approximate number of *M. aestuarina* consumed per fish per day was 1200 and 300 respectively. Taking the average wet weight of a *M. aestuarina* as 20 µg (Price & Warwick, 1980*a*) and of a goby as 0·67 g (Table 2), the estimated consumption of *M. aestuarina* was between 1 and 4% of body weight day^{-1} over the experimental period. Calculating the uptake of spionids

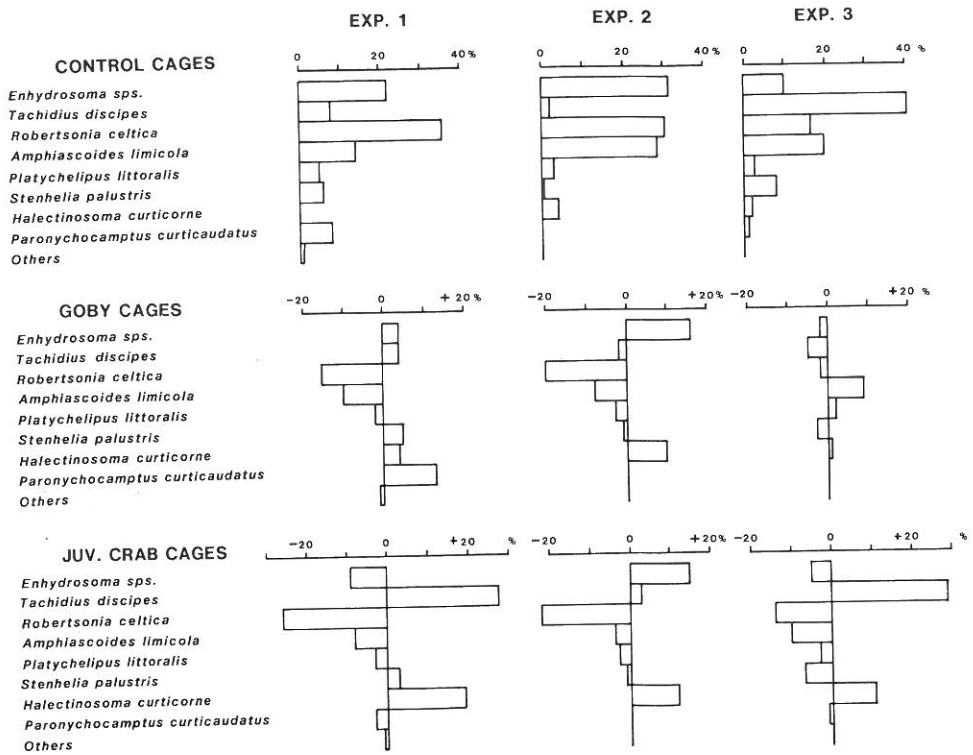

Figure 2. Percentage species composition of harpacticoid copepods in the control cage sediment and the relative changes in species abundance in sediment from the goby and juvenile crab cages.

[Fig. 1(b)] in the same way (using an overall relative growth rate of 0·015 and a mean wet weight per worm of 150 μg) gave an average daily consumption of 2·8% of body weight day^{-1}. Thus the total consumption of small annelids over the course of the experiment was approximately 5% of body weight day^{-1}. Table 3 shows that these organisms constituted about 33% of the volume of digestible food found in the gut of caged gobies which would suggest a daily food intake considerably in excess of 5% of body weight.

Meiofauna, almost all harpacticoid copepods, constituted a significant part of the diet of caged gobies (Table 3). Nematodes were rarely found and *Protohydra leuckarti* Greef never recorded but this is not surprising as these small, soft-bodied animals would be very rapidly digested. Figure 1(a), however, indicates that *P. leuckarti* were significantly reduced in the goby cages compared with the controls. This was not the case with harpacticoid copepods and predation had no effect on their total abundance. Figure 2, however, shows that there were differences in the relative species abundance of the control and goby cage sediment harpacticoids. The control cage population was dominated by *Robertsonia celtica* (Monard), *Amphiascoides limicola* (Brady) and two species of *Enhydrosoma, E. garienis* Guerney and *E. longifurcatum* Sars. The copepods recovered from the fish guts, however, were dominated by *Harpacticus* sp., *Tisbe* sp. and *R. celtica*. Both the former genera are associated with epiphytic algae and are therefore rarely encountered in sediment samples. By the end of this experiment some *Enteromorpha* spp. were growing on the inside of the cage bases and the *P. microps* were obviously feeding to some extent on its associated fauna (as described previously in Warwick *et al.*, 1982). In the goby cage sediments, however, the mesopsammic forms *R. celtica* and *A. limicola* were reduced in relative abundance, whereas the endopsammic *Enhydrosoma* species were not.

