

Effects of the green macroalga *Enteromorpha intestinalis* on macrobenthic and seagrass assemblages in a shallow coastal estuary

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ABSTRACT: A common symptom of eutrophication in temperate estuaries is the proliferation of ephemeral, floating macroalgae. Information on the effects of blooms on underlying assemblages mostly originates from non-vegetated intertidal and subtidal habitats. Blooms also often settle in large aggregations over seagrasses, where they decompose. To test hypotheses concerning the effect of dense mats on underlying assemblages of benthic invertebrates within a seagrass meadow, biomass of the green macroalga *Enteromorpha intestinalis* was experimentally manipulated in the Tuggerah Lakes estuary, New South Wales, Australia. Algae, equivalent to a naturally occurring bloom (~4.5 kg wet wt m⁻²), were added to caged plots (1 m²) at 2 sites in the seagrass meadow. After 3 mo, the *E. intestinalis* population began to decompose in the treatment plots and in shallow habitats adjacent to the foreshore. Dramatic declines in the biomass of seagrass and components of the infauna were detected in plots containing decomposing macroalgae. The results have implications for managing estuaries, since assemblages of seagrasses and macrobenthic organisms are considered to be important in nutrient-cycling and food-webs.

KEY WORDS: Macroalgae · Bloom · Seagrass · Macrobenthos · Eutrophication

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INTRODUCTION

There is much interest in the effect of excessive growth or 'blooms' of unattached macroalgae in estuarine systems worldwide. Blooms of these algae occur naturally in estuaries, but have increased in their frequency, magnitude and persistence in many areas, particularly in shallow systems with limited tidal exchange (Raffaelli et al. 1998). These changes are thought to be a symptom of eutrophication (Lavery et al. 1991, Sfriso et al. 1992, Kinney & Roman 1998, Raffaelli et al. 1998). Information on the effects of blooms to underlying assemblages originates mainly from studies on non-vegetated intertidal (Hull 1987, Bolam et al. 2000) or subtidal (Thrush 1986, Ólafsson

1988, Everett 1994, Norkko & Bonsdorff 1996a) habitats. Declines in seagrass in some estuaries are also thought to be related to blooms of opportunistic macroalgae (Williams Cowper 1978, Shepherd et al. 1989, Holmquist 1997, Raffaelli et al. 1998).

Seagrass meadows commonly support more diverse and abundant assemblages of fauna than do the surrounding areas of unvegetated sediments (Orth 1973, Stoner 1980, Peterson 1982, Edgar 1990, Ferrell & Bell 1991, Boström & Bonsdorff 1997). One explanation for this pattern is that the physical structure of seagrass modifies the local environment relative to surrounding areas, by increasing complexity important to fauna (e.g. Edgar & Robertson 1992), reducing water-movement (Gambi et al. 1990, Boström & Bonsdorff

2000), trapping sediments, larvae and food (Grady 1981, Peterson et al. 1984, Boström & Bonsdorff 2000) and providing protection from predators (Peterson 1982, Boström et al. 2002). Increasing loss and fragmentation of seagrass habitat is causing growing concern, as it is considered to be of great importance for the ecology and productivity of coastal waters (Orth et al. 1984, Anderson 1989, Edgar et al. 1994, Edgar & Shaw 1995, Boström & Bonsdorff 2000).

Unattached macroalgae make important contributions to the structural complexity of seagrass meadows. Clumps of macroalgae often contain large numbers of fauna and can facilitate their dispersal as they are propelled across the landscape by water-currents (Holmquist 1994, Brooks & Bell 2001). Holmquist (1994) showed that drift macroalgae (25 cm in diameter) were efficient transporters of several species of molluscs, decapods, ophiuroids and fishes, sometimes moving up to 0.5 km in a day. This would effectively decrease the degree of isolation between fragments of seagrass within a landscape, particularly for fauna lacking planktonic larval stages (Holmquist 1994, 1998, Brooks & Bell 2001). Any positive contribution that drifting clumps may make to seagrass communities can, however, be offset if the algae coalesce into large, stationary mats (Holmquist 1994). In a related study, Isaksson & Pihl (1992) observed a reduction in the total abundance and biomass of epibenthic fauna in response to heavy overgrowth of seagrass by filamentous algae. Moreover, future blooms often develop, once bloom-forming algae become established at a site (Raffaelli et al. 1998).

