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Responses of benthic invertebrates and their avian predators to the experimental removal of macroalgal mats

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A field experiment investigating the effects of algal removal on benthic invertebrates and estuarine birds was carried out during September and October 2001. A randomized block experimental design was employed and three treatments were used: sites with algal cover maintained, when necessary by the addition of algae, sites with algal cover removed and control sites that were not manipulated in any way. Total invertebrate numbers increased during the experiment, but species varied in their response to the different treatments. Although *Hydrobia ulvae* showed the greatest increase in cleared sites after two months, there was no significant difference between treatments. *Corophium volutator* showed significant colonization of cleared sites during the experimental period, and numbers of *Phyllodoce maculata* also increased in the cleared sites. Results showed that while more sedentary benthic infauna are less capable of adjusting to the affects of algal clearance, more mobile epifauna and polychaetes show an ability to disperse to cleared sites in a relatively short period of time. Wading birds, however, did not enter the study site in any abundance during the experiment. Black-headed gulls (*Larus ridibundus*) were significantly more abundant in cleared sites than in algal cover-maintained or control sites when foraging.

INTRODUCTION

Increased nutrient inputs to marine coastal areas with resultant eutrophication have been recognized for many years (Rosenberg, 1985). Such enrichment, especially of the nutrients nitrogen and phosphorus, has been linked to an increased growth of macrophytes in many estuaries and coastal areas of the world, notably of fast-growing, mat-forming green algae such as *Enteromorpha* spp. In temperate regions algal mats may maintain high cover and biomass during the spring, summer and autumn before being broken down or buried in autumn and winter (Hull, 1987). While nutrients play a major role, other factors such as topography, local changes in hydrography (Raffaelli et al., 1998), light attenuation (Lavery et al., 1991) and degree of exposure (Pihl et al., 1999) influence the spatial distribution and biomass of the algae.

Many studies have documented the effects of algal mats on the estuarine system. In general, dense algal cover reduces oxygen exchange between the sediment and water column, resulting in anoxic conditions, accentuated by enhanced bacterial activity during algal decay (Hull, 1987). In addition reduced water flow under the mats and an increase in sedimentation rates (Hull, 1987), together with a possible accumulation of hydrogen sulphide may lead to significant effects on macrofaunal communities and the local ecology as a whole.

Field studies have shown a reduction in invertebrate fauna under algal mats, for example sedentary sediment/water interface feeders such as bivalve molluscs (Everett, 1994; Raffaelli et al., 1998) and species such as the burrowing amphipod *Corophium volutator* (Pallas) (Raffaelli et al., 1991). On the other hand, algal mats may provide a constant supply of detritus for burrowing and surface detrivores with species such as oligochaetes and capitellid worms increasing in number (Everett, 1994; Lopes et al., 2000). The mat itself may also serve as a refuge from predators for some epi-benthic mobile species such as gammarid amphipods. Algal mats are also known to effect the feeding, abundance and distribution of other animals, particularly wading birds (Tubbs & Tubbs, 1980; Lewis & Kelly, 2001) and fish (Isaksson et al., 1994).

While a number of field studies undertaken to investigate the effects of algal mats on invertebrates have adopted an experimental approach, most have quantified the effects of the addition of algae to areas of mudflat which were devoid of algae at the start of the experiment (e.g. Lopes et al., 2000), or where there was no previous history of algal cover (e.g. Hull, 1987). Our study, undertaken at Clonakilty Bay, West Cork, Ireland, adopts a different approach in that it was designed to assess the effects of removing algae from a mudflat area where extensive mats occur during the summer months. The experiment was designed to assess initial recolonization and recovery of invertebrates following algal mat removal, allowing comparison of algal covered areas, clear areas and areas undergoing natural algal breakdown.

Previous studies have shown that different species of wading birds have different responses to algal mats (Tubbs & Tubbs, 1980). For example, the black-tailed godwit (*Limosa limosa* L.) when foraging, has been shown to probe through clear spaces amongst patchy algal mats especially when the mats are in the process of breaking up (Lewis & Kelly, 2001). Therefore this study was also designed to test whether wading birds would move into the study area and 'sample' newly created clear areas when foraging.