Juvenile C. maenas cages. No data are available on the types and quantities of food present in the guts of juvenile *C. maenas* at the end of the experiment but their impact on the benthic fauna was qualitatively similar to that of the gobies, although in most cases it was greater in intensity (Table 4, Fig. 1). The counts of almost all the small annelid species were lower in the juvenile crab cages than in all other treatments and were significantly lower than the control cages or oligochaetes, *M. aestuarina* and *F. sabella*. It would appear that the rate of consumption of the sabellids was much higher than by gobies during the early part of the experiment. The number of *M. aestuarina* in the juvenile crab cages was significantly lower than in all other treatments after 10 days and continued to fall at approximately the same rate over the remainder of the experiment [Fig. 1(b)].

Among the meiofaunal groups *P. leuckarti* was significantly reduced, whilst again total harpacticoid copepods numbers were not. However, in the crab cage sediments all the mesopsammic and endopsammic species were reduced in relative abundance (Fig. 2), considerably so in the case of *R. celtica*, and this was compensated for by an increase in the relative abundance of the epipsammic forms *Tachidius discipes* Giesbrecht and *Halectinosoma curticorne* Boeck.

Benthic fauna – Experiment 2: September–October 1980

Two size groups of *P. microps* were included along with juvenile *C. maenas* in this experiment but in the light of the previous experiment adult *C. maenas* were not included and the larger benthic macrofauna not sampled (Table 1).

A block effect was again detected in the populations of *M. aestuarina* and additionally

TABLE 6. Experiment 2. Numbers of *C. crangon* per cage and mean number of *Manayunkia* and copepods per sample

	Treatment cages											
	Control			Juv. goby			Adult goby			Juv. crab		
	1	2	3	1	2	3	1	2	3	1	2	3
Crangon	25	—	9	15	4	—	1	8	1	19	3	16
Manayunkia	3	28	28	13	22	—	7	5	11	—	14	1
Copepods	13	29	14	11	13	—	16	10	17	1	17	6

in the copepods (Table 5). Whilst this effect was present over all treatments it was most marked in the control and juvenile crab cages. Shrimps, *Crangon crangon* (L), were common in these treatments at the end of the experiment and an analysis of their gut contents indicated that *M. aestuarina* and copepods were important food items. The number of *C. crangon* varied considerably between treatment cages and correlated inversely with the