Manipulative experiments by Holmquist (1997) and Hauxwell et al. (2001) demonstrated that overlying clumps of macroalgae can create sizeable gaps in a seagrass canopy. Recovery of seagrasses after a disturbance is often slow (Holmquist 1997, Butler & Jernakoff 1999, Hauxwell et al. 2001). Whilst the algae can provide an alternative structure for many fauna, species of drift macroalgae are often ephemeral (i.e. persisting for months; Virnstein & Carbonara 1985, Sogard & Able 1991, Holmquist 1997). Changes in the availability and spatial distribution of the seagrass habitat ultimately affect the structure and function of the seagrass landscape (Stamps et al. 1987, Wiens 1992, Boström & Bonsdorff 2000, Brooks & Bell 2001). Disturbances that affect the distribution of the seagrass habitat can greatly affect associated fauna (Heck & Thoman 1981, Worthington et al. 1991, Doak et al. 1992, Skilleter 1994, Holmquist 1997, Eggleston et al. 1999, Boström & Bonsdorff 2000).

In addition to destroying the primary habitat of the majority of seagrass-associated species, the decomposition of clumps can alter the physical characteristics of the underlying sediments. The handful of studies that

have directly examined the effects of such events on animals associated with seagrasses have focused on mobile fauna (e.g. Holmquist 1997). Results from studies examining the effects of decomposing algae on assemblages of benthic macroinvertebrates in unvegetated habitats have been equivocal. A number of factors may be attributed to the differences in responses: differences in biomass or species composition of macroalgae, hydrological regimes, characteristics of the sediments, and in the spatial and temporal scales examined (Raffaelli et al. 1998). For example, breakdown of small amounts of macroalgal material may stimulate production of many deposit-feeders, but larger amounts may reduce oxygen concentrations and cause migration or mortality (Hull 1987, Norkko & Bonsdorff 1996a, Hansen & Kristensen 1997). Consequently, studies examining their specific effects on seagrass and associated fauna are required.

Herein we expand on this topic by quantifying the effects of large stationary clumps of macroalgae on assemblages in a seagrass meadow near Sydney, Australia. Based on observations from the literature and in the field, we hypothesised that the formation and subsequent decomposition of persistent clumps of macroalgae cause decreases in the biomass of the underlying seagrasses and alter the structure of assemblages of benthic macroinvertebrates. Specifically, we hypothesised that small-scale experimental 'blooms' would have similar effects, and tested this by applying bloom-sized densities of the drift species *Enteromorpha intestinalis* to experimental plots in a seagrass meadow. *E. intestinalis* was chosen because it was abundant at the time of the study, and because it is a common bloom forming species in Australia and worldwide (King & Hodgson 1995, Raffaelli et al. 1998). Seagrass and infauna in plots to which algae were added and those in control plots were sampled after 3 mo, i.e. after the *E. intestinalis* population had begun to decompose on the surface.

MATERIALS AND METHODS

Location. The study was done in a seagrass meadow in the Tuggerah Lakes estuary on the central coast of New South Wales, Australia (Fig. 1). The estuary has a surface area of 75 km² and is open to the sea at the entrance via a narrow channel, which allows limited (<1%) tidal exchange and a tidal amplitude of approx. 0.1 m (King & Hodgson 1995, Roberts 2001). The sediments vary between sandy mud (50 to 95% mud) and muddy sand (5 to 50% mud; Roberts 2001). Massive and persistent (i.e. over a period of months) blooms of drift macroalgae, usually of the genera *Enteromorpha*, *Chaetomorpha* and *Cladophora* (class Chlorophyta)



Fig. 1. Tuggerah Lakes estuary, central coast of New South Wales, Australia

are common in several areas, often developing rapidly and then settling over seagrass meadows or accumulating along the foreshore, where they decompose (King & Hodgson 1995, Roberts 2001).

At the time of the study, the seagrass meadow was composed of *Halophila ovalis* (R. Brown), *Zostera capricorni* (Ascherson) and *Ruppia megacarpa* (Mason) ($63 \pm 10\%$, $21 \pm 8\%$ and $16 \pm 6\%$ of the total biomass, respectively; $n = 10$). Interspersed amongst the seagrasses were *Chondria succulenta* (J. Agardh) Falkenberg, *Chaetomorpha linum* (O. F. Müller) Kützing, *Microdictyon umbilicatum* (Vellay) Zanardini, *Enteromorpha intestinalis* and *Gracilaria edulis* (Gmelin) Silva in very low densities (<5 g wet wt m^{-2}). A dense band (approximately 15 to 20 m wide) of *E. intestinalis* was present in the shallow (<20 cm) unvegetated area adjacent to the shoreline.