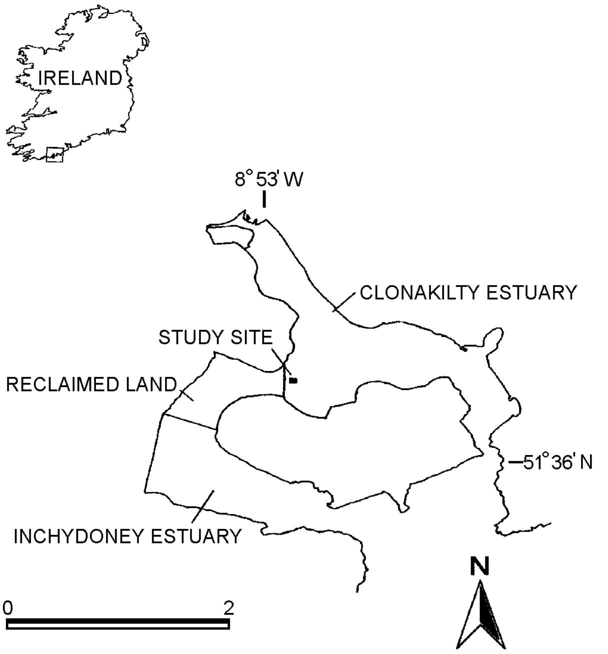

Figure 1. Clonakilty Bay, West Cork, Ireland and position of the study area. Scale bar: kilometres.

MATERIALS AND METHODS

Study site and experimental design

Clonakilty Bay is located on the south coast of Ireland and is a small estuary with mud and sand flats extending over approximately 272 hectares (Figure 1). The bay is divided by Inchydoney Island and an area of reclaimed land to give two distinct parts, a northern arm that is the estuary of the Feagle River and a southern arm which receives two small streams. The bay supports internationally important numbers of wading birds during the winter.

Algal mats have been observed in this bay for the past 10–15 years but vary from year to year in cover and biomass (T.C. Kelly, personal observation). A study site was chosen in a mudflat area of the northern arm of the bay where algal mats are extensive and cover over 70% of the sediment in the summer months.

A randomized block design was chosen so as to prevent any gradients in initial sediment parameters or algal cover from masking the effects of treatments during analysis. Within the designated study area 12 sites, each measuring 10 m^2, were arranged in a 3×4 grid. Sites were marked with short canes in an attempt to make the markers as unobtrusive as possible. Sites were positioned 2 m away from each other. The design was blocked in that there were four blocks, set parallel to the tide edge, the furthest block down shore being assigned as Block 1. Within each block three sites were each randomly assigned a treatment: A+ (a site with algal cover maintained), A− (a site with algae removed) and C (a control site with no manipulation). Each treatment was therefore replicated four times.

Study site manipulation

Following initial sampling, algae were removed from the sites assigned the treatment A− (September 2001). This task was performed using a light rake and by one person only to minimize disturbance to the sediment. Algae removed were transported as far away as possible from the study area. The experiment ran until the end of October 2001 when storms started to break-up the mat in the study site and caused the A+ sites to begin to lose their cover. During the two-month experimental period it was once necessary to maintain the A+ sites by adding a small amount of washed algae to any clear patches that had developed. Algae were removed from the A− sites a further three times to remove any algae that had drifted onto these sites. Control sites were left undisturbed at all times.

Sampling methods

In August 2001 initial sampling was undertaken within all sites prior to algae being removed from the A− sites. Sampling for all parameters consisted of three replicate samples per site, a random numbers table determining their position. The outer 1 m edge of each site was not sampled to reduce edge effects.

Algal biomass was determined using an 18-cm diameter core that was pushed into the sediment. Algae were removed, washed in seawater to remove sediment and invertebrates, and then weighed to determine fresh weight per unit area (FW m^{-2}). The algae were then dried in an oven at 70°C to obtain dry weight per unit area (DW m^{-2}).

