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Effects of macroalgal mats on intertidal sandflats: an experimental study

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Abstract

The growth of green macroalgal mats is becoming increasingly common in many marine intertidal habitats. While the ecological effects of such growth has previously been experimentally investigated on mudflats, such experiments have rarely been performed on intertidal sandflats. This study investigated the ecological effects of macroalgal cover on a moderately exposed intertidal sandflat, Drum Sands, Firth of Forth, Scotland. Artificially implanted *Enteromorpha prolifera* (Müller) caused marked changes in the macrobenthos, together with significant changes in all the measured sediment variables. After 6 weeks, the weed significantly increased the macrofaunal diversity. The numbers of *Pygospio elegans* (Claparède) were significantly reduced under weed mats, while those of *Capitella capitata* (Fabricius), oligochaetes and gammarids increased. Percent water, organics and silt/clay contents, medium phi and sorting coefficient significantly increased in the sediments under weed mats which also became significantly more reduced between 1 and 8 cm depth. After 20 weeks, a macrofaunal community numerically dominated by *C. capitata,* with a significantly reduced diversity, was present under weed mats, while sediment variables were no longer significantly different from controls. The negative effect of *E. prolifera* on *P. elegans* was mainly due to larval filtering, suggesting that weed is likely to have detrimental effects on population maintenance of most species which rely on planktonic larval recruitment. These results are broadly similar to those obtained from algal manipulation experiments performed in much more sheltered, muddier environments. We suggest that a predictable deterioration in environmental quality results from the growth of macroalgal mats in soft-bottom habitats. However, the longer term effects of such algal growth are less predictable and depend upon the spatial distributions of the most abundant infaunal species and the spatial heterogeneity of weed mat establishment.

Keywords: Macroalgal mats; Macrobenthic community; Sandflats; Sediment variables

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1. Introduction

Excessive growth of green macroalgae is becoming an increasingly common phenomenon in estuaries and sheltered bays (Fletcher, 1996; Pihl et al., 1999). In temperate regions, the growth of mat-forming algae occurs mainly in the spring and is capable of persisting at high densities throughout the summer before disappearing in the late autumn (Hull, 1987). The effects of such growth have been well documented (Perkins and Abbott, 1972; Fahy et al., 1975; Wharfe, 1977; Nicholls et al., 1981; Soulsby et al., 1982, 1985; Reise, 1983, 1985; Tubbs and Tubbs, 1983; Thrush, 1986; Hull, 1987, 1988; Ólafsson, 1988; Sundback et al., 1990; Everett, 1991, 1994; Raffaelli et al., 1991; Bonsdorff, 1992). Generally, macroalgal mats, usually of the genera *Enteromorpha*, *Cladophora*, *Chaetomorpha* and *Ulva*, cause the underlying sediments to become more reducing, often leading to anoxia and the accumulation of toxic hydrogen sulphide (Wharfe, 1977; Reise, 1985). These physicochemical changes within the sediments cause a general decline in species richness (Reise, 1985; Raffaelli et al., 1991) and an increase in opportunists (Thrush, 1986) similar to the changes occurring in areas of high organic loading (Pearson and Rosenberg, 1978). The resulting changes may have direct effects on the numbers of birds (Fahy et al., 1975; Nicholls et al., 1981; Soulsby et al., 1982; Tubbs and Tubbs, 1983) and fish (Perkins and Abbott, 1972) that these areas are able to support.

Generalisations concerning the effects of weed mats upon soft-sediment invertebrate assemblages are not straightforward (Everett, 1994; Raffaelli et al., 1999). Differences in hydrodynamic environment, algal genus, whether the alga is attached or floating, and differences in weed biomass all vary between studies making comparisons difficult.

Controlled experimental manipulations provide the most rigorous approach to investigating the effects of weed mats on the sediments and their fauna. Previous experiments have been carried out either by adding macroalgal material to undisturbed areas (e.g., Thrush, 1986; Hull, 1987) or by removing algae from within affected areas (e.g., Reise, 1985; Everett, 1991; Cha, in preparation), although the two approaches seem to produce generally similar results (Raffaelli et al., 1999). Because of the practical difficulties associated with artificially establishing weed mats on more exposed habitats, algal implantation experiments have previously only been carried out on relatively sheltered, intertidal mudflats. These field experiments have reported negative impacts on a variety of taxa, especially burrowing amphipods, deposit-feeding polychaetes and deeper-burrowing bivalves, with few taxa, such as capitellid worms, showing positive effects (Hull, 1988; Raffaelli et al., 1991; Everett, 1994). In the present study, we use an algal implantation experiment on Drum Sands, Firth of Forth, Scotland, to test whether the macrofaunal effects of algal mats on moderately exposed intertidal sandflats are similar to those reported for more sheltered mudflats. Furthermore, we investigate the mechanisms of algal mat–invertebrate interactions with reference to the most dominant infaunal species on Drum Sands, *Pygospio elegans*, and discuss the possible long term ecological effects of such algal growth.