Experimental design. To test the hypotheses that small-scale experimental 'blooms' would cause declines in the biomass of the underlying seagrasses and alter the structure of assemblages of benthic macroinvertebrates, bloom-sized densities of *Enteromorpha intestinalis* were applied to experimental plots in a seagrass meadow. To secure the macroalgae, wire mesh was used to fence off plots (1 × 1 m and 0.9 m high) within the seagrass meadow. The 1.5 × 1.5 cm mesh-size of the wire was small enough to retain the macroalgae, but sufficiently large to ensure that water circulation was not restricted significantly. The bottom edges of

each fence were raised to 10 cm above the substratum, allowing macrobenthic organisms to move in and out of the plots. Plots were chosen randomly within 2 sites (each approx. 25 × 20 m, and 50 m apart) located 100 m from the shore at a depth of 0.5 to 1.0 m. To test for possible confounding effects of the fences, various procedural controls were used. The experiment involved 4 treatments: (1) algal addition (AA), whereby *E. intestinalis* was added to fenced plots; (2) untouched controls (UC), which were undisturbed areas haphazardly chosen in the seagrass meadow; (3) a fenced control (FC), whereby panels were removed to allow animals such as fishes free access, thus controlling for the effect of the fenced structures (no algae were added); (4) an exclusion control (EC), whereby fences were intact, to control for the effect of the fenced structures and the exclusion of movement of animals in and out (no algae were added).

There were 5 replicates of each treatment (AA, UC, FC, EC) at each site. *Enteromorpha intestinalis* was collected from nearshore areas and added to AA plots in August 1999, at a weight and cover equivalent to those in seagrasses in some areas in the estuary or equivalent to those close to the shore at the study location (a 15 cm thick algal mat ~ 4.5 kg wet wt m^{-2} or ~ 0.45 kg dry wt m^{-2} , respectively). Large numbers of the hydrobiid gastropod *Potamopyrgus antipodarum* (Gray) and species of epifaunal amphipods and isopods were present in the algae added to the plots. These animals were not removed, since dispersal of benthic organisms via clumps of drift macroalgae occurs naturally (Holmquist 1994) and it was considered important to disturb the algae as little as possible.

The sites were visited weekly to assess the condition and cover of the macroalgae in each of the AA treatment plots and to ensure that the fenced structures had not trapped drift algae. Structural breakdown of the *Enteromorpha intestinalis* population began in experimental plots and adjacent to the foreshore after 11 wk. The plots were left for a further week, during which breakdown of the algae occurred rapidly, and then sampled using a corer (10 cm diameter, 10 cm deep). We collected 1 core sample from the centre (to avoid possible edge effects) of each of the replicate treatment (AA, UC, FC, EC) plots at each site. Samples were collected by carefully penetrating the plant material and sediment with the corer, which was then capped to create sufficient suction to retain the sample. Samples were sieved through a 0.5 mm mesh, placed into labelled plastic bags, fixed with 7% buffered formalin/seawater (v/v), and then sorted under a binocular microscope. Above-ground parts of seagrasses were sorted to species and oven-dried to a constant weight at 105°C for 48 h prior to weighing to the nearest 0.01 g. Polychaetes were identified and

enumerated as families, bivalves and gastropods were identified to species. Other faunal groups counted were oligochaetes, infaunal amphipods, nemertean, platyhelminths and anthozoans. Warwick (1988), James et al. (1995) and Chapman (1998) found that, whilst analyses at family level were weighted by the pattern of the most abundant species of benthic fauna, similar patterns in assemblages occurred irrespective of the level of taxonomic resolution used, justifying the use of taxonomic levels higher than species for some organisms in our study.