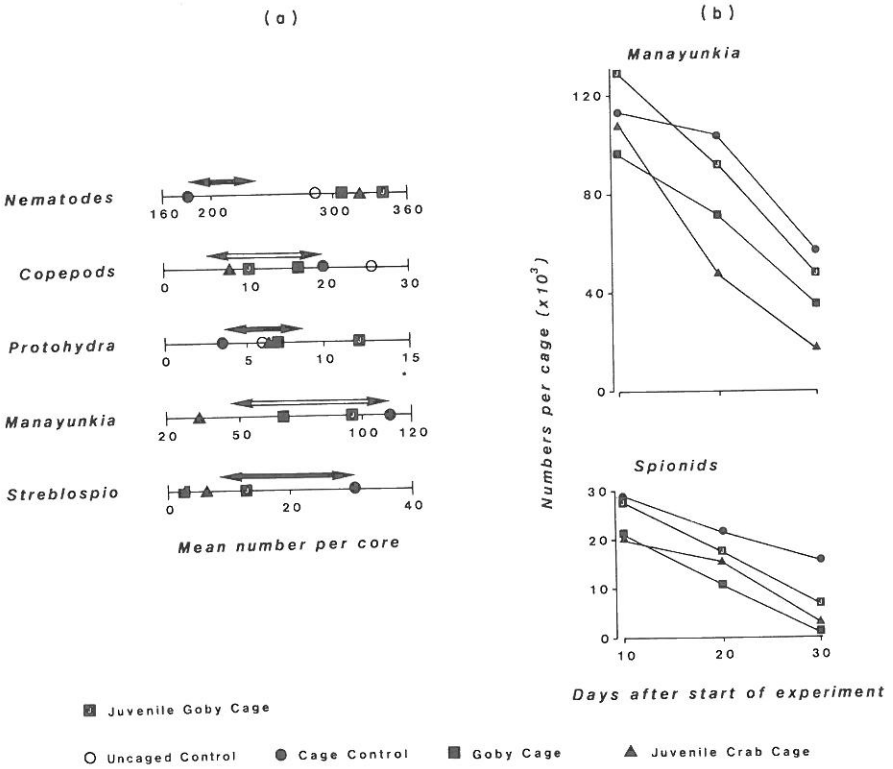

Figure 3. Experiment 2. (a) Showing the mean number per core of each species in each treatment. Bar length indicates the least significant difference between any pairs of means, a solid bar when each core is a treatment replicate, an open bar when all cores from each treatment are a treatment replicate. (b) Mean numbers of *M. aestuarina* and spionids in each treatment at each sampling.

TABLE 7. Experiment 2. Mean number (± SE) of animals in each treatment at termination and *F* values and significance levels

Species	Treatments					*F* values and significance (ANOVA)
	Uncaged control	Caged control	Adult goby cages	Juvenile goby cages	Juvenile crab cages	
No. 0·5 cm^{-2}						
Nematodes	285·0±22·5	180·0±3·6	306·0±12·8	339·0±13·5	322·0±7·7	21·20***
Harpacticoids	25·5±5·2	19·5±4·6	16·7±1·0	10·5±1·4	8·2±3·3	1·94
Protohydra	6·0±2·0	3·5±0·7	6·8±1·1	11·8±1·1	6·8±0·6	6·03**
No. 4·4 cm^{-2}						
Manayunkia		111·0±19·7	68·2±18·1	96·2±10·6	33·7±16·5	1·95
Fabricia		2·0	2·0	2·3	2·0	
Streblospio		30·7±10·2	2·3±1·5	12·8±3·6	6·2±3·6	4·91*
Pygospio		0·5	0	0	0	
Peloscolex		9·5±3·6	2·5±1·2	14·8±5·0	5·5±1·5	2·70
Oligochaetes		3·7±1·3	6·5±1·9	1·8±1·2	5·5±2·5	2·50
No. 0·2 m^{-2}						Mann-Whitney
Crangon		11·3	3·3	9·5	12·7	ns
Palaemon		0·7	0	1·0	0·7	ns
Gammarus		0·3	0	0·5	0·7	ns
Carcinus		7·3±1·5	2·7±1·3	7·5±2·5	[5·7]	
P. microps		1·3	[8·3]	[6·0]	2·3	
Biomass 0·2 m^{-2} (g)						
Carcinus		0·5	0·3	0·4	[5·8]	
P. microps		0·1	[6·9]	[1·8]	0·04	

*$P<0·05>0·01$, **$P<0·01>0·001$, ***$P<0·001$. Boxed figures represent treatment animals.

number of *M. aesturarina* and copepods (Table 6). Thus any natural spatial heterogeneity in the distribution of these organisms may have been reinforced by small, uncontrolled predators to produce a block effect. In the control cages there was no increase in abundance of individual species (Table 7). Indeed in all the meiofaunal groups the counts in the control cages were *lower* than in the uncaged controls and in the case of nematodes were significantly lower [Fig. 3(a)]. A similar but less significant phenomenon occurred in the first experiment. In both these cases the number of very small *C. maenas* (2–9 mm carapace width) were higher in the control cages than in the treatment cages (where they were presumably eliminated by predation by adult *P. microps* and cannibalism by larger juvenile *C. maenas*).