Organic matter was determined by taking three randomly placed cores of sediment (depth 3 cm) from each site, algae removed from the sediment surface beforehand. Organic content was estimated by the loss-on-ignition method (Holme & McIntyre, 1984) at 550°C for six hours. Silt content was measured following the method of Holme & McIntyre (1984) to establish the percentage of material passing through a 63-μm wet sieve.

Invertebrate infauna was sampled using a 10-cm diameter core to a depth of 15 cm, three cores randomly placed in each site. Sediment cores were sieved on a 500-μm mesh sieve and the fauna retained were fixed in 4% formalin/seawater solution prior to being identified to the lowest possible taxonomic level.

At the end of the experiment (end of October 2001) sampling was undertaken for invertebrate infauna and sediment parameters as before.

Bird usage of the study sites during the four-hour period leading up to low tide was monitored by performing scans of birds in the study area on randomly assigned days. On each sampling occasion, the number of birds within the study area was counted at 15 min intervals and a record made of the position of each bird in relation to all sites. In addition a record was made of the time of the tidal cycle and weather conditions. The number of birds in the vicinity of the study area was assigned as Low: less than 50 birds with scattered distribution; Medium: 50 or more birds with scattered distribution or High: flocks of birds or 100+ scattered individuals.

Data analyses

Univariate community measures were calculated: total individuals, species richness, Shannon–Wiener diversity (H′), Simpson's (D) for dominance, 1/D Simpson's reciprocal index and Shannon evenness (J). The three

Table 1. *Algal biomass and sediment measures prior to the algal removal experiment and after two months. Mean ± standard error of un-pooled data (N=12).*

		Before			After		
		A+	A−	C	A+	A−	C
Algal biomass	Kg FWm^{-2}	2.44 (0.58)	2.52 (0.25)	3.38 (0.80)			
	g DW m^{-2}	206.15 (34.79)	246.17 (26.85)	276.73 (60.54)			
Organic matter	%	13.19 (0.42)	13.39 (0.44)	13.82 (0.37)	14.25 (0.38)	14.38 (0.33)	14.33 (0.39)
Silt content	%	88.78 (1.27)	85.66 (1.71)	88.45 (1.08)	91.08 (0.68)	90.21 (0.99)	93.17 (0.71)

Table 2. *Macroinvertebrate community composition before algal removal and after two months of experimental algal removal. (Pooled data from cores, mean ± standard error, N=4.)*

