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The impact of infauna (*Nereis diversicolor* and *Saduria entomon*) on the redistribution and biomass of macroalgae on marine soft bottoms

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Abstract

Mass occurrence of macroalgae is a phenomenon attributed to eutrophication, and can lead to drastic changes in the benthic communities on soft bottoms. While the negative effects of macroalgal blooms on the macrozoobenthos have been studied extensively, the effects of the infauna on the macroalgal material have not previously been studied in the northern Baltic Sea. The impact of the infaunal species *Nereis diversicolor* and *Saduria entomon* on the burial and biomass of *Enteromorpha* spp., *Cladophora glomerata* and *Fucus vesiculosus*, was assessed through a series of microcosm experiments. Results show that *S. entomon* did not significantly affect the biomass of the algae, nor actively relocate them. *N. diversicolor* redistributed the filamentous green algae into the sediment, down to 4 cm at most, and decreased the biomass of the filamentous algae by 140–360%. Furthermore, the loss of biomass promoted in presence of polychaetes proved to be a density dependent process. The effect on the perennial macroalgal species, *F. vesiculosus*, was less clear, as no redistribution or significant change in macroalgal biomass was observed. Our findings show that infauna can contribute to a loss in macroalgal biomass through feeding and burrowing activities leading to the redistribution and incorporation of the detritus into bioturbated sediment.
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1. Introduction

One of the effects of elevated nutrient levels is mass development of annual macroalgae (Schramm and Nienhuis, 1996), which has been reported from several coastal areas around the world (Bonsdorff, 1992; Fletcher, 1996; Valiela et al., 1997; Raffaelli et al., 1998; Pihl et al., 1999; Bäck et al., 2000; Vahteri et al., 2000; Nelson et al., 2003). Intermediate amounts of

benthic drift algae increase the habitat complexity of the otherwise bare soft bottoms (Norkko, 1997; Raffaelli et al., 1998) and offer the fauna alternative resources (Norkko et al., 2000; Salovius et al., 2005), which enable relatively high species and interaction diversity (Norkko, 1997). It is under such conditions, i.e. before the algal mats induce highly unfavourable conditions, that benthic invertebrates are most likely to be able to utilize the extra organic material (Raffaelli, 2000).

In their review, Raffaelli et al. (1998) list several species of grazers that often occur in high abundances in association with macroalgal mats; gastropods, amphipods, shrimps and polychaetes, which are suggested

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to be able to modify macroalgal blooms by preventing the establishment, reducing the intensity, or accelerating the decline of the bloom. Infauna, such as members of the family Nereidae, Oligochaeta, *Capitella capitata* Fabricius, as well as epifaunal gammarids have been shown to increase in abundance under macroalgal mats (Norkko and Bonsdorff, 1996a,b; Bolam et al., 2000; Raffaelli, 2000; Rossi and Underwood, 2002). Studies performed on intertidal flats have revealed some organisms to be able to affect the biomasses of attached algal assemblages. Raffaelli (2000) reported of *Nereis* (syn. *Hediste*) *diversicolor* O.F. Müller decreasing the aboveground biomass of *Enteromorpha* sp. through bioturbation and grazing, as did Hughes (1999). *Corophium volutator* Pallas, commonly found on the tidal flats, did not, however, affect the green algae (Hughes, 1999; Raffaelli, 2000), nor did *Hydrobia ulvae* Pennant (Raffaelli, 2000).

While the detrimental effects of macroalgal mats on the benthic macrofauna have been thoroughly examined in the northern Baltic Sea (Ólafsson, 1988; Bonsdorff, 1992; Bonsdorff et al., 1995; Norkko and Bonsdorff, 1996a,b,c), the beneficial effects on the infauna have not been as rigorously studied in this area. Thus, the aim of this paper is to assess whether the infauna can gain from the occurrence of macroalgae, i.e. extra organic material, and thereby harbours a potential to affect the biomass of macroalgae on marine soft bottoms in the brackish northern Baltic Sea.

