FAUNISTIC CONTROL OF *ENTEROMORPHA* BLOOMS:
A FIELD EXPERIMENT

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Abstract: Gobies, *Pomatoschistus microps* (Krøyer), were introduced to a series of cages on an estuarine mud-flat during the period in which the cover of *Enteromorpha* sp. was declining. They fed selectively on the grazers which either ingested *Enteromorpha* directly or browsed on micro-organisms attached to it and, therefore, significantly affected the breakdown rate of the alga. It is suggested that the balance between grazers and their predators may be at least partially responsible for the irregular development of *Enteromorpha* on estuarine mud-flats from year to year.

INTRODUCTION

The development of the green alga *Enteromorpha* spp. on estuarine mud-flats has a profound effect on the general ecology of estuaries (e.g. Owens *et al.*, 1978; Nicholls *et al.*, in press). A bloom of *Enteromorpha* occurs as a more or less dense covering on mud-flats in the Lynher estuary, Cornwall, U.K. in certain summers but not in others, and in some years may reach a biomass of ≈ 250 g dry wt $\cdot$ m^{-2} (Joint, 1978). This sporadic occurrence has also been noted in other areas, and development of the bloom has been attributed largely to environmental factors such as climatic conditions or nutrient run-off from the land (Wilkinson, 1980; Nicholls *et al.*, in press). However, experimental evidence is beginning to accumulate to suggest that grazing organisms, particularly Crustacea, may play an important role in the breakdown of macrophyte material, either directly by maceration and ingestion (Welsh, 1975) or indirectly by feeding on attached micro-organisms thus keeping them in the log-phase of growth and accelerating microbial degradation (Lopez *et al.*, 1977). The question arises, therefore, as to whether such grazers, in the natural densities at which they occur in the field, can significantly affect the relative rates of growth and breakdown of *Enteromorpha* and thus play a role in controlling the magnitude of the bloom.

Field manipulations have shown that grazers on rocky shores, particularly gastropods and limpets, play an important role in controlling algal development (see Underwood, 1980, for recent review). Such experiments involve removal of algae or grazers from experimental sites and subsequently either enclosing or excluding the grazers with cages of various forms. Potential grazers such as shrimps, amphipods and juvenile crabs could not be cleared from among the strands of

Enteromorpha on the Lynher mud-flat without destructive sampling of the alga, or at best causing severe disturbance. As *Pomatoschistus microps* is an efficient predator of epibenthic Crustacea, our approach has been to retain these gobies in field cages in numbers much greater than natural densities in order to control the numbers of grazers with the minimum of disturbance. We have compared the performance of *Enteromorpha* in these cages with that in control cages without gobies. Problems of interpretation of results arising from the physical effects of caging (Virnstein, 1978) are partly eliminated by controlled experiments of this kind.

METHODS

The peak of the *Enteromorpha* bloom in the Lynher usually occurs in September (Joint, 1978). Cages were set out on September 13, 1979, at a site near Antony in the Lynher estuary (described by Warwick & Price, 1975). The base of each cage consisted of a square aluminium frame 300 mm high, enclosing an area of 0.2 m^2, pushed into the mud so as to leave 50 mm above the mud surface: a wooden frame 250 mm high, covered in nylon mesh with 2-mm apertures, was clipped to the top of each base (Fig. 1). Eight cages, each 2 m apart, were arranged in a 2×4 array.
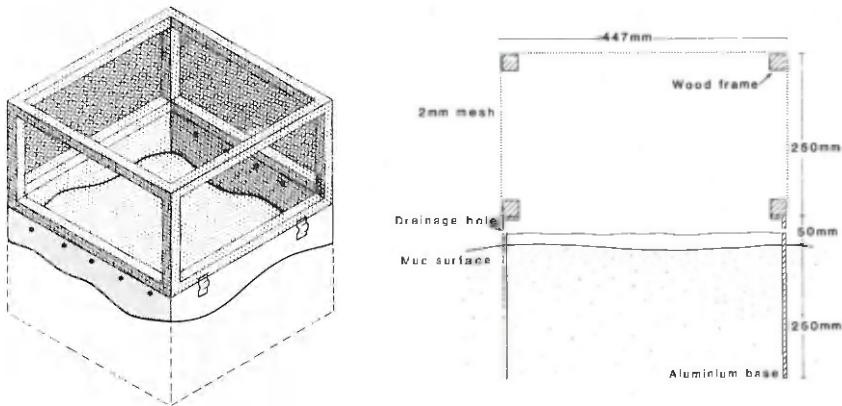

Fig. 1. Sketch and cross-section of an enclosure.