	Initial			2 Months		
Species/taxa	A+	A−	C	A+	A−	C
Oligochaetes	7.25 (5.71)	5.50 (4.52)	1.00 (0.58)	10.00 (6.88)	5.25 (5.25)	9.25 (5.12)
Eteone longa	0.00	0.00	0.00	0.25 (0.25)	1.75 (0.48)	1.00 (0.58)
Phyllodoce maculata	0.75 (0.48)	1.5 (1.19)	0.25 (0.25)	1.25 (0.48)	6.00 (3.34)	1.00 (0.41)
Hediste diversicolor	0.00	0.00	0.00	0.00	0.25 (0.25)	0.25 (0.25)
Malacoceros fulignosus	8.75 (4.59)	8.00 (2.38)	5.25 (1.32)	21.75 (8.23)	10.50 (9.84)	43.00 (17.96)
Pygospio elegans	5.25 (1.97)	5.25 (1.93)	3.5 (1.32)	2.00 (0.71)	2.25 (1.60)	2.0 (1.35)
Arenicola marina	0.5 (0.29)	0.00	0.5 (0.5)	0.25 (0.25)	0.25 (0.25)	0.00
Carcinus maenas	1.25 (0.63)	0.25 (0.25)	0.25 (0.25)	0.00	0.25 (0.25)	0.20 (0.25)
Hydrobia ulvae	33.25 (22.98)	8.25 (4.25)	18.5 (4.29)	57.25 (20.03)	68.75 (9.03)	59.75 (18.23)
Gammarus spp.	0.25 (0.25)	0.00	0.00	2.00 (0.71)	0.25 (0.25)	0.75 (0.48)
Corophium volutator	1.25 (1.25)	0.00	0.00	0.50 (0.50)	31.25 (18.09)	2.50 (0.32)
Crangon crangon	0.00	0.00	0.00	0.25 (0.25)	1.00 (0.71)	1.25 (0.95)
Scrobicularia plana	1.00 (0.41)	1.00 (1.00)	0.5 (0.29)	0.25 (0.25)	0.25 (0.25)	0.25 (0.25)
Cerastaderma edule	0.75 (0.25)	0.75 (0.48)	0.5 (0.5)	1.50 (0.87)	1.00 (1.00)	1.25 (0.75)
Total individuals	61.75 (21.12)	30.75 (3.09)	30.75 (4.13)	96.75 (40.7)	131.75 (17.62)	124.00 (19.14)
Species richness	8.00 (1.08)	5.25 (1.38)	5.25 (1.55)	7.5 (0.87)	7.75 (0.63)	8.25 (1.55)
H′	1.34 (0.22)	1.20 (0.20)	1.16 (0.20)	1.12 (0.13)	1.16 (0.11)	1.11 (0.18)
D	0.37 (0.12)	0.36 (0.05)	0.42 (0.10)	0.44 (0.05)	0.42 (0.05)	0.45 (0.07)
1/D	3.37 (0.69)	2.91 (0.35)	2.87 (0.68)	2.34 (0.25)	2.50 (0.36)	2.37 (0.35)
J	0.65 (0.11)	0.82 (0.06)	0.67 (0.08)	0.55 (0.04)	0.57 (0.05)	0.54 (0.05)

replicate cores from each site were pooled to give a single value for each site. As non-parametric tests were deemed suitable for these non-normal data, comparisons between initial values and values after two months were analysed using Mann–Whitney U-tests. Site environmental parameters were analysed using Kruskal–Wallis tests.

Densities of selected and the most abundant invertebrate species were analysed using a randomized block analysis of variance (ANOVA). The raw data were transformed ($\log_{10}$ n+1) and variances checked for homogeneity using Levene's test. In two cases a Friedman's test (non-parametric randomized block) was performed.

RESULTS

Environmental parameters

All experimental sites were covered in a dense and uniform algal mat prior to the start of the experiment, the dominant species being *Enteromorpha muscoides* (Clemente y Rubio). The algal biomass was relatively stable across the experimental sites (Table 1). There was no significant difference between the biomass (g DW m^{-2}) of the sites assigned the treatments A+, A− or C prior to the start of the experiment (H=1.92, P=0.383) or between experimental blocks (H=5.13, P=0.163, Kruskal–Wallis test).

No significant differences were determined in the % organic matter content of the sediment of the sites prior to the start of the experiment (H=1.70, P=0.427, Kruskal–Wallis test) (Table 1). Block 1 however, exhibited significantly lower % organic matter (H=10.24, P=0.017, Kruskal–Wallis test). The % silt content showed no significant difference between sites prior to the experiment (H=1.73, P=0.42) or between blocks (H=5.72, P=0.13, Kruskal–Wallis test) (Table 1).

Following the two month duration of the experiment, the % organic matter content of the sediment was still significantly lower in Block 1 (H=7.88, P=0.05), but there