In the period between experiments 1 and 2 the numbers of small annelids had been falling rapidly and in the control cages during the experiment [Figure 3(b)] numbers continued to fall sharply and at about the same rate as in the predator treatment cages. Only the sharper rate of decline between 10 and 20 days in the juvenile crab cages made the numbers of *M. aestuarina* in this treatment significantly lower than in the controls at 20 days. The spionid *S. shrubsoli* was also significantly lower in the goby and crab cages at termination.

The effect of the predators on the relative species abundance of the harpacticoids was essentially the same as in the first experiment (Fig. 2). The cage gobies, however, were feeding almost exclusively on *R. celtica* at the end of the experiment. The populations of this species were relatively reduced in the goby and crab cage sediment compared to the

TABLE 8. Experiment 3. Mean number (±SE) of animals in each treatment at termination and *F* values and significance levels

Species	Treatments				*F* values and significance (ANOVA)
	Uncaged control	Caged control	Adult goby cages	Juvenile crab cages	
No. 0·5 cm^{-2}					
Nematodes	288·0±18·6	295·0±31·5	388·0±23·9	293·0±22·8	3·80*
Copepods	35·1±3·4	32·3±2·6	44·6±4·3	72·1±5·3	20·56***
Protohydra	7·0±0·7	16·0±0·9	5·9±0·6	4·8±0·7	46·62***
No. 4·4 cm^{-2}					
Manayunkia	152·0±18·8	108·0±12·0	96·0±7·2	17·6±4·2	22·32***
Fabricia	9·2±2·2	8·6±1·9	7·3±0·7	1·4±0·4	6·0**
Streblospio	8·4±2·0	10·9±1·4	7·4±1·1	4·4±1·3	3·17*
Pygospio	5·5±1·0	4·6±0·6	4·3±0·8	1·3±0·4	6·12**
Peloscolex	5·4±1·2	5·1±0·9	6·1±1·5	8·2±1·9	0·99
Oligochaetes	5·4±1·2	3·5±0·9	5·3±1·3	2·8±0·9	1·42
No. 0·2 m^{-3}					
Gammarus		0	0·5	0·3	
Neomysis		3·8	0	0·3	
Carcinus		0·3	1·0	[11·0]	
P. microps		0	[4·5]	0	
Biomass 0·2 m^{-2} (g)					
Carcinus		0·25	0·05	[10·7]	
P. microps		0	[2·4]	0	

*$P<0·05>0·01$, **$P<0·01>0·001$, ***$P<0·001$. Boxed figures represent experimental animals.

controls, whilst the *Enhydrosoma* species and *H. curticorne* were relatively more abundant.

Benthic fauna – Experiment 3: April 1981

There was no significant block effect in this experiment (Table 5) but there was a significant difference between treatments in all species and groups identified except small oligochaetes (including *P. benedeni*) (Table 8, Fig. 4). The difference between caged control and uncaged control blocks was only significant in the case of *P. leuckarti* where