2. Methods

To evaluate the impact of infauna on macroalgae on marine soft bottoms, a series of microcosm experiments in a laboratory environment were conducted in the summer of 2003. The four experiments focused on the links between the infaunal species *Nereis diversicolor* O.F. Müller and *Saduria entomon* L., and the algae *Fucus vesiculosus* L., *Cladophora glomerata* (L.) Kützing and *Enteromorpha* spp.

2.1. Test organisms

N. diversicolor (Polychaeta, Phyllodocida) occurs in marine and brackish waters in the North Temperate Zone (Smith, 1977). *N. diversicolor* is one of the largest (up to 10 cm) and one of the most commonly occurring polychaetes on the shallow soft bottoms of the Åland Islands (Bonsdorff, 1981; Perus and Bonsdorff, 2004). The polychaete is an active predator on crustaceans, other polychaetes, insect larvae and bivalves (Fauchald and Jumars, 1979; Reise, 1985; Rönn et al., 1988)

N. diversicolor shows considerable versatility in feeding and is truly omnivorous as it also functions as a suspension feeder (Riisgård, 1991), deposit feeder and herbivore (Fauchald and Jumars, 1979; Olivier et al., 1995). *N. diversicolor* is euryhaline and eurytherm and is also tolerant to hypoxia, anoxia and hydrogen sulphide (Theede et al., 1973; Vismann, 1990). The polychaetes were collected with an Ekman–Birge grab at 1–2 m depth in a shallow bay in the inner archipelago. The samples were sieved (≤500 μm) in the field and intact, adult (≥3 cm in size) *N. diversicolor* specimens were brought back to the laboratory. The polychaetes were kept in 11 l glass aquaria with mud–sand sediment. The aquaria were oxygenated through air bubbling. The polychaetes were fed crushed mussels and phytoplankton while stored.

S. entomon (Crustacea, Isopoda) is a glacial relict species in the Baltic Sea, where it occurs throughout the depth range and can grow up to about 9 cm (Haahtela, 1990). *S. entomon* is an omnivorous scavenger (Green, 1957) and functions as a key invertebrate predator and community regulator (Sandberg and Bonsdorff, 1990). The isopod feeds on bivalves, crustaceans and polychaetes (Sandberg, 1996) as well as carrion and conspecifics (Green, 1957; Leonardsson, 1991). *S. entomon* is highly tolerant to hypoxia, anoxia and hydrogen sulphide (Hagerman and Szaniawska, 1990; Vismann, 1991). Traps baited with fish were used for catching *S. entomon* at about 10 m depth in the outer archipelago of the NW Åland Islands. The isopods were kept in 11 l glass aquaria with sand as sediment, and were fed pieces of fish. The aquaria were oxygenated through air bubbling.

The experiments were conducted with annual, filamentous green macroalgae, *Enteromorpha* and *C. glomerata*, as well as a perennial, leathery species belonging to the brown algae, *F. vesiculosus*. At least six species of *Enteromorpha* occur in the Baltic Sea; *E. intestinalis*, *E. compressa*, *E. clathrata*, *E. flexuosa*, *E. procera* and *E. prolifera*. Identification to species level is difficult due to large differences within species and small differences between species (Tolstoy and Österlund, 2003). The macroalgae were collected by hand in the upper littoral zone in the outer archipelago, NW Åland Islands.

2.2. The experimental set-up

In experiment 1, the impact of *N. diversicolor* and *S. entomon* on the biomass of *Enteromorpha* was investigated. The experiment consisted of three treatments: (1) a control without invertebrates, which enables mea-