Data analysis. The PRIMER software package (Plymouth Marine Laboratory) was used to test hypotheses about multivariate differences among assemblages of macrofauna. Nonmetric multidimensional scaling (nMDS) ordinations of all replicates were plotted based on non-transformed abundances and Bray–Curtis similarities; 1-way analyses of similarities (ANOSIM; Clarke & Warwick 1994) tested for differences in the structure of assemblages among treatments within each site. The percentage contributions of taxa to dissimilarities between pairs of treatments within sites were calculated using the SIMPER program (Clarke & Warwick 1994). Differences in abundances of selected variables collected from core samples were tested by 2-factor analyses of variance. Treatment (4 levels) was fixed and site (2 levels) was random. Data were examined for het-

erogeneity of variances using Cochran's C-test and means were compared by Student-Newman-Keuls (SNK) tests.

RESULTS

Following cover by *Enteromorpha intestinalis* for almost 3 mo and then rapid breakdown of the algae, there were considerable differences in the rank abundance of major taxonomic groups between algal addition (AA) and control (UC, FC, EC) treatments (Table 1). Polychaetes were most abundant in control plots, whilst gastropods were numerically dominant in plots to which macroalgae had been added (Table 1). Larger taxa or deeper burrowing forms, such as orbinid polychaetes, the bivalve *Tellina deltoidalis* Lamarck and the gastropod *Batillaria australis* (Quoy & Gaimard), were present in small numbers in control plots, but were generally absent from AA plots. The vertical sediment profiles of core samples collected from AA treatment plots were black to a few centimetres below the surface and had a strong hydrogen sulphide odour typical of anoxic sediments. Mean (\pm SE; n = 5) biomass estimates (g dry wt core⁻¹) of *E. intestinalis* collected from core samples at each of the 2 sites were 0.92 (\pm 0.41) and 0.94 (\pm 0.41), respectively.

Table 1. Percentage (mean \pm SE; n = 5 plots) of different macrofaunal taxa in experimental plots at each site. AA: algal addition; UC: untouched control; FC: fenced control; EC: exclusion control

Taxon	Site 1				Site 2			
	AA	UC	FC	EC	AA	UC	FC	EC
Polychaetes	14 \pm 5	54 \pm 5	43 \pm 4	44 \pm 6	20 \pm 17	71 \pm 3	47 \pm 7	57 \pm 4
Gastropods	72 \pm 8	13 \pm 3	35 \pm 5	29 \pm 10	73 \pm 19	11 \pm 1	27 \pm 7	13 \pm 3
Bivalves	10 \pm 3	19 \pm 5	13 \pm 4	14 \pm 7	5 \pm 2	12 \pm 2	12 \pm 4	19 \pm 1
Crustaceans	1 \pm 1	12 \pm 4	7 \pm 2	10 \pm 3	<1 \pm 0	5 \pm 1	11 \pm 2	9 \pm 2
Other	3 \pm 2	2 \pm 1	2 \pm 1	2 \pm 1	1 \pm 1	1 \pm 0	3 \pm 1	3 \pm 1

Table 2. Summary of mean Bray–Curtis dissimilarity values (untransformed data) and results of ANOSIM tests of differences in structure of assemblages of macrobenthic organisms among treatments within each site. Abbreviations as in Table 1. ns: not significant; *significant at p < 0.05; **significant at p < 0.01

	Site 1				Site 2			
	AA	UC	FC	EC	AA	UC	FC	EC
Within samples	50	37	35	47	66	30	37	31
Between samples								
AA		67**	50*	57*		82*	74*	81*
UC			41 _{ns}	42 _{ns}			38 _{ns}	33 _{ns}
FC				38 _{ns}				35 _{ns}

Multivariate analysis

The macrofauna assemblages differed significantly between AA and control treatments UC, FC, EC at each site (ANOSIM; Table 2). Pairwise comparisons revealed no significant differences among the control treatments at either site (Table 2), indicating no effects of the experimental procedure on infauna. This pattern was illustrated by a 2-dimensional ordination plot (nMDS; Fig. 2a).

