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Interactions between macro-algal mats and invertebrates in the Ythan estuary, Aberdeenshire, Scotland

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Abstract Blooms of opportunistic green macro-algae are a common feature of coastal areas and their effects on mudflat invertebrates can be dramatic. On the Ythan estuary, Aberdeenshire, Scotland, we have carried out a number of manipulative field experiments designed to evaluate the effects on invertebrates of different species of macro-algae with contrasting ecologies, and the effects of invertebrates on the development of the blooms. Macro-algal mats were found to have dramatic negative effects on the density of the amphipod *Corophium volutator*, with higher algal biomasses having greater impact. The mechanism for this interaction seems to be interference by the algal filaments with the feeding behaviour of the amphipod. In contrast, the polychaete *Capitella* spp. increases in abundance under macro-algal mats due to enrichment of the sediment with organic material. These two interactions are seen at all scales, in areas of less than 1 m² to the scale of the entire estuary, irrespective of the species composition of the macro-algal mats. Bioturbation by *Corophium* and grazing by the snail *Hydrobia ulvae* had little effect on macro-algal biomass, but there were less algae when the polychaete *Nereis diversicolor* was present. The most significant interaction in this system is the pronounced negative impact of algal mats on the abundance of *Corophium*, probably the most important invertebrate species in the diets of the estuary's shorebirds, fish and epibenthic crustaceans.

Key words *Corophium* · *Enteromorpha* · Eutrophication · Ythan estuary · Macro-algae