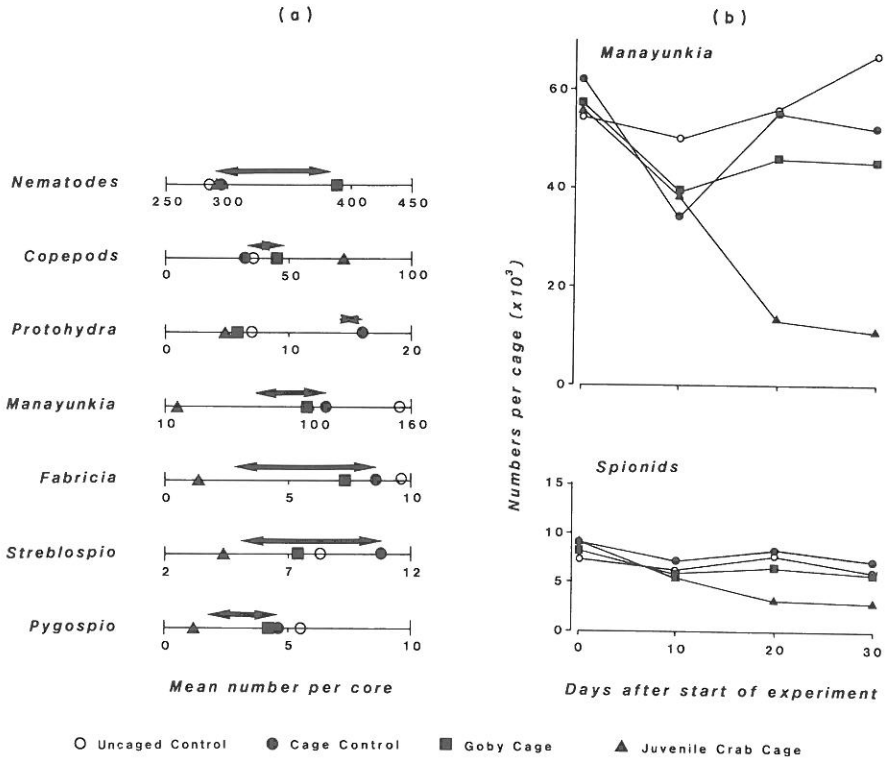

Figure 4. Experiment 3. (a) Showing the mean number per core of each species in each treatment. Bar length indicates the least significant difference between any pair of means, a solid bar when each core is a treatment replicate, an open bar when all cores from each treatment are a treatment replicate. (b) Mean number of *M. aestuarina* and spionids in each treatment at each sampling.

counts in the control cages were double those in other treatments. There were no other significant differences between the control cages and the *P. microps* treatment (with the possible exception of nematodes which were unaccountably higher in the *P. microps* cages). At no stage during the experiment were the *M. aestuarina* and spionid counts significantly different from the controls [Fig. 4(b)] and this at a time when both wild and caged *P. microps* were feeding most heavily on *M. aestuarina* (40–50% by volume of the total food, Table 3). The population in the control cage at the start of the experiment was at the same level as it was in the previous October and remained so throughout most of

the experiment. The loss of worms from all treatments during the first 10 days was probably due to a week of freezing temperatures and snow not usually encountered at this time of year.

In all cases the significant differences between treatments indicated by the one-way ANOVA (Table 8) are between the juvenile crab cages and other treatments. This is shown for *M. aestuarina* in Fig. 4(b). The decrease in this species shown for all treatments in the first 10 days continued in the crab cages so that they were significantly lower after 20 days and at termination.

In this experiment there was a significant increase in copepod numbers in the juvenile *C. maenas* cages, due entirely to increases in the epipsammic *T. discipes* and *H. curticorne* (Fig. 2) which presumably were not preyed upon by crabs.

Discussion

As pointed out by Arntz (1977), caging experiments in soft sediments are much more difficult to design and execute than those on rocky shores. While we believe our cages and experimental design overcame most of the problems associated with alteration of the physical environment and fouling, some biological difficulties were not overcome. The most important of these was the inability to exclude all unwanted predators from the cages, particularly very small *C. maenas* (less than 6 mm carapace width) and the shrimp *C. crangon*. These were either present in the mud surface when the cages were put in position or settled out of the plankton through the cage meshes during the course of the experiments. Reise (1977, 1978), Bell and Coull (1978) and our own observations of the gut contents of *C. crangon* indicate that small annelids, nematodes and copepods are preyed on by this species. There is some evidence to suggest that the presence of these species in the control (and other treatment) cages in the June and September 1980 experiments may have contributed to the block effect discerned and to the lower counts of nematodes in the control cages. An inevitable consequence of confining predators to cages on the intertidal flats is the interference with tidal migration behaviour and its possible effects on feeding rhythms and foraging behaviour. Naylor (1962) and ourselves have shown that adult *C. maenas* and *P. microps* migrate from the deeper water channel onto and off the mudflat with the tide. The prevention of this movement may have been the cause of caged *P. microps* not feeding on macrofauna to the same extent as wild fish. Juvenile *C. maenas* (less than 20 mm) on the other hand either remain on the mudflat during low water (Klein Breteler, 1976) or seek shelter under macroalgae higher up the shore (Crothers, 1968) coming out onto the mudflat to feed at high water.