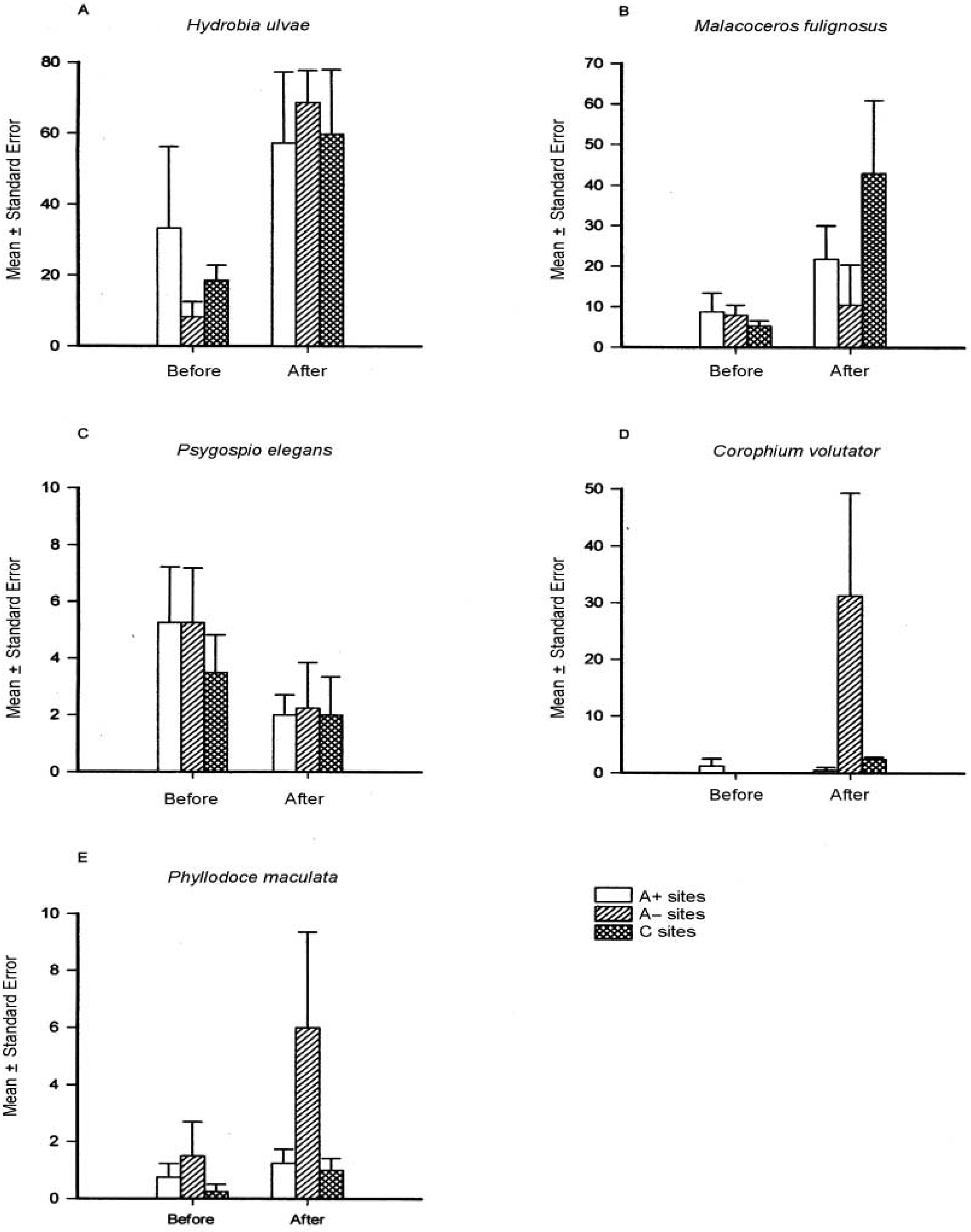

Figure 2. Mean abundance of selected invertebrate species, before the experiment when all treatment sites were covered in algae, and after two months of algal removal. A+ sites: algal cover maintained; A− sites: algal cover removed; C sites: undisturbed control sites. (Mean number ±standard error, N=4.)

was no significant difference amongst A+, A− or C treatments (H=0.36, P=0.84, Kruskal–Wallis test). After two months % silt content was significantly lower in the A− sites (H=6.47, P=0.04, Kruskal–Wallis test).

Measures of diversity

No significant differences were found for any of the diversity measures between the assigned treatments (A+, A− and C) or between blocks when considering the two sampling periods separately (Table 2) or when comparing initial values with those after two months. Although species richness increased over time in both the A− and C sites the increase was not significant at either site (U=3.00, P=0.139, Mann–Whitney U-test).