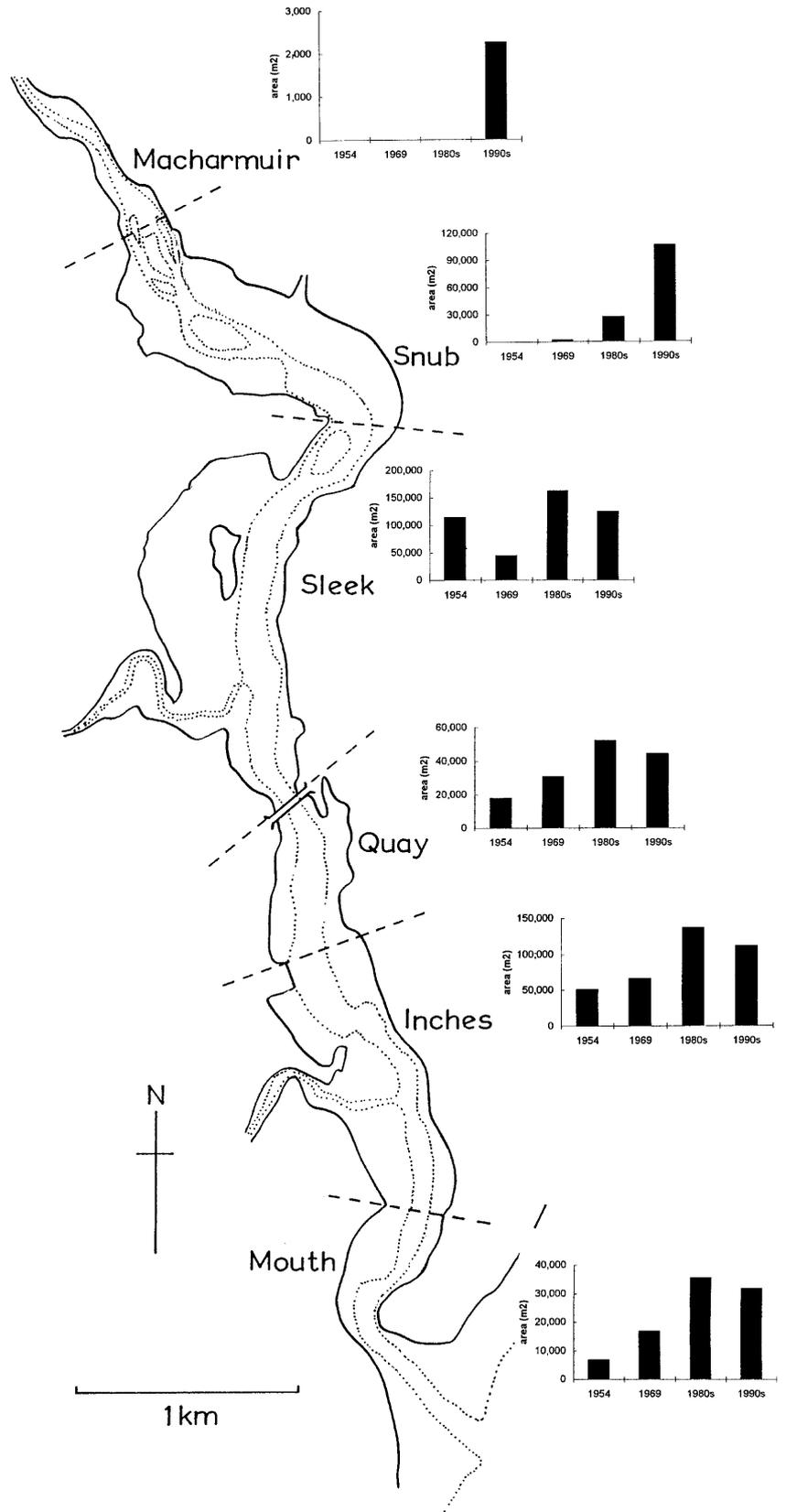
Introduction

Large-scale blooms of opportunistic macro-algae have been reported from many coastal shallow-water areas world-wide (Fletcher 1996), including the Wadden Sea (Reise and Siebert 1994). These mats can impact significantly on invertebrate assemblages, causing declines in some species and increases in others (Raffaelli et al. 1998). Nowhere is this seen more clearly than in the Ythan estuary, 20 km north of the city of Aberdeen on the east coast of Scotland. The estuary is only 8 km in length and only a few hundred metres (max) in width. The river Ythan drains about 650 km² of land, almost all of which is under intense arable agriculture. In line with much of the rest of Europe, the amount of nitrogenous fertiliser applied to crops in the catchment has increased substantially and there has been a shift towards cereals and oil-seed rape (Raffaelli 1998, 1999). Not surprisingly, the levels of dissolved oxidised nitrogen in the river have increased over the past 30 years and these levels are reflected in the receiving estuary (Balls et al. 1995; Raffaelli 1999). Analysis of aerial photographs taken in mid-summer at low tide show that in 1954 and 1969, green macro-algal mats (only biomasses >1 kg m⁻² wet weight show up on the photographs) were then much less widespread than in the 1980s and 1990s (Fig. 1), and there have been concomitant changes in the Ythan's invertebrates and shorebirds (Raffaelli et al. 1999). Whilst most of the interactions described to date concern the negative impacts of macro-algal blooms on invertebrates (Raffaelli et al. 1998), invertebrates may also have impacts on macro-algae, especially at low algal biomasses. In this paper, I discuss these interactions for the Ythan estuary, with particular emphasis on the amphipod *Corophium volutator*. This species seems particularly sensitive to macro-algal mats and is a major food item for most of the Ythan's shorebirds, fish and epibenthic crustaceans (Hall and Raffaelli 1991).

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Fig. 1 Temporal changes in the area of macro-algal mats in different sections of the Ythan estuary, Aberdeenshire. Data from aerial photographs, on which biomasses $>1 \text{ kg m}^{-2}$ (wet weight) are apparent (modified from Raffaelli et al. 1999)



Effects of mats on invertebrates

Evidence for negative impacts of macro-algal mats on invertebrates comes from four kinds of investigation carried out over a range of spatial and temporal scales.

Small-scale studies

The spatial distribution of algal mats is heterogeneous over a range of scales. At the estuary scale, mats are confined to certain sections (see below) and within mat-affected areas, there are often mat-free patches, several square metres in extent. Small-scale comparisons of patches (<1 m²) of mudflat with and without a covering of macro-algal mats have consistently revealed few *Corophium volutator* (sometimes none) and many *Capitella* spp. under mats, whilst the converse is true for mat-free patches (Fig. 2). These small-scale effects have been reproduced on many occasions in numerous undergraduate and postgraduate projects carried out at the University of Aberdeen, and the effects are consistent and predictable, at least for these two taxa.

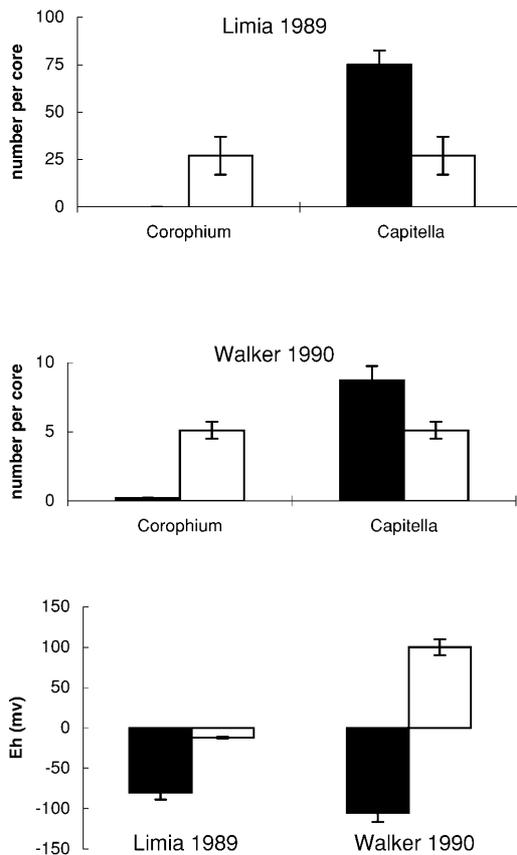


Fig. 2 Mean abundance (7.5 cm diameter corer) of *Corophium volutator* and *Capitella* spp., and redox potential at 4 cm depth, in small-scale patches of sediment covered by macro-algal mats (solid bars; $n=5$ cores) and in algal-free areas (open bars; $n=5$ cores), Newburgh Quay, autumn 1987 (Limia 1989) and summer 1990 (Walker 1990)