There appeared to be greater variability in the structure of assemblages among AA plots than among replicate control plots (see Fig. 2a). Warwick & Clarke (1993) proposed that disturbance increases variation in assemblages at different spatial scales, although Chapman et al. (1995) found the opposite. To test formally the hypothesis that addition of algae significantly altered the variability in assemblages among replicates, Bray–Curtis measures of dissimilarity were calcu-

Table 3. Summary of SIMPER analyses indicating rank (1 to 5 presented only) and percentage contributions (in parentheses) of taxa to dissimilarities between pairs of treatments within each site (1 = taxon that contributed most to difference). Abbreviations as in Table 1. –: no data

Taxon	Site 1						Site 2					
	AA vs UC	AA vs FC	AA vs EC	UC vs FC	UC vs EC	FC vs EC	AA vs UC	AA vs FC	AA vs EC	UC vs FC	UC vs EC	FC vs EC
Polychaetes												
Capitellidae	4 (8)	3 (13)	2 (11)	3 (14)	4 (14)	2 (15)	3 (12)	2 (11)	3 (11)	3 (15)	3 (13)	4 (15)
Nereididae	–	–	–	–	–	–	–	–	–	–	–	5 (7)
Opheliidae	2 (11)	2 (15)	3 (10)	4 (11)	3 (14)	4 (14)	2 (12)	3 (7)	2 (12)	2 (23)	1 (26)	2 (21)
Amphipods												
Infaunal amphipods	5 (7)	5 (6)	4 (7)	5 (8)	5 (9)	5 (7)	–	4 (6)	5 (5)	4 (11)	5 (10)	–
Gastropods												
<i>Potamopyrgus antipodarum</i>	1 (49)	1 (46)	1 (54)	1 (35)	1 (24)	1 (36)	1 (63)	1 (64)	1 (57)	1 (28)	4 (14)	1 (21)
Bivalves												
<i>Arthritica helmsi</i>	3 (9)	4 (8)	5 (6)	2 (15)	2 (19)	3 (14)	4 (3)	5 (5)	4 (7)	5 (9)	2 (19)	3 (17)

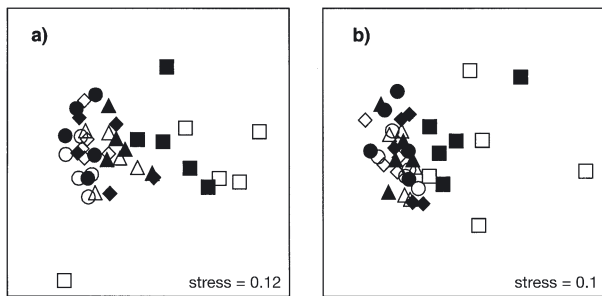


Fig. 2. Non-metric multidimensional scaling (nMDS) ordination of (a) all taxa and (b) all taxa excluding gastropod *Potamopyrgus antipodarum*, based on non-transformed abundances and Bray–Curtis similarities (n = 5 cores). Squares: algal addition; circles: untouched control; triangles: fenced control; diamonds: exclusion control; closed symbols: Site 1; open symbols: Site 2

siderably smaller in AA plots than in control plots. *P. antipodarum* also contributed to dissimilarities among control treatments, due to it being consistently more abundant in FC and EC plots than in UC plots at both sites, possibly indicating that the snails were attracted to the caged structures, or that the cages provided some protection from predation. The percentage contributions of taxa ranked as contributing most to dissimilarities among control treatments were relatively small, either because most taxa had similar densities or because they were sparse and patchy (Table 3). Given the relatively great importance of *P. antipodarum* in differences among treatments, and that it was probably introduced into the habitat with the algae, assemblages were analysed without the data for this snail. The results were essentially the same as those achieved when the snail was included (Fig. 2b; Table 4).

lated between 2 pairs of replicates from each treatment for each site (see Underwood & Chapman 1998). This gave n = 2 independent measures of percentage dissimilarity. There was no significant (ns) difference in variability among each of the 4 treatments ($F = 0.57$ ns, $df = 3, 3, p < 0.05$). Although there were few replicates, the lack of significance probably reflects no difference, rather than being a lack of power, since variation among treatments was not much larger than the variation among samples.

Dissimilarities among treatments were due primarily to differences in the relative abundances of taxa rather than the presence or absence of specific taxa (SIMPER; Table 3). *Potamopyrgus antipodarum* contributed most to differences between AA plots and control plots; the abundances of all other ranked species were con-

Populations analysis

The biomass of the seagrass was drastically reduced in plots to which macroalgae had been added compared to control plots at each site (AA < UC, EC, FC; Fig. 3;

Table 4. Summary of mean Bray–Curtis dissimilarity values (untransformed data) and results of ANOSIM tests of differences in structure of assemblages of macrobenthic organisms among treatments within each site, with *Potamopyrgus antipodarum* omitted. Further details as in Table 2