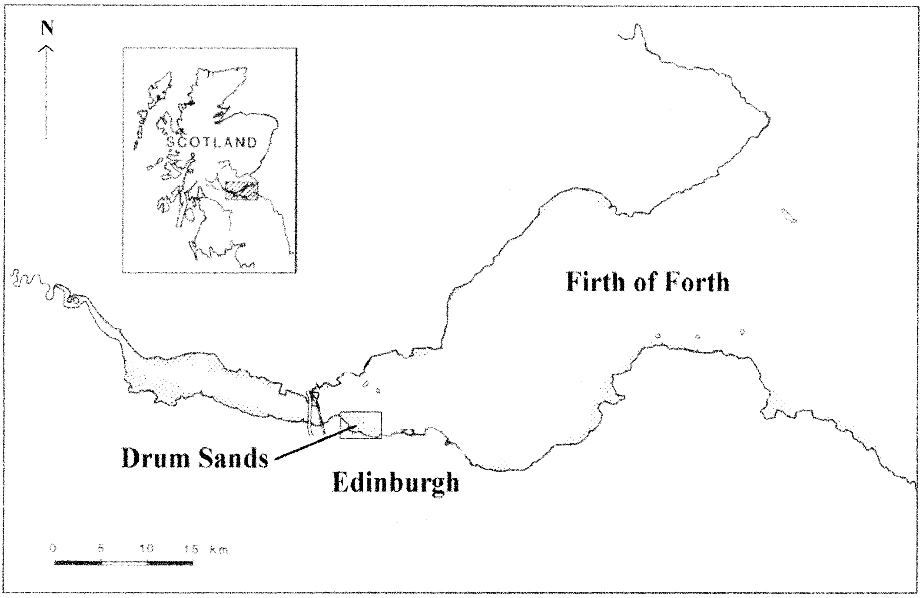

Fig. 1. Map of the Firth of Forth, Scotland, showing the position of Drum Sands.

2. Materials and methods

2.1. Study site

Drum Sands is located in the Firth of Forth on the east coast of Scotland (Fig. 1). A full account of the general ecology and environment of the area can be found in Webb and Metcalfe (1987), F.R.P.B. (1993) and Bolam (1999). Generally, the biological and chemical qualities of this sandflat are good with no detectable effects from the nearby oil exporting terminal and treated ballast water outfall (F.R.P.B., 1993). Dominating macrofauna are the polychaete *Pygospio elegans* and the bivalves *Cerastoderma edule* (L.) and *Macoma balthica* (L.). Macroalgal mats (*Enteromorpha prolifera* and *Vaucheria* sp.) have established on this site during recent years (Bolam, 1999). Drum Sands is relatively flat and the majority lies below mid tide level. An area of 250×400 m was staked out on the sandflat, within which the sediments were moderately sorted with a median particle size of 2.6 ϕ, loss on ignition 3–5%, and with no obvious environmental gradient.

2.2. Experimental design

Within the 250×400 m study area, six experimental blocks were set out in a line perpendicular to the tide edge. Within each block, three 1 m^2 plots were marked out, 0.5 m apart and at least 1.5 m away from those of neighbouring blocks. The plots were randomly assigned as unmanipulated control, weed plot or net plot, the latter treatment was included because of the method of attachment of algae to the sediment surface. The sediment surface in the selected area was well oxidised.

Algal material (identified as *Enteromorpha prolifera*) was collected from Dalgety Bay, on the north coast of the Firth of Forth, approximately 5 km distant. On collection it was washed thoroughly in seawater to remove any associated fauna, subsequent checks revealing few invertebrates except for *Hydrobia ulvae* (Pennant) which was omitted from later analysis.

On June 1st, 1997, sediment and faunal samples were taken, together with redox potential measurements from each plot to establish the initial values at the start of the experiment. The fauna was sampled by taking three cores (each 6×6 cm in area, 10 cm depth), located within each plot by random numbers. Cores were sieved on a 500 μm mesh sieve and preserved using neutralised, saline formaldehyde solution (10%) with 0.01% Rose Bengal, and the organisms identified to the lowest possible taxonomic level. The three cores were then pooled to provide a single value for each plot.

The sediment samples were taken within each plot by three randomly located cores (2.4 cm I.D., 3 cm depth) and the data pooled as above. Later, weed was carefully removed from the sediment surface before the cores were inserted to ensure that differences in organic content were not due to above surface weed. Water content was determined by weight loss on drying at 100°C, organic content by weight loss on ignition at 480°C for 4 h and particle size analysis was carried out after Holme and McIntyre (1984). Percentage silt/clay (or <63 μm), median particle size (Md ϕ) and sorting coefficient (inclusive graphic standard deviation) were derived from graphical plots of the particle size distributions.

Redox potential was measured at 1, 2, 4, 6 and 8 cm depths after Pearson and Stanley (1979) using a RL100 meter (Russel). Only one set of redox measurements were taken in each plot.