A similar pattern of abundance is seen when macro-algae are cleared from large (4 m×4 m) areas from within extensive contiguous mats of *Enteromorpha*. *Corophium* is able to recolonise algal-free areas (Fig. 3), but within a few weeks these individuals are excluded as the mats re-develop (Okora 1989). *Corophium* juveniles can probably disperse widely in the Ythan (Lawrie and Raffaelli 1998) but, if the mats are sufficiently dense (>2–3 kg m⁻² wet weight) so that they generate a hostile sediment environment, or so extensive that recruits have to travel large distances from an unaffected area, then algal-free patches within mats are only slowly recolonised, if at all. This is clearly seen in Fig. 3, where the amount of recolonisation declines with increasing distance of the cleared plot from the nearest source of *Corophium*, an unaffected area of mudflat.

Similarly, if *Chaetomorpha* is experimentally removed during the summer by clipping 0.25 m² plots to prevent mat development, then these algae-free areas have higher *Corophium* densities than in sediments underlying *Chaetomorpha* mats (Fig. 4; Cha, in preparation).

Intensive study at a single site over a long time

Larger-scale evidence of interactions between algal mats and invertebrates comes from one particularly well-documented area of the Ythan (Newburgh Quay), where estimates of *Corophium* have been made over many years in relation to the feeding ecology of shorebirds (Raffaelli et al. 1991). Here, there have been changes in the local population of *Corophium* over time, concomi-

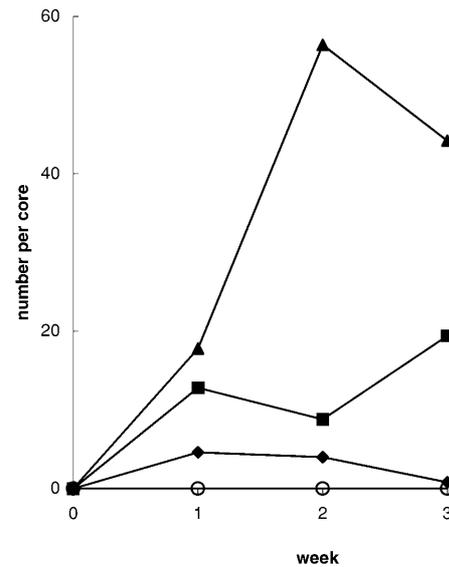


Fig. 3 Recolonisation of *Corophium volutator* in three 16 m² areas cleared within dense extensive algal mats, summer 1989. Solid triangles are nearest to unaffected areas of mudflats (source of *Corophium* recruits) and solid diamonds are furthest away (see text). Open circles are data from an adjacent macro-algal mat (2 kg m⁻² wet weight). Week 0 is 1 June. Data from Okora (1989)

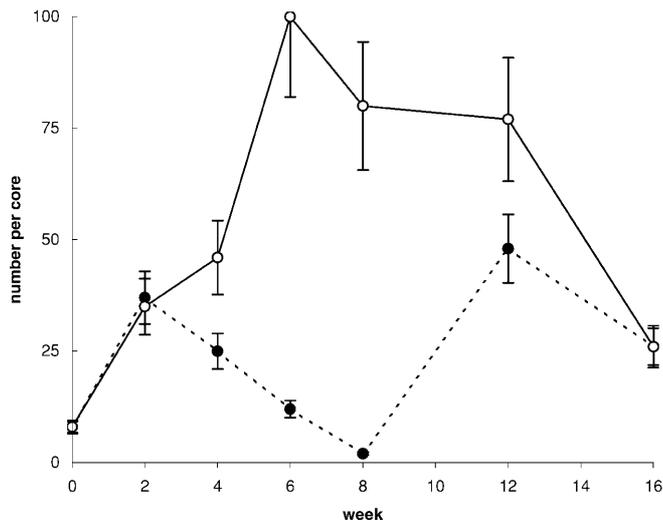


Fig. 4 Mean abundance (7.5 cm diameter corer) of *Corophium volutator* in replicate ($n=6$) 0.25 m² areas on the Sleek of Tarty, Ythan estuary, from which *Chaetomorpha* was regularly clipped at the sediment surface (open circles) and under developing mats of *Chaetomorpha* (solid circles). Week 0=1 May 1994. Data from Cha, in preparation

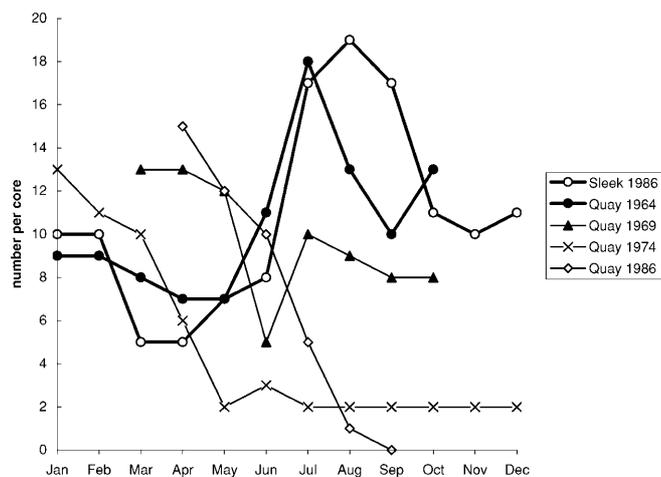


Fig. 5 Seasonal cycle of abundance of *Corophium volutator* at South Quay between 1964 and 1986, when macro-algal biomass was increasing from a few hundred g m⁻² to several kg m⁻², and at the Sleek of Tarty in 1986, at that time relatively unaffected by macro-algae. Data from Raffaelli et al. (1991). Densities scaled to a standard corer size of 7.5 cm diameter