	Site 1				Site 2			
	AA	UC	FC	EC	AA	UC	FC	EC
Within samples	52	40	37	44	68	30	36	31
Between samples								
AA		59*	57*	53 _{ns}		67**	66**	71**
UC			36 _{ns}	41 _{ns}			34 _{ns}	34 _{ns}
FC				37 _{ns}				34 _{ns}

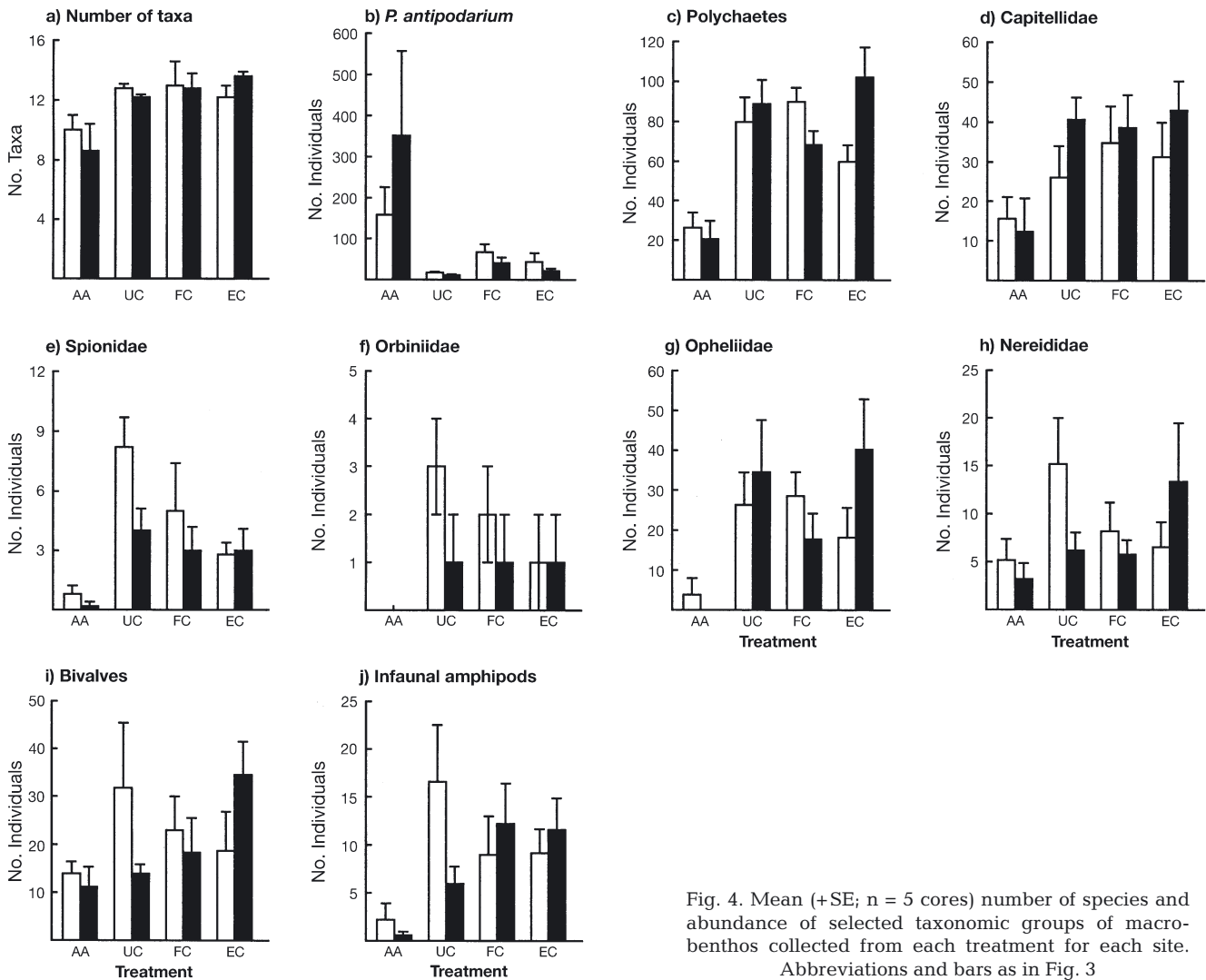


Fig. 4. Mean (+SE; n = 5 cores) number of species and abundance of selected taxonomic groups of macrobenthos collected from each treatment for each site. Abbreviations and bars as in Fig. 3

most diverse and abundant infauna in the various controls, but were considerably less abundant in plots to which algae had been added. Generally, larger taxa and deeper burrowing forms, including orbinid worms, the bivalve *Tellina deltoidalis*, the snail *Batillaria australis* and infaunal amphipods, appeared to have been eliminated from plots to which algae had been added. In contrast, the small (3 to 5 mm) epifaunal gastropod *Potamopyrgus antipodarium* was very abundant. These important effects occurred despite the small spatial scale (1 × 1 m² plots) and relatively short duration (3 mo) of the experiment.