A 2 kg amount fresh weight (FW) of algae was added to each weed plot and pinned to the surface with plastic netting (5 cm mesh size). Preliminary experiments had shown that 30–40% of weed is lost soon after implantation at this site, so that the actual biomass was approximately 1 kgFW/m^2 [pers. obs.]. The netting treatment to control for the effects of the mesh was simply 1 m^2 of plastic mesh. The weed plots were examined after 2 weeks and more weed added in areas where the weed had not properly established.

After 6 and 20 weeks, the plots were sampled for invertebrates and sediments, and redox measurements taken. Only 6% of each plot had been sampled by the end of the experiment.

Weed biomass was determined after 6 weeks (maintained density) and 20 weeks (during decay) by defining a 6×6 cm area within each plot and removing the enclosed weed. The weed was later washed in water to remove any fauna or sediment and dried at 80°C for 24 h to constant weight (Everett, 1991).

2.3. *Pygospio elegans* size distribution

Size measurements were carried out on *P. elegans* only since this species is numerically dominant on Drum Sands and exhibits a spatial distribution which has important implications for the spatial dynamics of other species (Bolam, 1999). Size determination was carried out by measuring the width of the 5th setiger using a dissecting microscope (× 40 magnification) fitted with an eyepiece micrometer.

2.4. Data analyses

Only those species with a mean abundance of more than one individual per core for any one plot type were included in the analyses. All data were checked for normality using the Anderson–Darling test and for homogeneity of variances using the Bartlett test. Data not meeting these criteria were transformed appropriately (see Zar, 1984) and again checked for normality and homoscedasticity. One-way ANOVAs were carried out followed by a Tukey test if significant. *P. elegans* size distributions were compared between unmanipulated control and weed treatment plots by Kolmogorov–Smirnov tests using the formula for large sample sizes given by Smirnov (1948).

3. Results

3.1. Community parameters

The effects of *Enteromorpha prolifera* on the total number of individuals and species, together with Simpson's diversity index values, are given in Table 1. There was no significant change in the mean number of individuals until 20 weeks after algal implantation when the numbers significantly increased under *E. prolifera* to 126.5±10.2 (S.E.) individuals per sample. The mean number of species did not significantly change throughout the experiment, remaining between 6 and 9 per sample in all treatments. *E. prolifera* significantly affected the macrofaunal diversity during this experiment. In the short term, after 6 weeks, diversity significantly increased in the weed plots to

Table 1
Mean number of individuals, species and diversity index values (mean±S.E., $n = 6$) for each treatment at the start of the experiment and 6 and 20 weeks after algal implantation

		No. individuals per sample	No. species per sample	Simpson index
Initial	Control	40.5±7.9	8.5±1.0	0.68±0.07
	Net	30.7±5.6	6.2±0.8	0.56±0.08
	Weed	38.5±6.4	8.0±0.7	0.65±0.07
6 Weeks	Control	34.5±7.2	6.0±0.6	0.5±0.07
	Net	33.5±3.8	6.7±0.4	0.59±0.04
	Weed	30.5±3.8	7.0±0.4	0.77±0.03
20 Weeks	Control	76.8±6.2	7.7±0.2	0.65±0.05
	Net	64.7±3.6	7.8±0.5	0.64±0.03
	Weed	126.5±10.2	8.7±1.1	0.40±0.05

0.77±0.03 while in the longer term, during weed decay, these plots had a significantly lower diversity compared to control plots (0.40±0.05).

3.2. Species abundances

Only five taxa were sufficiently abundant at the start of the experiment for statistical analyses, the polychaetes *Pygospio elegans* and *Capitella capitata*, the bivalves *Cerastoderma edule* and *Macoma balthica* and oligochaetes (Fig. 2i). Prior to setting up the experiment, there were no significant differences in abundance. After 6 weeks, *Gammarus* spp. had increased in density within the weed treatments, and six taxa were analysed (Fig. 2ii). Four species revealed a significant effect of weed. *C. capitata*, oligochaetes and *Gammarus* spp. had higher densities in the weed treatment plots compared to the net plots, whilst *P. elegans* significantly decreased in density. The two bivalve species, *C. edule* and *M. balthica*, showed no treatment effect. For all these species the net treatment was not significantly different from the controls, suggesting there were no artefacts associated with the method of weed attachment after 6 weeks.

After 20 weeks, eight taxa were analysed since the polychaetes *Anaitides mucosa* (Oersted) and *Spio martinensis* (Mesnil) were now sufficiently abundant (Fig. 2iii). Five taxa showed significant responses to weed: *C. capitata*, oligochaetes and *Gammarus* spp. maintained their increased abundance in the weed treatments, while *P. elegans* was significantly reduced under the weed mats. *S. martinensis* was significantly reduced by both the weed treatment and the netting. *C. edule*, *M. balthica* and *A. mucosa* did not differ between treatments.