tant with an increase in the biomass of opportunistic green macro-algae at that site (Raffaelli et al. 1989). In the 1960s, when macro-algal biomass was typically a few hundred g m⁻² (dry weight) at this site, the seasonal cycle of abundance of *Corophium* was similar to that observed in areas unaffected by macro-algae, such as the Sleek of Tarty area of the Ythan (Fig. 5). It seems that the normal increase in *Corophium* in the spring has been progressively impacted by the macro-algal bloom which develops at the same time. At low algal biomasses in the 1960s this had little effect on *Corophium*, but at the high

biomasses recorded in the 1980s, *Corophium* is effectively excluded from this site.

Unfortunately, there are few data available for other invertebrate taxa at this location, except for *Hydrobia ulvae*, but these data are difficult to interpret (Shearer 1997). Densities of *Hydrobia* increased dramatically at this site up to the mid-1970s, with a subsequent decline through the 1980s and 1990s. However, the *Hydrobia* data from the 1970s are from studies (Buxton 1975; Green 1977; Joffe 1978) which employed a smaller mesh size (0.5 or 0.25 mm) than those in the 1960s and 1990s, so that these trends may be more apparent than real. Also, Armonies and Hartke (1995) have shown that in the Wadden Sea, hydrographic factors may drive distribution patterns in this species because of its floating habit, so that it may reflect local environmental conditions less well.