Adult gobies were caught by seine-netting close by, and 30 animals were put in the water retained by the base of each of four cages in one row after they had been covered by one tide. The remaining four cages acted as controls. The gobies were all ≈ 35 mm standard length with an individual wet weight of ≈ 0.5 g. The cages were visited frequently to keep the meshes free of loose *Enteromorpha* and to remove any dead gobies, which were not replaced. The experiment was terminated after 4 wk. To determine the terminal densities of various faunal components and the

biomass of *Enteromorpha* on the mud surface the following samples were taken from the cages.

(1) Three 4.9-cm^2 sediment cores taken at random for analysis of meiofauna (nematodes, harpacticoid copepods, ostracods, kinorhynchs, *Protohydra leuckarti* Greef). Only the copepods were identified to species level, because this was the only group which featured significantly in the diet of the gobies.

(2) Two 30-cm^2 sediment cores taken at random for analysis of smaller annelid macrofauna, *Manayunkia aestuarina* (Bourne), *Fabricia sabella* (Ehrenberg), *Streblospio shrubsoli* (Buchanan), *Pygospio elegans* Claparède, *Peloscolex benedeni* (Udekem) and other oligochaetes.

(3) Thorough hand-netting of the whole cage area with a square framed net of fine mesh to collect the gobies, epifaunal invertebrates, and *Enteromorpha*. The gut contents of the larger epibenthic Crustacea associated with *Enteromorpha* outside the cages during the experiment and of the caged gobies (after preservation in formalin) at the end of the experiment, were examined in the laboratory and the dry weight of the surface *Enteromorpha* was determined. Because of the small numbers of many of the taxa in each core, it was felt necessary to pool the cores from each cage and carry out a two sample *t*-test with four observations in each group. For nematodes, harpacticoids and *M. aestuarina*, however, sufficient numbers were present to allow a full 2-factor mixed model analysis of variance (ANOVA) separating out variation between similarly treated cages from variation between cores within cages.

RESULTS

ENTEROMORPHA

During the course of this experiment the surface *Enteromorpha* disappeared from the mud-flat as well as from the four control cages, although some was still present buried below the mud surface. All four goby cages, however, still contained a luxuriant growth of 8.85 g dry wt $\cdot$ m^{-2} of surface *Enteromorpha* (Table I). This was the most immediately obvious and dramatic result of the experiment.

Benthos: mean ($\pm$ SD) of number or weight per cage (0.2 m^2) at termination of the experiment and values for Student's t: *, $P < 0.05$; n.s., not significant ($P > 0.05$); N.A., not applicable.

	Goby cages	Control cages	t (d.f. 6)
Surface			
Enteromorpha (dry wt g)	1.77 $\pm$ 0.43	0	N.A.
Meiofauna (no. $\times$ 1000)			
Nematoda	1116 $\pm$ 165	1145 $\pm$ 162	-0.25 n.s.
Harpacticoids	59 $\pm$ 14	84 $\pm$ 16	-2.36 *
Protohydra leuckarti	3.6 $\pm$ 1.6	5.1 $\pm$ 3.8	-0.73 n.s.
Small annelids (no. $\times$ 1000)			
Manayunkia aestuarina	62 $\pm$ 25	55 $\pm$ 16	0.47 n.s.
Fabricia sabella	4.5 $\pm$ 1.0	4.7 $\pm$ 2.2	-0.17 n.s.
Streblospio shrubsoli	6.0 $\pm$ 4.2	7.3 $\pm$ 3.2	-0.49 n.s.
Pygospio elegans	0.8 $\pm$ 0.5	1.0 $\pm$ 0	-0.80 n.s.
Peloscolex benedeni	2.8 $\pm$ 2.9	2.3 $\pm$ 1.3	-0.31 n.s.
Oligochaetes	13 $\pm$ 0.5	14.5 $\pm$ 2.1	-1.39 n.s.
Epifauna (no.)			
"Small" *P. microps*	0	6.8 $\pm$ 3.9	N.A.
Crangon crangon	0	5.3 $\pm$ 3.3	N.A.
Palaemon serratus	0	45.2 $\pm$ 73.3	N.A.
Carcinus maenas	8.8 $\pm$ 5.2	11.8 $\pm$ 7.6	-0.65 n.s.
Chaetogammarus marinus	64 $\pm$ 49	72.8 $\pm$ 55.7	-0.24 n.s.