3.3. Sediments

At the start of the experiment there were no significant treatment differences for any of the sediment physical variables measured (Fig. 3i). Six weeks later, the levels of all of the measured sediment variables were significantly higher in the weed treatment (Fig. 3ii). There were no significant artefacts associated with the plastic mesh for any of these variables. After 20 weeks, when the majority of the implanted weed had degraded, these differences had disappeared, suggesting that the effects of the weed on the sediment variables were short-lived (Fig. 3iii).

3.4. Redox potential

The redox potential values at the start of the experiment were similar for all three plot types and the values for the control plots only are shown in Fig. 4i. At all the sediment depths measured, the redox potentials were significantly lower in the weed treatment after 6 weeks. Although the mean redox potential for the weed treatment was never negative (except for 8 cm depth with a mean of −2.3 mV), the sediments at this time were black just below the sediment surface. In contrast, the sediments did not appear black until a depth of 7–8 cm within the net and control plots. After 20 weeks, when the majority of the weed had disappeared, the sediments within the weed treatment plots

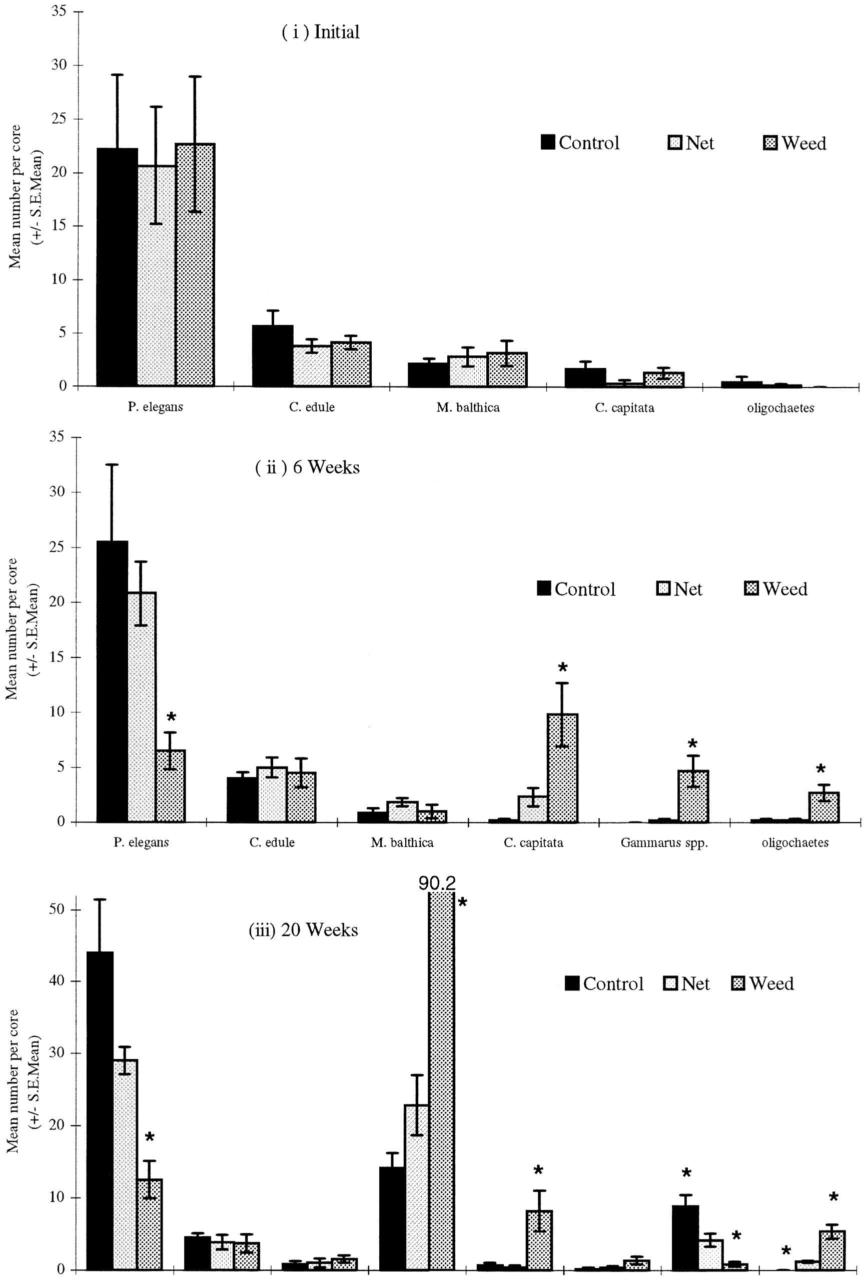

Fig. 2. (i–iii) Mean abundance per core for initial, 6 weeks and 20 weeks results (mean±S.E., $n = 6$). *Denotes statistical significance from net plot values using One-way ANOVA with Tukey multiple comparison test at 5% level of significance.