Invertebrate densities

Analysis of total individuals showed a significantly higher number across all treatments after two months compared with the initial values ($F_{1,15}$=47.20, P=0.001, ANOVA) (Table 2). Although the greatest increase in individuals over time was apparent in A− sites, analysis showed no significant effect of treatment ($F_{2,15}$=0.22, P=0.803), block ($F_{3,15}$=0.77, P=0.531), or any significant time×treatment interaction ($F_{2,15}$=2.92, P=0.085).

Numbers of *Hydrobia ulvae* (Pennant) increased significantly over time ($F_{1,15}$=16.40, P=0.001) (Figure 2A). The greatest mean numbers after two months were found in A− sites, but there was no significant effect of treatment ($F_{2,15}$=0.69, P=0.514) or any time×treatment interaction ($F_{2,15}$=1.79, P=0.201). There was no effect of block ($F_{3,15}$=0.14, P=0.936).

Although *Malacoceros fuliginosus* (Claparède) increased in number over time this was found to be non-significant ($F_{1,15}$=2.35, P=0.146) (Figure 2B). There was also no significant effect of treatment ($F_{2,15}$=2.55, P=0.112) although significant differences were found between blocks ($F_{3,15}$= 5.67, P=0.008). After two months, numbers in C sites had increased greatly resulting in a significant time×treatment interaction ($F_{2,15}$=4.34, P=0.033). In contrast, the spionid polychaete *Pygospio elegans* (Claparède) showed a significant decrease in numbers over time in all sites ($F_{1,15}$=10.38 P=0.006) but no significant differences between treatments ($F_{2,15}$=0.36, P=0.707) or blocks ($F_{3,15}$=0.65, P= 0.593) (Figure 2C). A non-significant time×treatment interaction ($F_{2,15}$=0.66, P=0.530) indicated no difference between treatments in either of the time periods.

Corophium volutator were only present in sufficient numbers to permit analysis after two months of experimental algal removal (Figure 2D). Significantly greater numbers were found in A− sites than in A+ or C sites (χ^2_2=6.12, $P<0.05$, Friedman's test). Similarly, numbers of *Phyllodoce maculata* (L.) could only be analysed after two months. Although greater numbers were found in A− sites, no significant difference was found between the three treatments (χ^2_2 =1.50, $P>0.05$, Friedman's test) (Figure 2E).

Response of estuarine birds

During 30 hours of observation time only 57 counts recorded bird presence. Five species of bird were seen within the study site: black-headed gull (*Larus ridibundus* L.), oystercatcher (*Haematopus ostralegus* L.), black-tailed godwit (*Limosa limosa*), curlew (*Numenius arquata* L.) and hooded crow (*Corvus corone cornix* L.). Of these, only the black-headed gull occurred with any regularity, being present in 79% of scans. Due to the low sample sizes, analysis was only performed on the black-headed gull to ascertain whether their distribution was homogenous amongst the A+, A− or C treatments. Results showed that there was a significant departure from homogeneity (χ^2=15.54, $P<0.01$) and that significantly more birds were observed in the A− sites than in the A+ or C sites. Low numbers of all bird species in the vicinity of the study area (i.e. less than 50 scattered individuals) were recorded in 75% of all scans.

DISCUSSION

Prior to algal removal, oligochaetes together with *Malacoceros fulignosus* and *Hydrobia ulvae* dominated the invertebrate community. *Malacoceros fulignosus* is tolerant of organic rich sediments (Pearson & Rosenberg, 1978) and may often be observed in high densities under algal mats or under patches of decomposing seaweed (Thrush, 1986). After two months of algal removal, this species exhibited lower numbers in the A− sites compared to increased numbers in the A+ and Control sites. This may suggest a tolerance of algal cover, perhaps the algal mat providing a refuge from predation. Indeed, invertebrates may have been subject to increased predation pressure in the A− sites, as predators may aggregate in clear areas adjacent to algal patches. A predator exclusion experiment would therefore have been a useful addition to the current study. It is also possible that any increased predation in the A− sites may have led to an underestimation of the actual increases of species such as *Corophium volutator* and *Hydrobia ulvae*.