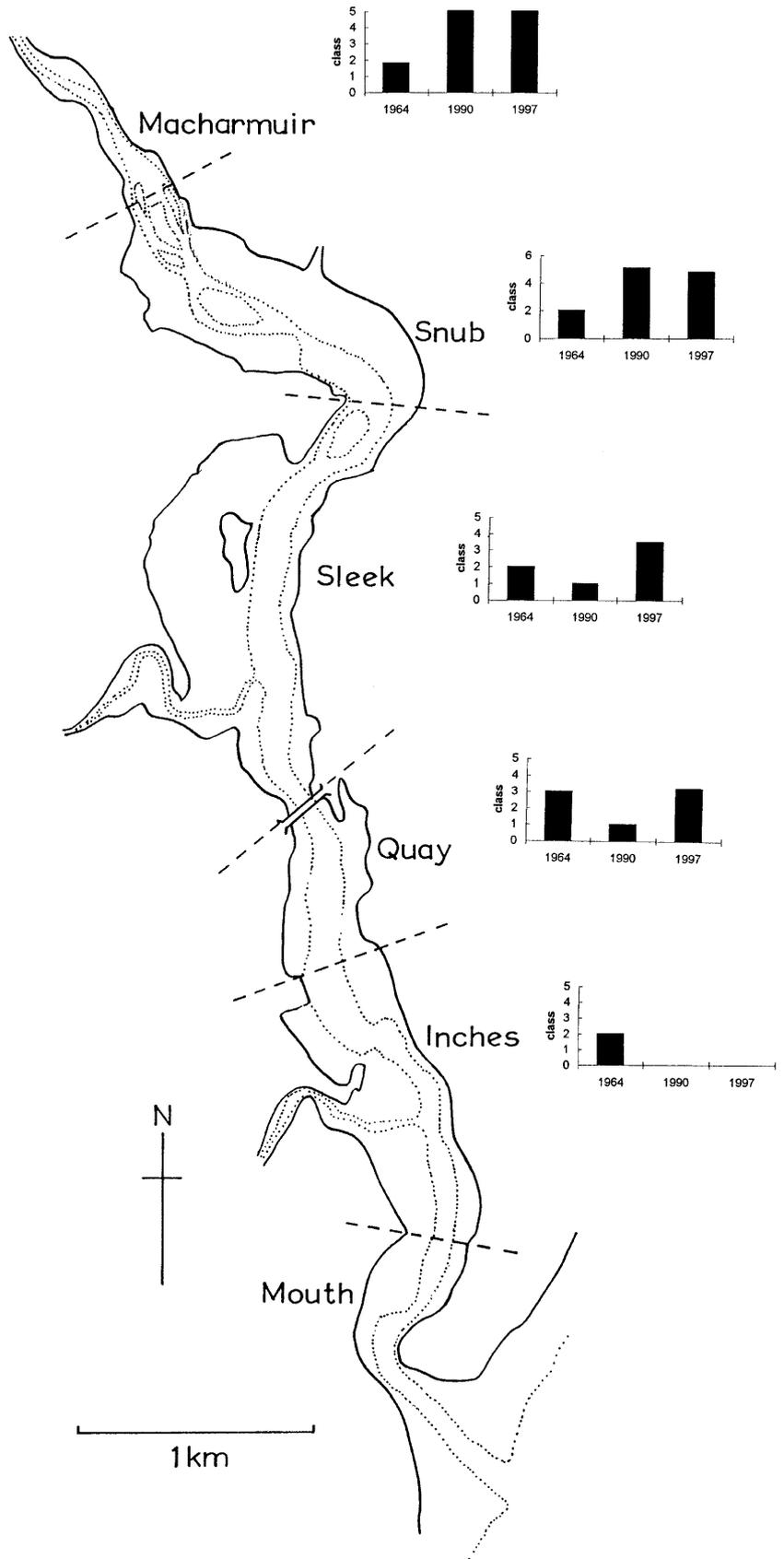
Long-term, estuary-scale changes

Estuary-scale invertebrate data are available for the late winter–early spring period of 1964, 1990 and 1997 (Raffaelli et al. 1999) for *Corophium volutator*, *H. ulvae*, *Macoma balthica* and *Nereis diversicolor*. The 1964 survey was undertaken by Goss-Custard (1966) to provide information on the densities of invertebrates important in the diet of wading shorebirds. At this time macro-algal blooms were not a prominent feature of the estuary (Raffaelli et al. 1999). The 1990 survey represents a period when macro-algal mats (>1 kg m⁻² wet weight) were widespread, covering about 40% of the intertidal area (Fig. 1). It should be noted that the algal biomasses shown in Fig. 1 at upstream locations in the 1990s were not present when the 1990 survey was carried out and, in any case, represent only small biomasses (note scale on y-axis). The 1997 survey was carried out in response to an unusually low macro-algal biomass recorded the previous (1996) summer, probably a result of a major flood event during the 1995–1996 winter (Raffaelli et al. 1999).

Analysis of these three surveys (Fig. 6) reveals: (1) a decline in *Corophium* between 1964 and 1990 in areas of the estuary then affected by macro-algal mats, (2) an increase in *Corophium* between 1964 and 1990 in areas of the estuary (mostly upstream) then not affected by mats, and (3) a recovery in *Corophium* between 1990 and 1997 in those areas (mostly downstream) from which mats had disappeared the previous summer (Fig. 6). *Macoma* and *Nereis* (but not *Hydrobia*) also increased in upstream (unaffected) locations between 1964 and 1990, probably due to an overall increase in the Ythan's productivity (Raffaelli et al. 1999).

The decline of *Corophium* between 1964 and 1990 in areas affected by algal mats is consistent with the results of the small-scale surveys and the long-term trends seen at Newburgh Quay (see above). The low macro-algal biomass in the summer of 1996 was accompanied by an increase in *Corophium* densities the following winter and

Fig. 6 Abundance of *Corophium volutator* in different sections of the Ythan estuary in 1964, 1990 and 1997. Abundances are in classes in order to conform to the initial survey carried out by Goss-Custard (1966), as follows: 1=<14, 2=15-29, 3=30-44, 4=45-59, 5=60-120, 6=>120, individuals per 100 m². Data from Raffaelli et al. (1999).