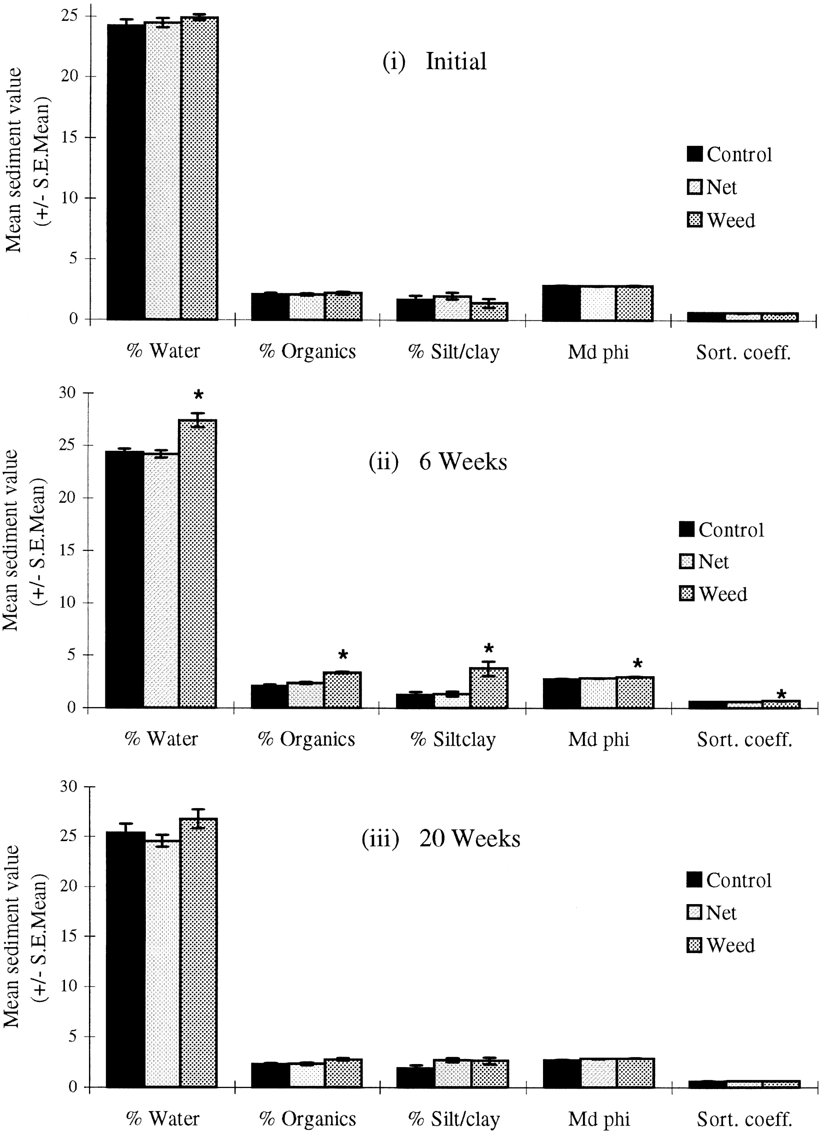

Fig. 3. (i–iii) Sediment results for initial values, 6 and 20 weeks (mean±S.E., $n = 6$). *Denotes statistical significance from net plot values using One-way ANOVA with Tukey multiple comparison test at 5% level of significance.

were no longer significantly more reduced than those of the net or control plots (Fig. 4ii).

3.5. Algal biomass

The *Enteromorpha prolifera* used in this experiment successfully established within