The spionid polychaete *Psygospio elegans* has shown mixed responses to algal mats in previous studies. Hull (1987) found reductions in numbers under a high biomass of algae (3 kg FW m^{-2}) but numbers increased under lower biomasses. In contrast, Österling & Pihl (2001) reported higher numbers of this polychaete under algal bags and cages (1.2 kg FW m^{-2}) than in clear controls. The current study showed a relatively low density of *P. elegans* at all sites prior to algal removal. Although the responses of *P. elegans* are clearly complex, this study suggests that a low population density is characteristic of prolonged algal cover. The interference of algal mats with spionid feeding mechanisms (Hull, 1987) or the mat's ability to filter out pelagic larvae thereby reducing recruitment (Olafsson, 1988) are possible reasons for low abundance.

Colonization of sites following algal removal could have occurred by the processes of reproduction or immigration. Given the short study period and timing of the current experiment and with population increases via reproduction and recruitment being higher in the summer months, important recruitment periods were missed. However, benthic invertebrates can show recovery via mobile juvenile (postlarval) stages in winter. Adults of some species also have considerable dispersal abilities through drifting or swimming in the water column or by movement through sediment (Beukema et al., 1999).

In general sedentary sediment/water interface feeders such as bivalves occur in lower densities under algal mats (Raffaelli et al., 1998) as seen in the case of *Scrobicularia plana* (da Costa) and *Cerastaderma edule* (L.) in the present study. With horizontal movements relatively limited, particularly in the case of *S. plana* (Hughes, 1970), increases in abundance would rely on settlement of larvae or spat. A longer study would have therefore been required to determine recolonization patterns of bivalves and given that algal mats in the study area are absent for only a short time during the winter, to determine how successful recolonization would be. Filamentous algae does not form such a barrier between the sediment and water column as does laminar forms, but due to the extensive cover and high biomass of algae in the area, together with reduced sediments and the filtering mechanism of algae, successful recruitment may be limited.

More mobile invertebrates include *Hydrobia ulvae*. While dispersal is chiefly through a planktonic larval stage, adult dispersal is also possible through crawling, floating behaviour or being rolled across the sediment surface (Barnes, 1981). *Hydrobia ulvae* has been reported to occur in high densities within algal mats (Hull, 1987) or to be unaffected by algal cover (Lopes et al., 2000). In the current study while *H. ulvae* showed the greatest increase in numbers within A− sites, a non-significant effect of treatment suggests no distinct preference for either clear mud or algal habitats.

Hediste diversicolor (O.F. Müller) is also extremely mobile in all life stages and is considered highly tolerant of anoxic conditions. The low numbers of this polychaete found in the present study suggest that high algal biomass and prolonged cover are factors that influence distribution and warrant further consideration.

Thus although some benthic invertebrates exhibit considerable dispersal capabilities throughout their life cycle, recolonization of the A− sites appeared negligible during the present study with the exception of *Corophium volutatotor* and *Phyllodoce maculata*. Raffaelli et al. (1991) found significant declines in *C. volutator* under algal mats suggesting that declines were due to an interference with the amphipod's feeding behaviour rather than organic enrichment of the sediment. Hull (1987) found that *C. volutator* rapidly recolonized areas cleared of algae. Our results confirm both of these findings, colonization of A− sites by *C. volutator* highlighting the dispersal capacity of the species and also showing that organically rich sediment, the previous presence of algal mats and conditions of the sediment following algal removal, do not deter successful colonization.

Counts of birds during the experimental period were expected to show some degree of patch choice by foraging birds. Few wading bird species foraged within the study site or were present in the vicinity of the study area during observation periods. However, black-headed gulls made preferential use of the cleared sites. This species was often observed foot-paddling while foraging within the clear sites, but never within A+ or Control sites, suggesting that the presence of algal cover prevents such behaviour from occurring. The black-headed gull is a less gregarious forager than flocking wintering waders such as the black-tailed godwit. This characteristic, together with a variable feeding method and diet may have enabled *Larus ridibundus* to make patch choice decisions quickly within the study area.