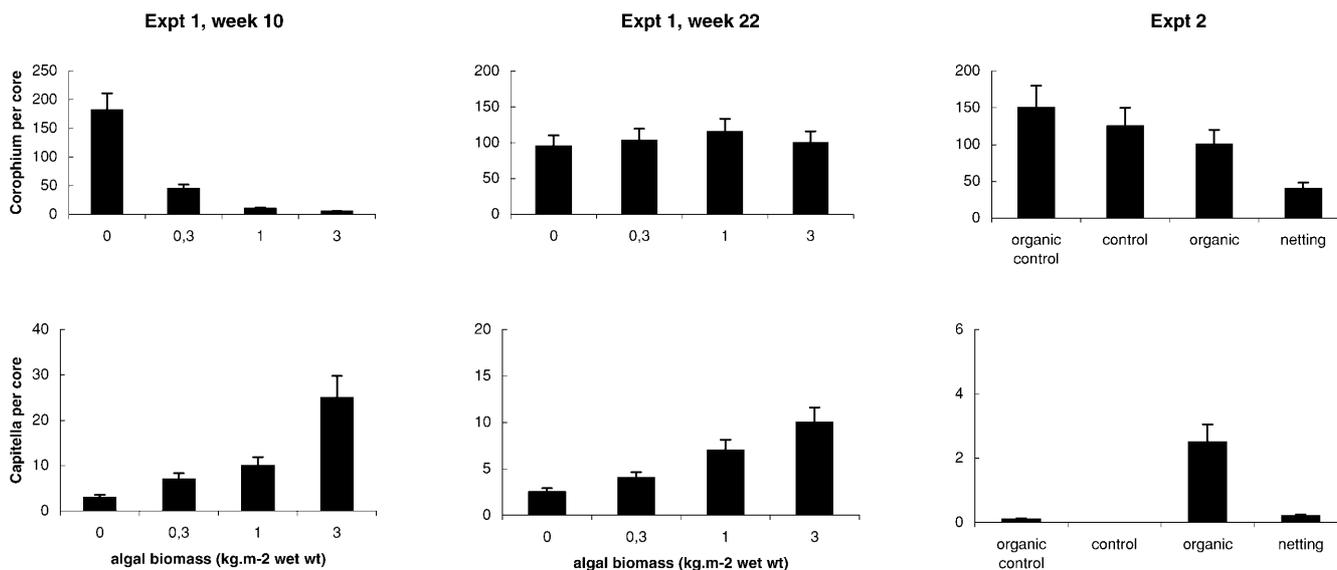


Fig. 7 Abundance of *Corophium volutator* and *Capitella* spp. in two field experiments, Sleek of Tarty, Ythan estuary. In the first experiment, macro-algal biomasses were applied to replicate areas of previously unaffected mudflat and sampled at weeks 10 (left) and 22 (centre). In the second experiment, replicate areas of sediment were treated with organic material (O), fine nylon netting (N), with appropriate controls of undisturbed sediment (C) and sediment treated in the same way as in the organic enrichment treatment (OC). Data from Raffaelli et al. (1998). Corer size was 7.5 cm diameter in both experiments

can be viewed as a natural large-scale experimental test of the hypothesised negative impact of macro-algal mats on this species.

Field experiments

Controlled manipulative experiments at the estuary-scale are not feasible, but such experiments have been performed at an appropriate small-scale by Hull (1987, 1988) and Laurent and Raffaelli (in preparation). In Hull's first experiment (Hull 1987), replicate 5 m² areas of previously unaffected mudflat were dosed with zero, 300 g, 1 kg or 3 kg (wet weight) m⁻² of green macro-algae (mostly *Enteromorpha* spp.) and sampled after 10 and 22 weeks. After 10 weeks, numbers of *Corophium* had declined and numbers of *Capitella* had increased with increasing macro-algal biomass (Fig. 7). By week 22, the macro-algae had been removed from the experimental plots by attrition, wave action and burial and *Corophium* recovered, whilst densities of *Capitella* remained high in the high biomass plots (Fig. 7). On the basis of these results, Hull (1987) suggested that the effect of macro-algal mats on *Corophium* is mostly physical, the algal filaments interfering with the normal deposit-feeding behaviour of *Corophium* at the sediment-water interface. In contrast, the effects on *Capitella* are probably due to an enrichment of the sediment, which persisted even when the surface macro-algal material was removed.

To test these propositions, Hull carried out a second experiment where the physical and enrichment effects were separated by applying inert nylon filaments to the sediment surface or adding finely-ground dried *Enteromorpha* (Hull 1988; Raffaelli et al. 1991). As predicted, *Corophium* abundance was significantly affected by the nylon filaments but not by enrichment, whilst *Capitella* increased only in the enrichment treatment (Fig. 7). The responses of other species in these experiments were inconsistent, but have been discussed elsewhere (Raffaelli et al. 1998).

In summary, small-scale studies, long-term intensive and extensive surveys and controlled manipulative experiments all provide compelling evidence that macro-algal mats have pronounced negative effects on *Corophium volutator*. This species occurs in the diets of many shorebirds, fish and epibenthic crustacean predators on the Ythan (Hall and Raffaelli 1991) and its decline over large areas (40%) of the intertidal flats is of concern. Restoring *Corophium* populations in the Ythan will require measures targeted at macro-algal mats. These mats comprise at least three genera *Enteromorpha*, *Ulva* and *Chaetomorpha* and probably many species. The estuary-scale data on long-term trends in macro-algal mats (Fig. 1) probably confounds all three genera, since these cannot be distinguished on the aerial photographs and they were unlikely to be separated in the biomass estimates made at Newburgh Quay between the 1960s and 1980s. It is also likely that the mats used in the field experiments described above were a mixture of different species.

Ulva, *Enteromorpha* and *Chaetomorpha* might be expected to have different impacts on invertebrate assemblages because of the gross differences in their growth form and ecology. On the Ythan, *Ulva* is only loosely associated with the sediment surface, sometimes simply lifting off the surface with the tide. *Ulva* tends to be more abundant in the upper reaches of the estuary, reaching peak abundance in late summer-early autumn

Fig. 8 Seasonal changes in the mean ($n=5$ quadrats) biomass (dry weight per 0.25 m²) of main green macro-algal genera at different sites on the Ythan estuary (2=downstream, 7=upstream), over the summer of 1998