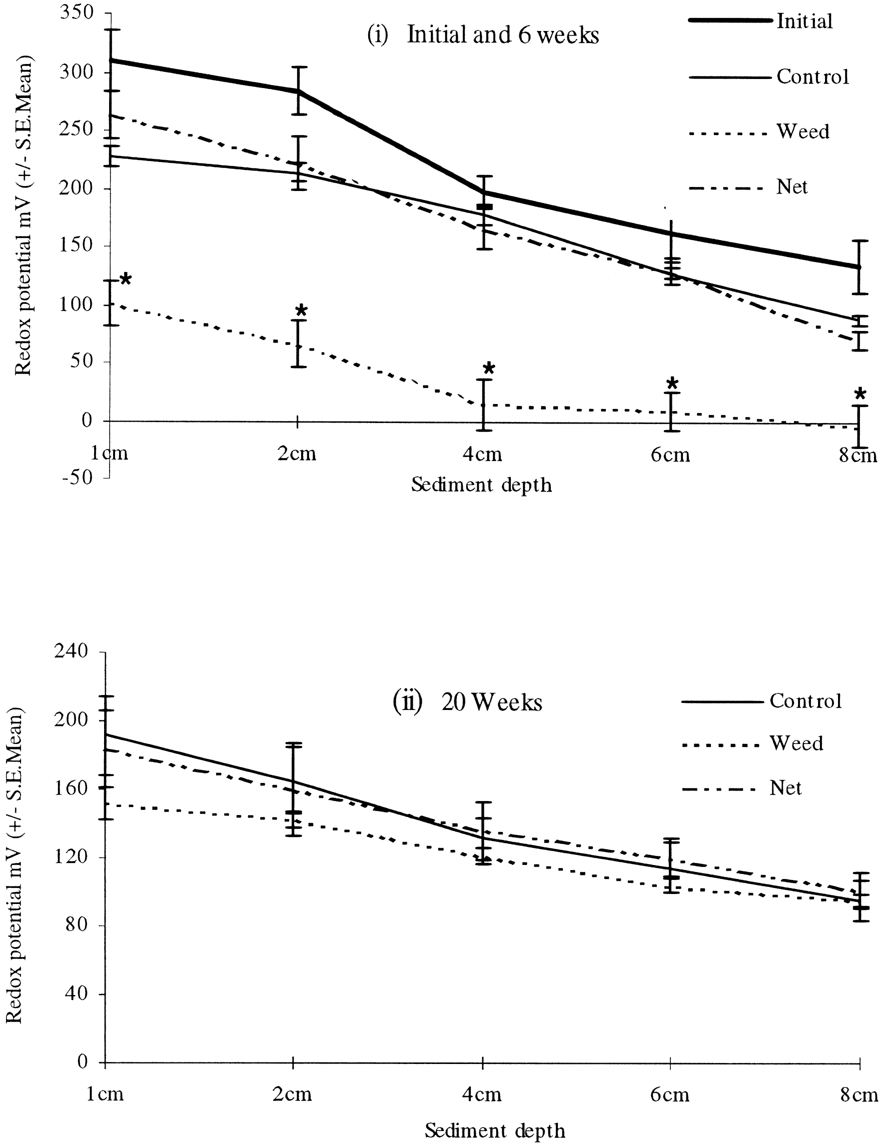

Fig. 4. (i–ii) Redox potential values; initial, 6 and 20 weeks results (mean±S.E., $n = 6$). *Denotes statistical significance from net plot values using One-way ANOVA with Tukey multiple comparison test at 5% level of significance.

the weed treatment plots while weed growth did not occur in either the net plots or the unmanipulated controls. The weed disappeared during October, approximately 20 weeks after the experiment was initiated.

The biomass of the *E. prolifera* estimated after 6 weeks (maintained density) and 20 weeks (during decay) was 139 and 66 gDW/m^2, respectively. These densities are realistic when compared with those in other experimental studies (Table 2).

Table 2
Mean algal biomasses used in controlled weed manipulation experiments

Weed	Mean weed biomass (gDW/m^2)	Implantation/removal	Authors
E. prolifera	66–139	I	Present study
Ulva spp.	450–890	R	Everett (1991, 1994)
Enteromorpha spp.	60[a], 200 and 600	I	Hull (1987)
Pilayella, Ectocarpus, Stictyosiphon and *Dictyosiphon* sp.	440.4	I	Norkko and Bonsdorff (1996)
Rhodomela,Ceramium and *Polysiphonia* spp.	180[a] and 360	I	Sundback et al. (1990)
Enteromorpha spp.	157	R	Cha (in preparation)

[a] Indicates that dry weight has been obtained from wet weight measurements using a wet/dry ratio of 5 (Ramus and Venable, 1987).

3.6. *Pygospio elegans* size distribution

The *P. elegans* size-frequency distributions from the unmanipulated control and weed treatment plots after 6 weeks and 20 weeks are shown in Fig. 5i–ii. The results suggest that after 6 weeks of weed cover, although there was no significant difference in the size distributions between the two plot types, the significant decrease in *P. elegans* abundance under weed mats (Fig. 2ii) was mainly due to a reduction in the smaller individuals. After 20 weeks, Fig. 5ii suggests that the acute larval recruitment phase which occurred on Drum Sands did not successfully occur within the weed treatment plots. The significant difference in *P. elegans* size distribution between these two plot types ($P < 0.05$; Kolmogorov–Smirnov test) was mainly due to those individuals in the smallest size classes, < 0.33 mm 5th setiger width.

4. Discussion

After 6 weeks, the *Enteromorpha prolifera* implanted in this study caused marked changes in the macrobenthos of Drum Sands, together with significant changes in all the measured sediment variables. The algae caused significant increases in the number of individuals after 20 weeks and after an initial increase in diversity after 6 weeks, the weed significantly decreased infaunal diversity. While the numbers of *Pygospio elegans* were significantly reduced, those of *Capitella capitata*, oligochaetes and epibenthic gammarids increased under weed mats. Percent water, organics and silt/clay contents, medium phi and sorting coefficient significantly increased in the sediments under weed mats which also became significantly more reduced between 1 and 8 cm depth. After 20 weeks, during weed decay, the effects of the weed were similar to those after 6 weeks and a community numerically dominated by *C. capitata* was present under weed mats, while the sediment variables were no longer significantly different from controls.