BENTHIC FAUNA

The results of the ANOVA for harpacticoid copepods are given in Table II in which part A shows that there was no significant difference between cages within treatments. It was, therefore, appropriate to form a new ANOVA table (part B) with a pooled residual, to test for treatment effects. It can be seen that the difference in number of harpacticoids in the goby and control cages is significant for $P < 0.05$. This process was repeated for nematodes and *Manayunkia aestuarina* counts but there was no significant difference between treatments. Two sample t-tests on the other meiofauna and small annelid species indicated that there was no difference between treatments. The most striking differences were found in the terminal populations of various epifaunal species, notably *Crangon crangon* (L.), *Palaemon serratus* (Pennant) and small "O" group gobies (< 20 mm long) which were absent from the goby cages at the end of the experiment (Table I). Although there was no significant difference between the numbers of the amphipod *Chaetogammarus marinus* (Leach) in the goby and control cages, there was a marked difference in

TABLE II

ANOVA for harpacticoid copepods in cores from goby and control cages: *, $P < 0.05$; n.s., not significant.

A. Source	SS	d.f.	MS	F ratio
Treatment	23126	1	23126	
Cages	24296	6	4049	1.3 n.s.
Residual	48770	16	3048	
Total	96193	23	–	

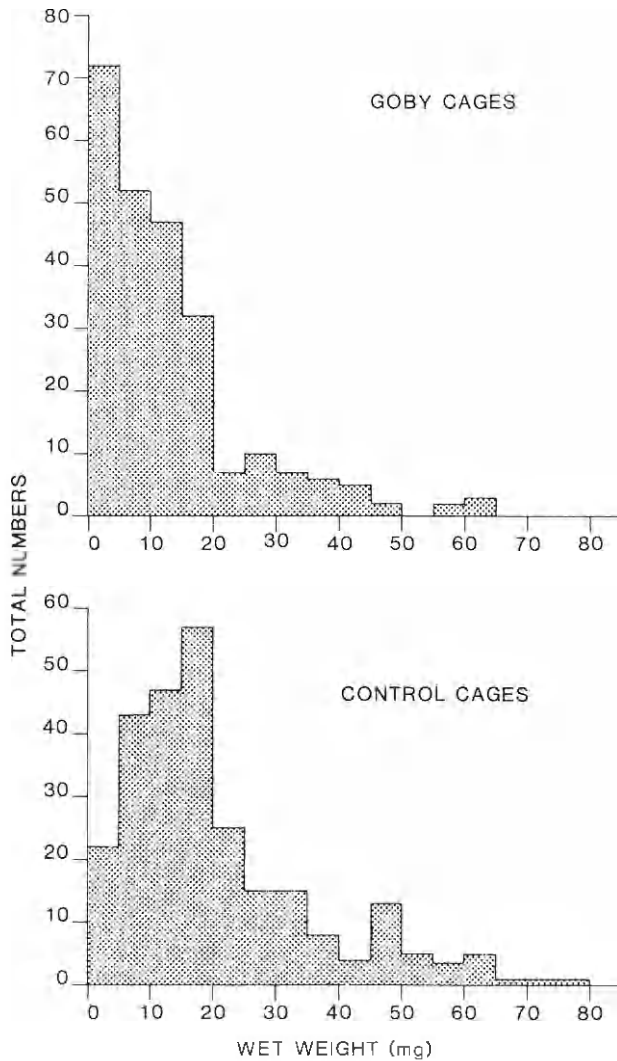| B. Source	SS	d.f.	MS	F ratio
Treatment	23126	1	23126	6.96 *
Pooled residual	73066	22	3321	
Total	96193	23	--	

Fig. 2. Size frequency histograms of *Chaetogammarus marinus* in goby and control cages.

the size structure (Fig. 2) of the populations, presumably the result of size-selective predation by the fish.

GUT CONTENTS OF GOBIES

In all, 80 gobies were removed from the treatment cages at the end of the experiment. Table III shows the percentage occurrence and number per fish of various food items in the whole gut of 38 of these. Among the meiofauna,

TABLE III

Gut contents of 38 caged gobies at the termination of the experiment.