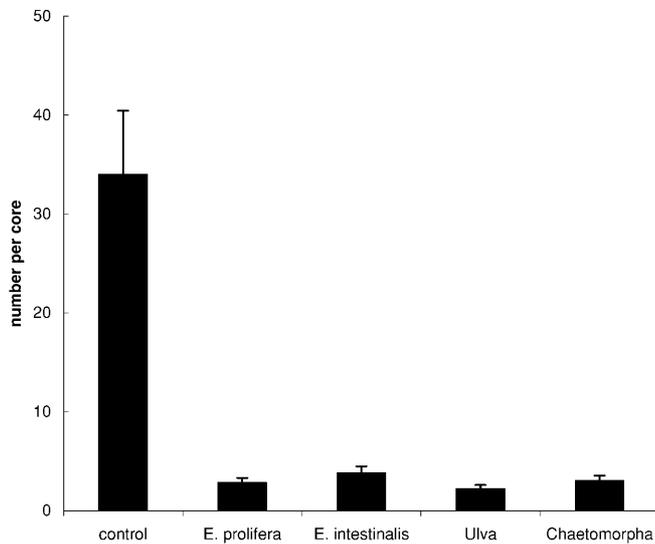
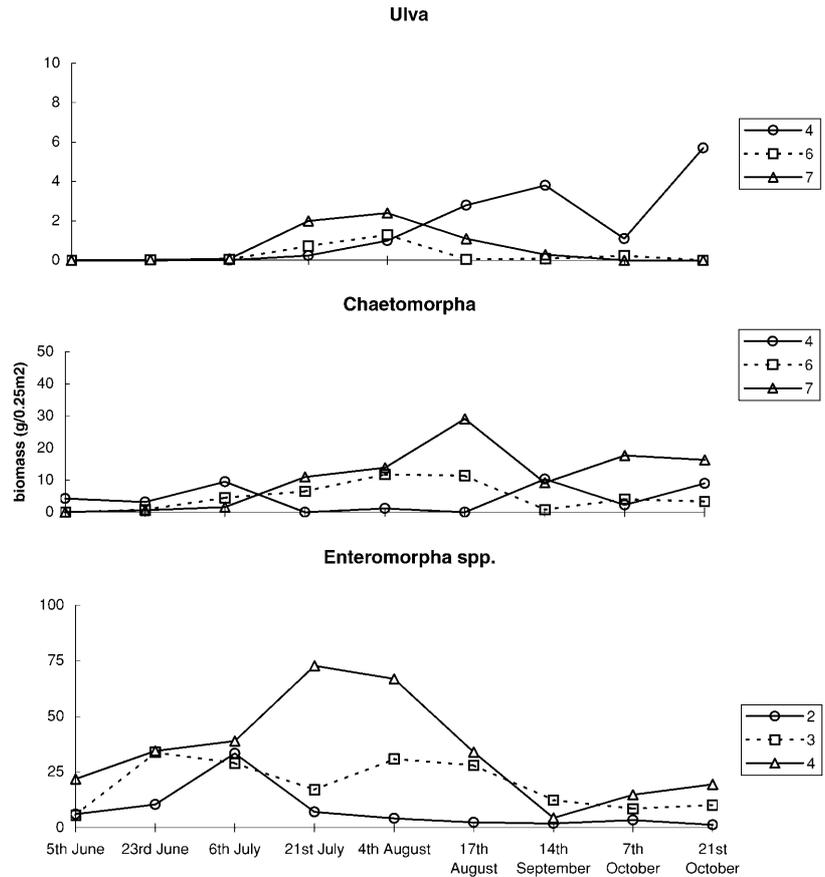


Fig. 9 Abundance of *Corophium volutator* after 6 weeks under equivalent biomasses (1 kg m⁻² wet weight) of different algal taxa, and in algal-free controls, autumn 1997, Tarty Burn, Ythan estuary. Data from Laurent and Raffaelli, in preparation

(Fig. 8). In contrast, *Chaetomorpha* is intimately associated with the sediment, often creating a dense matrix of filaments extending several cm beneath the surface. *Chaetomorpha* is characteristic of the middle and upper reaches of the estuary and blooms somewhat earlier than

Ulva, in mid-summer (Fig. 8). *Enteromorpha* is widespread in the lower and middle reaches of the Ythan and is often anchored in the mud so that it also forms a dense filamentous matrix. There are probably several (undetermined) species of *Enteromorpha* on the Ythan (Rebecca Taylor, personal communication), which reach peak biomass at different times of the year (Fig. 8).

Given their different ecologies, it is possible that these three macro-algal genera will have different effects on invertebrate populations. Laurent and Raffaelli (in preparation) tested this hypothesis in a manipulative field experiment whereby mats of biomass 1 kg m⁻² (wet weight) of *Ulva*, *Chaetomorpha* and two “species” of *Enteromorpha* were applied to replicate areas of mudflat. The effects on *Corophium* were similar for all three algal taxa – a dramatic decline in abundance (Fig. 9). The effects on other species will be discussed elsewhere (Laurent and Raffaelli, in preparation).