The effects of weed cover on species abundances are both dramatic and complex and can play an important role in structuring benthic assemblages. Hull (1988) suggested

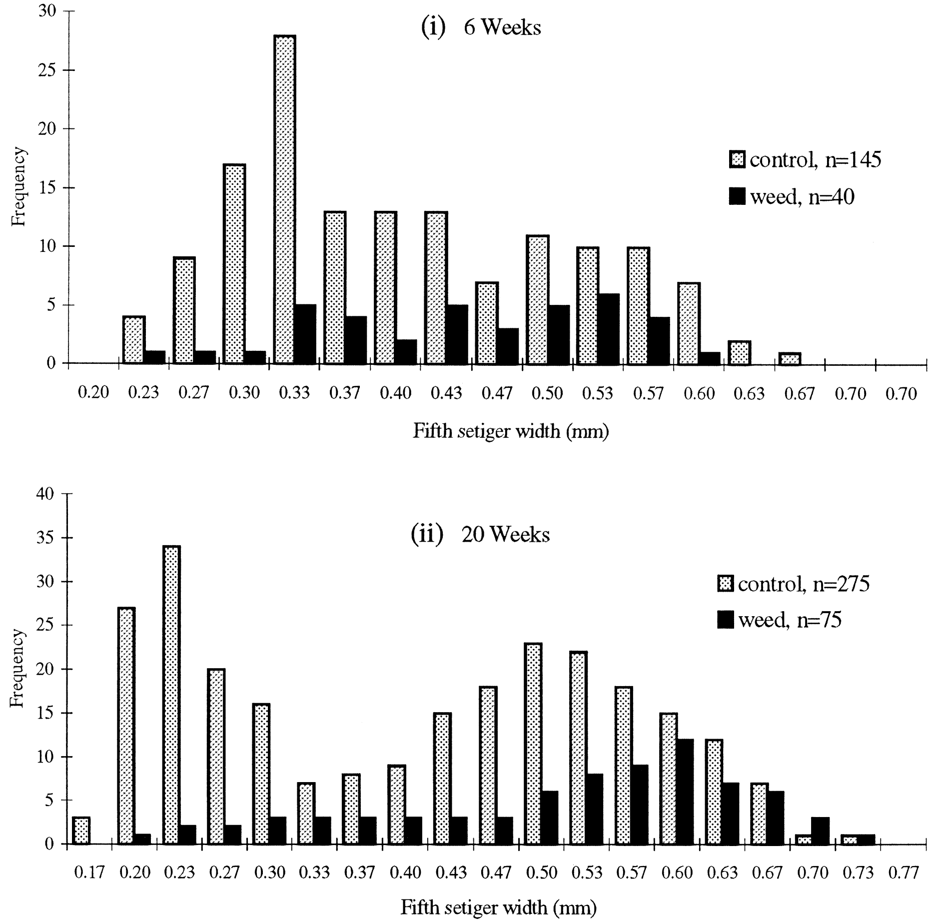

Fig. 5. (i–ii) Size-frequency histograms of *P. elegans* from unmanipulated control and weed treatment plots after 6 and 20 weeks. Total number of individuals measured for each treatment is given in legend.

that the observed changes result from the interaction of many factors. These include a reduced current velocity enhancing larval settlement, shelter from predation, a reduction in oxygen exchange between the sediment surface with the overlying water, accumulation of silt, anoxia and the production of toxic H_2S and prevention of burrowing. Consequently, the effects of weed cover on the fauna (Bonsdorff, 1992) and the mechanisms by which these effects are brought about (Raffaelli et al., 1991) are poorly understood.

Many of the effects previously observed in controlled algal manipulation experiments on intertidal mudflats are similar to those resulting from organic enrichment (Pearson and Rosenberg, 1978), notably the large increases in *C. capitata* and *Malacoceros fuliginosus* (Claparède) (Hull, 1987, 1988; Cha, in preparation). On intertidal mudflats such as the Ythan estuary, Aberdeenshire, the benthic community is naturally comprised of many such species and therefore likely to cope with the anoxic environment which algal mats create (Hull, 1987). This is in contrast to Drum Sands, a much sandier site, where *C. capitata* was present in very low numbers and *M. fuliginosus* was absent in control sediments suggesting that the fauna there is likely to show a more dramatic response to the disturbance imposed by weed cover. While *C. capitata* has previously been found to greatly increase under weed mats establishing on intertidal mudflats (Nicholls et al., 1981; Hull, 1988), the present study suggests that this response also occurs on more exposed sandflats. The recruitment of *C. capitata* in October (Warren, 1976) presumably enabled this species to increase in numbers under the favourable conditions created by weed mats at Drum Sands, possibly facilitated by a reduction in water flow. The long term numerical dominance of *C. capitata* after weed degradation, which has been found to occur on the Ythan estuary (Hull, 1988), also occurred on Drum Sands.