A further difficulty was that this cage design was not suitable for use with all types of predators and therefore it is not possible to assess the overall effects of all predators. The principal predators on this mudflat not included in this study are the flounder (*Platychthys flesus* L.) and wading birds. Both prey principally on macrofauna and both are most abundant in winter. Longhurst and Warwick (unpublished) have estimated that Redshank, Dunlin and Shellduck consume considerable quantities of macrofauna. The number of flounders feeding on the mudflat, on the other hand, is very small and transitory and their effect presumably less important.

Thus it is necessary to interpret the results of these types of experiment with caution (Virnstein, 1978). Nevertheless, they do suggest that the different predators studied affect the various elements of the benthic community in different ways.

Adult *C. maenas,* which are most abundant over the mudflat during the summer months (George, unpublished) were the only experimental predator likely to affect the abundance of the larger macrofauna species. They were included in the June 1980 experiment for this reason but no effect was observed. This is in contrast to the results of Scherer and Reise (1981) who demonstrated that adult *C. maenas* preyed significantly on the macrofauna, taking species according to their abundance but with males preferring molluscs and females concentrating on annelids. All the *C. maenas* in our experiment were females and *N. hombergi* was the dominant macrofaunal annelid but no change in the abundance of this annelid species was indicated. In the presence of adult *C. maenas* the small annelid species seemed to increase rather than decrease in abundance. Although Scherer and Reise (1981) show that adult crabs do feed on smaller polychaetes, Virnstein (1977) suggests that the disturbance caused by their burrowing activity may also affect the benthic fauna. Some oligochaetes, in particular *P. benedeni,* have been considered as indicators of disturbance (Gray, 1976) and the significant increase in number of these organisms in the adult crab treatment in the June 1980 experiment would suggest that the fauna was responding to crab disturbance.

From considerations of size and gut contents, the main impact of predation by juvenile crabs and gobies would be expected to fall on the small annelid and meiofaunal elements of the community. In all experiments the number of small annelids were always lower in the juvenile crab cages than in the controls. Numbers of each annelid species were generally reduced in proportion to their dominance in the community with the most significant effects being demonstrated on the small sabellid *M. aestuarina.* In addition to being the dominant small annelid in the community, this species may be more vulnerable to predation because not only are they confined to the top few millimeters of the sediment but one of us (JTD) has observed that, in the laboratory, and in contrast to the spionids, this species does not withdraw into its tube in response to vibration disturbance simulating the approach of a potential predator.

Populations of *M. aestuarina* reach a peak on the mudflat in late spring and early summer, during their breeding season. This is also the time of year during which the particular size group of *C. maenas* used in these experiments also reaches a peak (George, unpublished; Klein Breteler, 1976) and when natural densities are approaching the stocking density of the caged juvenile *C. maenas.* The June experiment covers this period and the results, demonstrating a rapid increase in the *M. aestuarina* populations in the control cages and the considerable decrease in the juvenile crab cages, would suggest that predation may significantly affect recruitment success of *M. aestuarina* and therefore the year to year abundance of this species. On the other hand *M. aestuarina* populations on the mudflat decrease naturally during the autumn and winter and while the September 1980 and April 1981 experiments showed that the rate of decrease was accelerated in the juvenile crab cages, their exclusion from the control cages did not significantly alter the rate of reduction. This would suggest that the seasonal fluctuations in density of *M. aestuarina* are not caused by predation and therefore that not all mortality is due to predation.

The effects of predation by *P. microps* on the small annelids shown in these experiments are somewhat anomolous and lead to difficulties in interpretation when the seasonal abundance and food preferences of the fishes are taken into account. *P. microps* are most abundant in the autumn when estimated densities of fish over 20 mm SL reach about $2{\cdot}0\,m^{-2}$ (Gee, unpublished) and in the autumn and spring *M. aestuarina* form about 50% of the diet of these fishes. It would therefore be expected that the impact of

P. microps predation on small annelids would be greatest in the September 1980 and April 1981 experiments, especially as the density of caged gobies was much higher than natural densities. However, there was no significant difference between the small annelids in the goby cages and control cages in these experiments.