Multivariate comparison revealed that the macrofauna assemblage of plots to which algae had been added differed distinctly from those in the various controls, mainly due to the relative abundances of a few species. *Potamopyrgus antipodarium* contributed most to dissimilarities, being present in greater numbers in plots to which algae had been added; however these

gastropods may have been directly introduced with the algae. When Hull (1987) added *Enteromorpha* spp. to experimental plots, he recorded increased numbers of *Hydrobia ulvae*, but cautioned that greater abundances could have been due to addition of snails associated with the algae: hydrobiid snails commonly inhabit clumps of drift macroalgae (Soulsby et al. 1982, Hull 1987, Norkko & Bonsdorff 1996a, Bolam et al. 2000, Norkko et al. 2000), and decomposition of the algae can directly and indirectly provide an abundant food supply for these deposit-feeding snails (see Levinton & Bianchi 1981, Levinton 1985).

In this study, few dead snails were found, suggesting that individuals transported with the macroalgae were able to avoid anoxic conditions. The abundance of hydrobiid snails can rapidly decline if conditions become anoxic (Norkko & Bonsdorff 1996a). For example, Norkko & Bonsdorff (1996a) measured massive declines in the abundance of *Hydrobia* spp. in re-

sponse to sediments being covered by macroalgae, whereas snails increased significantly in abundance in experimental compared to control plots within 5 d of the algae being removed. These authors suggested that the major source of colonisers was from surrounding areas, although they also found large numbers within the algal mat itself (Norkko & Bonsdorff 1996a). In a later experiment, Norkko et al. (2000) demonstrated that *Hydrobia* spp. were capable of moving up through the algal canopy to escape anoxic conditions. The apparent addition of snails to assemblages of fauna in plots to which algae had been added emphasises the potential role of drift macroalgae in contributing to colonisation of sediments (see Holmquist 1994, 1997).

Analysis of assemblages omitting data from *Potamopyrgus antipodarum* revealed differences among algal addition and control treatments that were essentially the same as those when the snail's data were included. Thus, the treatment effect was not solely due to distribution patterns of this snail. Opheliid and capitellid worms also considerably influenced assemblages structure. Opheliids were patchily distributed among replicate samples, but massive declines were recorded under the algal canopy. Capitellid worms were significantly less abundant in plots to which algae had been added, in contrast to studies which recorded increases in abundance of capitellids after addition of macroalgae (e.g. Thrush 1986, Hull 1987, Bolam et al. 2000) and other forms of organic enrichment (Pearson & Rosenberg 1978).

There are several reasons why one might expect capitellid worms to respond negatively to macroalgae. Generally, the densities of macroalgae added in this experiment were greater than those in the experiments cited above and are likely to have caused extreme anoxic conditions. Dramatic declines in capitellid populations have been observed after severe anoxic conditions have developed in sediments (Tsutsumi 1990). Moreover, the experimental plots in the present study were within a seagrass meadow, and it is well known that seagrass canopies can substantially reduce flow velocities in comparison to that in adjacent areas of unvegetated sediment (Scoffin 1970, Fonseca et al. 1982, 1983, Eckman 1987, Worcester 1995, Boström & Bonsdorff 2000). Reduced flow velocities could result in greater oxygen deficiency and longer burial of organisms by decomposing algae.