In contrast to the present study, Everett (1994) found that *Macoma balthica* decreased under weed (*Ulva*). He suggested that tellinid bivalves might be expected to suffer from the physical barrier formed by algae between the sediment surface and the overlying water column, consistent with the findings of Cha (in preparation). In contrast, Hull (1988) reported greater numbers of *M. balthica* under his experimentally-implanted algal-covered plots but these were juveniles whose recruitment may have been enhanced by the presence of weed filaments. The effect of weed mats on bivalves may depend upon the degree to which the sediments become reduced. Perkins and Abbott (1972) noted that *M. balthica* and *Cerastoderma edule* migrated up to the sediment surface to avoid the anaerobic conditions below. It is possible that such anaerobic conditions at the sediment surface are less likely in more exposed sandflats such as Drum Sands. Consequently, the effect of weed cover on bivalves on intertidal sandflats, like that observed on mudflats, is likely to be algal-biomass dependent, their numbers declining at higher algal biomasses to those reported in this study.

Pygospio elegans showed a significant decline in abundance within the weed plots during the experiment after 6 weeks and 20 weeks. The response of this species to weed varies in different experiments. For example, Bonsdorff (1992) found that drifting algal mats, in the shallow sandy bottoms of the Baltic, reduced numbers of adult *P. elegans* to zero. Cha (in preparation), working in the Ythan estuary, found that *P. elegans* density was lower in *Enteromorpha*-removed plots compared to those in weed plots, whilst Hull (1987), also working in the Ythan, found the effect was algal biomass-dependent. At lower biomasses, *P. elegans* increased, presumably as a result of an increased detrital-food supply, whilst at higher biomasses *P. elegans* declined, probably due to interference with the worm's feeding behaviour (Hull, 1987; Everett, 1994). *P. elegans* has also been recorded as an opportunistic species present in high densities around sewage outfalls (Anger, 1977) and other organic discharges (Pearson and Rosenberg, 1978), and therefore is not likely to decline in abundance due to the reducing sediments under weed mats. Size measurement analysis of *P. elegans* in this study suggested that juvenile *P. elegans* showed the greatest decrease in abundance under the implanted algal mats. Therefore, *Enteromorpha prolifera* either prevented the successful recruitment of *P. elegans* by 'filtering out' the larvae (Ólafsson, 1988) or the detrimental effect of weed on this species was predominantly on the young stages. The almost complete absence of new recruits under weed mats compared with the control plots supports the former. This 'larval filtering' mechanism probably occurs in addition to the direct physical effect of weed mats interfering with spionid feeding mechanisms (Hull, 1987; Everett, 1994), resulting in the large decrease in abundances shown in this and other studies. *P. elegans* has been shown to maintain high population densities on Drum Sands via two acute planktonic larval recruitment periods, April–May and November–December (Bolam, 1999). The adverse effects of weed mats on successful larval recruitment, as shown in this study, may have serious implications for the longer term population maintenance for this species and perhaps other species which rely on planktonic larval recruitment.

This study has revealed that the establishment of macroalgal mats on intertidal sandflats, as has been for intertidal mudflats, significantly affects the macrobenthic communities of these habitats. However, the significant reduction of certain species is likely to have important ecological implications in the longer term for the spatial distributions of these communities. For example, on Drum Sands, *Pygospio elegans* has been shown to form patches, 1–1.5 m^2, of increased density and that these patches represent distinct ecological areas (Bolam, 1999). These patches allow the presence of several species which are otherwise unable to survive on this sandflat and also represent a source of opportunists allowing rapid recolonisation of small-scale disturbances. Consequently, the mosaic of communities found on Drum Sands, in part due to the spatial heterogeneity of *P. elegans*, has important implications for the maintenance of spatio-temporal dynamics on this sandflat. Although weed implantation experiments give important information about species and community responses to the effects of weed mats, they give little insight into the direct and indirect long term changes in ecosystem functioning within these habitats. Similarly, the long term effects will undoubtedly be partly determined by the spatial distribution of the weed mats themselves (Raffaelli et al., 1999). Mats which cover large areas of intertidal sediments will have different ecological effects than smaller, spatially heterogeneous mats.

5. Conclusions

The results of the present experiment are broadly consistent with those carried out with other algal species (*Ulva*; Everett, 1994) and in much more sheltered, muddier environments (Hull, 1987; Cha, in preparation). In both habitats, deposit-feeding polychaetes such as spionids are negatively affected while sub-surface feeders such as capitellids and oligochaetes greatly increase in numbers. Higher algal biomasses to those reported in this study are likely to significantly reduce the densities of bivalves. We conclude therefore, that the immediate effects of algal mats are general and predictable and that a general deterioration in environmental quality is expected whatever the weed taxa or location. The long term ecological consequences of such algal growth are less predictable and depend upon the spatial distribution of the dominant macrofaunal species and the spatial heterogeneity of weed mat establishment.

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