Effects of invertebrates on macro-algae

All three genera of green macro-algae on the Ythan have a range of invertebrate consumers (Hall and Raffaelli 1991), and Green (1977) estimated that *H. ulvae* alone consumed 5–10% of the standing crop of *Enteromorpha*. Field experiments set up in early summer comprising replicate cages containing either 500 *Hydrobia* 100 cm⁻² or no *Hydrobia*, found no effect on *Enteromorpha* bio-

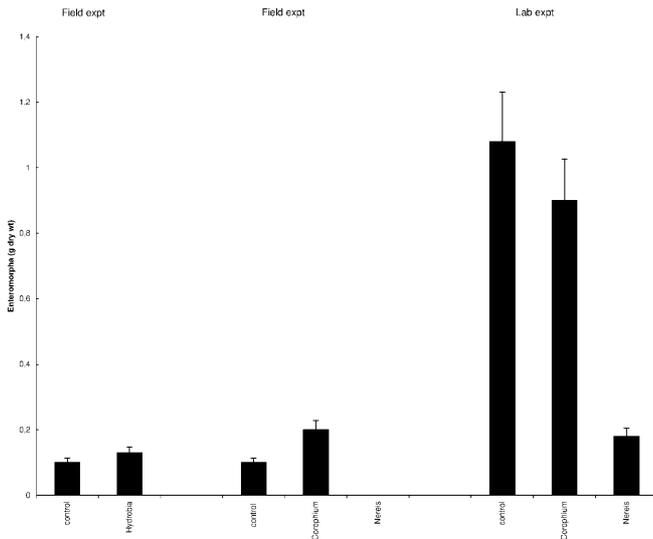


Fig. 10 Effects of *Hydrobia ulvae*, *Corophium volutator* and *Nereis diversicolor* on *Enteromorpha* biomass from field and laboratory experiments. In the field experiments, invertebrates were maintained in replicate ($n=5$) 10 cm diameter corers sunk to 10 cm depth and roofed with a 500 μ m mesh. The laboratory experiments were carried out using replicate ($n=4$) jars (8 cm diameter, 7 cm deep) for each treatment, half-filled with natural azoic sediment and topped with estuary water which was aerated. The field experiments ran for 5 weeks and the laboratory experiment for 16 days. Data from Shearer (1997) and Ventura (1997)



Fig. 11 Incidence of germlings of *Enteromorpha* on live ($n=50$, each site) and dead ($n=50$, each site) shells of *Hydrobia ulvae*. Large snails are >4 mm in shell height and small shells <4 mm. Macharmuir supports little macro-algae, whilst Inches regularly experiences algal blooms (see Fig. 1). Dead shells were aged according to their physical appearance. Data from Shearer (1977)

mass after 5 weeks (Fig. 10). Wilhelmssen and Reise (1994) similarly concluded that grazing by *Littorina littorea* is unlikely to control the development of macro-algal mats in the Wadden Sea. A similar experiment to assess the impact of *Corophium* (250 per 100cm²) and

Nereis (10 per 100 cm²) on the development of an *Enteromorpha* bloom in early summer (Ventura 1997) showed an effect of *Nereis* but not of *Corophium* (Fig. 10). These interactions were confirmed in laboratory experiments where *Enteromorpha* filaments were added to containers with either *Nereis* or *Corophium* (densities as above) or neither (Fig. 10). Here again, *Nereis* had a significant effect on above-ground algal biomass.

In the Wadden Sea, *Hydrobia* may play a positive role in the development of macro-algal mats by providing a suitable substrate for settlement and germination (Schories and Reise 1993). Live *Hydrobia* were collected from two areas on the Ythan during the summer from two sites: one with a long history of macro-algal blooms (Inches) and a second site (Macharmuir) where macro-algae are rare or absent (Shearer 1997). These data showed that large (>4 mm height) shells have a higher incidence of germling *Enteromorpha* than smaller shells, but the site which regularly experiences algal blooms had a lower incidence of fouling (Fig. 11), contrary to expectations.

Dead *Hydrobia* shells accumulate in large drifts in the middle section of the estuary (Sleek of Tarty), probably due to local circulation effects (Armonies and Hartke 1995). Examination of these shells also showed a significant number with germlings (Fig. 11), with proportionately more on recently dead shells (cf. Schories and Reise 1993). Most fouled shells only had one germling, with a maximum of six on some dead shells (Shearer 1997).

Reise (1983) argued that burrowing polychaetes might have a positive effect on the development of algal mats in the Wadden Sea, by anchoring filaments in the burrows. In the laboratory experiments described above, algal filaments were found attached up to 3.5 cm deep in the sediment in the *Nereis* treatment, the deeper filaments intertwined and glued together with mucus (Ventura 1997). There was no anchorage of filaments in the *Corophium* treatment.

Conclusions

Interactions between macro-algal mats and sediment invertebrates are complex and reciprocal. There is evidence from the Ythan that shells of *Hydrobia* could facilitate the recruitment of *Enteromorpha*, and *Nereis* draws algal filaments into its burrow, presumably in order to feed in safety. Neither *Hydrobia* nor *Corophium* had any effect on the *Enteromorpha* standing crop, but there was evidence for less above-ground algal biomass when *Nereis* was present. Although the mechanisms underlying the negative effects of *Nereis* are not well understood, it is possible that such interactions might explain in part the low abundance of macro-algae in the upper reaches of the estuary, where *Nereis* is most abundant. However, the most dramatic interaction documented on the Ythan is the negative impact of macro-algal

mats on *Corophium*, which seems to be independent of the algal species comprising the mats. Given the high occurrence of *Corophium* in the diets of the Ythan's consumers, it is vital that efforts are made to reduce the impact of macro-algal blooms in this estuary so that the conservation status that the Ythan presently enjoys may continue.

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