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REFERENCES

Barnes, R.S.K., 1981. Behavioural activities and ecological strategies in the intertidal gastropod *Hydrobia ulvae*. In *Feeding and survival strategies of estuarine organisms* (ed. N.V. Jones and W.J. Wolff), pp. 79–90. London: Plenum Press.

Beukema, J.J., Flach, E.C., Dekker, R. & Starink, M., 1999. A long-term study of the recovery of the macrozoobenthos on large defaunated plots on a tidal flat in the Wadden Sea. *Journal of Sea Research*, **42**, 235–254.

Everett, R.A., 1994. Macroalgae in marine soft-sediment communities: effects on benthic faunal assemblages. *Journal of Experimental Marine Biology and Ecology*, **175**, 253–274.

Holme, N.A. & McIntyre, A.D., 1984. *Methods for the study of marine benthos*, 2nd edn. Oxford: Blackwell Scientific Press.

Hughes, R.N., 1970. Population dynamics of the bivalve *Scrobicularia plana* (da Costa) on an intertidal mud-flat in North Wales. *Journal of Animal Ecology*, **39**, 333–356.

Hull, S.C., 1987. Macroalgal mats and species abundance: a field experiment. *Estuarine, Coastal and Shelf Science*, **25**, 519–532.

Isaksson, I., Pihl, L. & Van Montfrans, J., 1994. Eutrophication related changes in macrovegetation and foraging of young cod (*Gadus morhua* L.): a mesocosm experiment. *Journal of Experimental Marine Biology and Ecology*, **177**, 203–217.

Lavery, P.S., Lukatelich, R.J. & McComb, A.J., 1991. Changes in the biomass and species composition of macroalgae in a eutrophic estuary. *Estuarine, Coastal and Shelf Science*, **33**, 1–22.

Lewis, L.J. & Kelly, T.C., 2001. A short-term study of the effects of algal mats on the distribution and behavioural ecology of estuarine birds. *Bird Study*, **48**, 354–360.

Lopes, R.J., Pardal, M.A. & Marques, J.C., 2000. Impact of macroalgal blooms and wader predation on intertidal macroinvertebrates: experimental evidence from the Mondego estuary (Portugal). *Journal of Experimental Marine Biology and Ecology*, **249**, 165–179.

Olafsson, E.B., 1988. Inhibition of larval settlement to a soft bottom benthic community by drifting algal mats—an experimental test. *Marine Biology*, **97**, 571– 574.

Österling, M. & Pihl, L., 2001. Effects of filamentous green algal mats on benthic macrofaunal functional feeding groups. *Journal of Experimental Marine Biology and Ecology*, **263**, 159–183.

Pearson, T.H. & Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology. Annual Review*, **16**, 229–311.

Pihl, L., Svenson, A., Moksnes, P.-O. & Wennhage, H., 1999. Distribution of green algal mats throughout shallow soft bottoms of the Swedish Skagerrak archipelago in relation to nutrient sources and wave exposure. *Journal of Sea Research*, **41**, 281–294.

Raffaelli, D., Limia, J., Hull, S. & Pont, S., 1991. Interactions between the amphipod *Corophium volutator* and macroalgal mats on estuarine mudflats. *Journal of the Marine Biological Association of the United Kingdom*, **71**, 899–908.

Raffaelli, D.G., Raven, J. & Poole, L., 1998. Ecological impact of green macroalgal blooms. *Oceanography and Marine Biology. Annual Review*, **36**, 97–125.

Rosenberg, R., 1985. Eutrophication—the future marine coastal nuisance. *Marine Pollution Bulletin*, **16**, 227–231.

Thrush, S.F., 1986. The sublittoral macrobenthic community structure of an Irish sea-lough: effect of decomposing accumulations of seaweed. *Journal of Experimental Marine Biology and Ecology*, **96**, 199–212.

Tubbs, C.R. & Tubbs, J.M., 1980. Wader and Shelduck feeding distribution in Langstone Harbour, Hampshire. *Bird Study*, **27**, 239–248.

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