	% occurrence	Mean number of items per fish
Meiofauna		
Nematoda	15.8	0.29
Harpacticoidea	86.8	29.50
Ostracoda	7.9	0.18
Annelida		
Nephtys hombergi	5.2	0.05
Manayunkia aestuarina	63.9	9.90
Oligochaeta	2.6	0.03
Epifauna		
Caridea	5.2	0.05
Chaetogammarus marinus	52.6	0.74
Mysidea	5.2	0.08
Fish	2.6	0.03
Cyprid larvae	44.7	3.90
Isopod larvae	2.6	0.03
Other		
Filamentous green algae	21.0	
Inorganic detritus	63.2	

harpacticoid copepods were consumed preferentially in comparison with the other taxa. Comparison of the numbers in the gut with the numbers in the cage samples indicated that not all species of copepods were taken with equal preference, the order being algal-dwelling species > epibenthic species > burrowing species. The algal-dwelling *Harpacticus* sp. comprised 15% of the total numbers of copepods in the guts, but their relative abundance in the cages was < 1% of the total population.

The small sabellid polychaete *Manayunkia aestuarina* was numerically prominent in the diet, and the epibenthic crustaceans *Crangon crangon*, **Palaemon serratus** and *Chaetogammarus marinus* were volumetrically important. Small mysids were also preyed upon by gobies but it is possible that these organisms could have passed

TABLE IV

Stomach contents of Crustacea from among *Enteromorpha* in seine-net hauls taken during the experiment: food items expressed as mean percentage volume of total estimated gut capacity.

Species	Enteromorpha	Unicellular organisms (diatoms etc.)	Other algal and vascular plant detritus	Molluscs & annelids	Crustacea (mainly C. marinus)	Mean gut fullness (%)
Crangon crangon	56	–	19	11	–	86
Palaemon serratus	70	30	–	–	–	100
Chaetogammarus marinus	80	–	–	–	–	80
Carcinus maenas (juvenile)	42	–	17	27	7	93

through the 2-mm cage mesh because, at the end of the experiment, they were absent from the control cages as well as those containing gobies.

GUT CONTENTS OF EPIBENTHIC CRUSTACEANS

The approximate mean volume of identifiable stomach contents of epibenthic crustaceans collected from *Enteromorpha* during October 1979 was estimated visually by dissection under the microscope. In all species the gut contents were found to contain a high percentage of the parenchymatous tissue of *Enteromorpha* (Table IV).

DISCUSSION

It may be argued that increased nutrient levels in the goby cages, caused by either disturbance of the sediment or excretion of NH_4-N by the gobies could be responsible for continued *Enteromorpha* growth in these cages. Differences in nutrient levels between the cages seems unlikely, however, as the cages were flushed by the tides every 6 h. Furthermore, in subsequent experiments of the same kind (performed when *Enteromorpha* was not present on the mudflat) measurements of NO_3-N and NH_4-N levels in the water retained by the cage bases at the end of their exposure period failed to reveal significant differences between control and treatment cages. On a wider basis it seems clear from the data of Owens *et al.* (1978) that the decline of *Enteromorpha* in late summer is not due to nutrient limitation. These authors found no reduction in NO_3-N and NH_4-N in the water column of the Eden estuary at this time and Morris *et al.* (1981) made a similar observation in the Tamar–Lynher Estuary system. These latter authors also observed that phosphate levels do not decrease during this period.

The organisms which affect the breakdown rate of *Enteromorpha* are those which macerate and ingest the weed directly, as well as those that feed on micro-organisms attached to the weed. We have shown that the larger epibenthic crustaceans (*Crangon crangon, Palaemon serratus, Chaetogammarus marinus* and "O" group *Carcinus maenas* (L.) all fall into the former category, and we assume that the harpacticoids *Harpacticus* sp. are microbial browsers. The introduction of gobies, which are selective predators on all of these species (except *Carcinus maenas*), significantly affected the breakdown rate of the weed. The reduction of grazing pressure on the *Enteromorpha* may not simply be a result of direct ingestion of the grazers by the gobies, but in addition the gobies, in their constant pursuit of prey, may disturb the grazers and thus inhibit their feeding activity. In this case the grazers were responsible for the breakdown of 8.9 g dry wt $\cdot$ m^{-2} of *Enteromorpha* (i.e. the weight in the goby cages) over the 4-wk period of the study. If *Chaetogammarus marinus* and *Carcinus maenas* had been removed completely from the goby cages, this value may well have been higher. We therefore suggest that the balance between

grazers and their predators may be at least partially responsible for the variability, from year to year, in the development of *Enteromorpha* on estuarine mud-flats.

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