These observations lead one to question whether the observed reductions in *M. aestuarina* in the goby cages in the June 1980 experiment were genuinely the result of goby predation or an experimental artifact, especially as natural densities of gobies at this time of year are low (0·2–0·5 m^2) and *M. aestuarina* forms a much smaller percentage of their diet. When it is assumed that all reductions of *M. aestuarina* in this experiment were due to fish predation, then the calculated daily food intake by gobies of this species *alone* was approximately 4% of body weight day^{-1}. Estimates of food intake by gobies, made by other means, give a total daily intake of between 2 and 4% of body weight day^{-1} for the size group of gobies used in this experiment (Gee, unpublished; Healey; 1971). Thus the calculated intake of *M. aestuarina* alone in the June experiment would provide the total food requirements of the gobies. As they were also feeding on other items (Table 3) this does suggest that all the reductions of *M. aestuarina* in the June goby cages was not caused directly by goby predation. It would therefore appear that at the densities at which they occur naturally predation by *P. microps*, the dominant fish predator on the mudflat, is unlikely to significantly affect the abundance of *M. aestuarina* and other small annelids on either a seasonal or annual basis.

Among the meiofaunal groups studied in these experiments the expected changes in abundance were not observed except in *P. leuckarti* in the spring and summer. Generally speaking the numbers of copepods in all treatments were remarkably constant both within and between experiments except for higher counts in the juvenile *C. maenas* cages in April 1981. This was unexpected in the light of previous work (Sibert, 1979; Schmidt-Moser & Westphal, 1981) which suggests that predation by small fishes has a significant effect on copepod abundance. However, their conclusions were based on indirective evidence. More recently Alheit and Scheibel (1982), in a detailed analysis of fish uptake and benthic copepod abundance, demonstrated that at natural densities, the feeding pressure exerted by fish on harpacticoid copepod populations is negligible. Even at the high densities used in the present experiments, predation by gobies and crabs was not sufficient to alter the total abundance of copepods. However, there was evidence that the predators were capable of altering the relative abundance of individual species. *P. microps* reduced the relative abundance of the epipsammic and mesopsammic species, resulting in a relative increase in the endopsammic *Enhydrosoma* species. Juvenile *C. maenas* preyed upon all the mesopsammic and endopsammic forms and their reduction was compensated for by a relative increase in the epipsammic *T. discipes* and *H. curticorne*.

Heip (1980) has shown that in a similar estuarine intertidal copepod community none of the species maximize their breeding potential (in terms of the number of generations produced per annum) and that they avoid competition and possibly predation through the evolution of different life history strategies and differential timing of reproductive effort. However, if for some reason one species is reduced or eliminated, another species would take advantage of this by altering its timing of reproduction or by producing extra generations.

It is postulated, therefore, that the copepod population in these experiments were maintained at a relatively constant level either by an increase in the reproductive effort by those species not being preyed upon (e.g. *T. discipes* in the summer juvenile crab

cages) or by the predation being most effective on those species which were actually breeding at that time of year (e.g. *R. celtica* in both predator treatments in the autumn). Only when a species is not being preyed upon during its period of maximum reproductive effort would an increase in population number be observed, as was the case with *T. discipes* in the juvenile *C. maenas* cages in the spring.

In this paper we have regarded the epibenthic predators as the only ones present and all the infauna as potential prey. However, Ambrose (1984) has pointed out that many of the infaunal species themselves are predators; that in muddy substrates these tend to become proportionately more abundant when epibenthic predators are excluded and that prey species of predatory infauna may therefore be less abundant in the absence of epibenthic predators than when these latter are present. Some of the macrofaunal polychaetes, such as *Neries diversicolor* present in the Lyhner mudflat community, are potential infaunal predators and it may be that their influence on the abundance of the small annelids and meiofauna in this community is greater than that of the larger epibenthic crustacean and fish predators.

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