The declines in the abundance of tellinid bivalves and surface-feeding worms (e.g. spionids) after addition of macroalgae were broadly consistent with the results of several other studies (e.g. Ólafsson 1988, Everett 1994, Norkko & Bonsdorff 1996a). In contrast, Hull (1987) reported increases in tellinid abundance, after macroalgae addition, although most of the indi-

viduals he recorded were juveniles. He suggested that the positive results were largely due to algae enhancing the settlement of larval recruits by reducing flow velocities (Hull 1987). As sediments become more anoxic, larger adults are forced to migrate towards the sediment surface, where they are at greater risk of predation (Perkins & Abbot 1972, Norkko & Bonsdorff 1996a). Physical interference with feeding behaviour has also been implicated as an important mechanism causing migration of bivalves (Norkko & Bonsdorff 1996b) and spionid worms (Everett 1994) in areas covered by macroalgae. In the present study, the canopy of macroalgae was in close proximity to the sediment surface, so it is possible that its physical presence in addition to anoxic conditions contributed to declines in components of the benthic fauna.

Declines in above-ground biomass of seagrass were also recorded by Holmquist (1997) and Hauxwell et al. (2001) in response to macroalgae cover. Holmquist (1994, 1997) found that small (0.25 m diameter), mobile patches of macroalgae added structural complexity to seagrass meadows, but that large (1 m diameter) stationary patches eliminated underlying seagrasses after 6 mo. Hauxwell et al. (2001) manipulated the canopy height of macroalgae over plots (1 m diameter) of seagrass, and measured significant declines in above-ground summer production when the algal canopy height was greater than 9 to 12 cm. They attributed declines in density, recruitment, growth-rate and production of the seagrass to reduced light, hypoxic conditions and potentially toxic concentrations of ammonium (Hauxwell et al. 2001).

At the scale of this experiment, the local effects of cover by macroalgae were catastrophic. Although clonal plants, such as seagrasses, are considered to have adapted to dynamic environments (Caraco & Kelly 1991), recovery after disturbance can be slow (Holmquist 1997, Butler & Jernakoff 1999, Hauxwell et al. 2001). Even 18 mo after removing macroalgae, Holmquist (1997) measured significantly smaller biomass in experimental than in control plots. Whilst large patches of macroalgae can support a greater diversity and abundance of demersal organisms than the less structurally complex seagrass, these benefits are likely to be offset by their ephemerality and the negative effects of decomposition (Holmquist 1997). Few studies have directly examined the consequences of fragmentation of the seagrass habitat, but related studies have shown that changed sizes of patches and spacing between patches of seagrass may subsequently influence the dispersal of animals (Worthington et al. 1991, Doak et al. 1992, Eggleston et al. 1999) and the distribution, abundance and foraging behaviour of predators (Heck & Thoman 1981, Heck & Wilson 1987, Skilleter 1994).

In the present study, it was not possible to determine whether the decline in diversity and abundance of benthic infauna was due to migration from plots to which algae had been added or to mortality. The experimental plots were relatively small, so declines in diversity and abundance may have been due to emigration rather than mortality. Animals may have been able to seek refuge in adjacent patches of habitat. Their ability to survive in this manner could have significant implications in terms of the overall effect of a bloom. If a bloom of algae occurs as small clumps of plants dispersed throughout a seagrass meadow as opposed to an extensive mat, then organisms that are negatively affected could persist by moving into patches between algae-affected areas (Raffaelli et al. 1998). The remnant patches without algae could provide source populations for re-establishment in disturbed sediments. Thus, persistence of the assemblage would be less dependent on a supply of larvae from other habitats.

In a review, Raffaelli et al. (1998) stated that it is still unclear whether there is a direct relationship between increases in macroalgae abundance and concomitant declines in seagrass beds in estuaries around the world. Moreover, few published studies have investigated the effects on assemblages of macrobenthic organisms in seagrass meadows. Through experimental manipulation of the biomass of *Enteromorpha intestinalis*, this study has demonstrated that overlying mats of macroalgae can cause sizeable gaps in the seagrass canopy. Components of the infauna responded negatively to factors associated with cover and decomposition of the macroalgae, but large numbers of hydrobiid snails (probably introduced together with the algae) were found. Thus, aggregations of drift macroalgae can greatly influence the patterns of distribution and abundance of seagrass and associated fauna. Assemblages of seagrasses generally support greater diversity and abundance of fauna than adjacent areas of unvegetated sediments, so the formation of blooms and subsequent declines in the components of seagrass meadows could have considerable implications for productivity at larger scales. The present study provides quantitative information on changes in assemblages at the small spatial scale relevant to some blooms in the seagrass habitat. Further work is needed to determine the underlying mechanisms and the integrated causes and effects on the scale of an estuary. Quantification of temporal changes and potential rates of recovery of the benthic community is also essential.

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