surement of any autogenous changes in macroalgal biomass; (2) a *Nereis* treatment; and (3) a *Saduria* treatment. In addition to measuring the changes in *Enteromorpha* biomass, samples were taken in three replicates of the algae, the sediment and *N. diversicolor* in order to measure the carbon and nitrogen content in these. This was complemented with a control treatment containing only *N. diversicolor* and sediment. Samples of *N. diversicolor* consisted of intact polychaete specimens. The contribution of *N. diversicolor* to a loss in biomass of *Enteromorpha* was further investigated by comparing the impact of different of densities of polychaetes (experiment 2). Apart from the control, the treatments consisted of densities of *N. diversicolor* ranging from 35 to 345 ind m^{-2}. Experiment 3 examined the changes in *C. glomerata* biomass in the presence of infauna, which was then repeated with *F. vesiculosus* (experiment 4, see Table 1 for abundances and densities). The densities of infauna used in this study correspond to natural densities observed in the field. *N. diversicolor* occurs along the entire Finnish coastline and is common at depths <20 m, although specimens can be found down to 50 m depth. The densities vary from 1 to more than 1500 ind m^{-2} (Bonsdorff et al., in prep.). The densities of 300 *N. diversicolor* m^{-2} used in this study correspond to values found under algal net bags simulating drifting algae in the field (Norkko and Bonsdorff, 1996c). The isopod *S. entomon* was used in densities corresponding to 100 ind m^{-2}, which is higher than the average natural densities recorded. However, *S. entomon* shows a patchy distribution, with high densities on occasion (Haahtela, 1990). The amounts of algal material used correspond to low amounts frequently observed in the field (Holmström, 1998; Berglund et al., 2003).

The experimental set-up was a flow-through system where filtered (≤25 μm) seawater was led to the aquaria through silicon tubes perforated with needles. Small plastic aquaria (100 cm^2; 0.75 l) were used. In the density dependency experiment, larger plastic aquaria (289 cm^2; 3.0 l) were used. A net (≤500 μm) prevented the organisms to escape through the outlet. The sediment in the experimental aquaria consisted of 50% dried, sieved (≤500 μm) sand and 50% frozen (−18 °C, 48 h), sieved (≤500 μm) mud. The mud–sand mixture had an organic content of 1.7%. The depth of the sediment in the aquaria was 4 cm. Two containers were used, into which the replicates were randomly placed for stabilization of the temperature. Each experiment ran for 7 days. Samples for analysis of carbon and nitrogen content were frozen (−18 °C) prior to

freeze-drying (−70 °C). The samples were analyzed at Umeå Marine Sciences Centre, Umeå University, Sweden. The light conditions followed normal diurnal rhythm and periodicity. The hydrographical conditions (oxygen, salinity, pH, temperature) were analyzed at least every second day. Samples for analysis of total phosphorus, nitrogen and chlorophyll-*a* were taken from the incoming water at the beginning and termination of the experiment.

The wet weight of the infauna was measured by placing the individuals on a paper towel before weighing. The fauna was checked for anomalies under a dissection microscope and no individuals carrying eggs were included in the experiments, since these individuals may differ in behaviour. The infauna was randomly placed into the experimental aquaria without food for 48 h in order to acclimatize to the experimental conditions before the trial started. Before the experiment started, the algae were carefully rinsed with seawater and associated fauna and epiphytes were removed under a dissection microscope. Excess water was gently squeezed out of the algae, which were then patted with paper towels. The wet weight of the algae was measured before and after the experiment. Equal amounts of algae were randomly placed in the aquaria. As the experiment was terminated, the water and eventual loose lying algae were poured into a sieve (500 μm) and rinsed free of any sediment with filtered (25 μm) seawater. This was followed by placement of the hose into the aquarium, which gently allowed the sediment to resuspend and run through the sieve. Fragmented algal fronds and the polychaetes were thereby retained in the sieve, after which they were rinsed free from any particles smaller than 500 μm.

2.3. Data analysis

The experimental set-up was a one-way ANOVA design with treatment as fixed factor and change in macroalgal biomass as dependent variable. The material was tested for normality (Kolmogorov–Smirnov test) and for homogeneity of variances (Levene's test) prior to analysis. When normality or homogeneity of variances was not obtained even with transformation, Kruskal–Wallis' non-parametrical test was used. Replicates containing animals that died or shed skin during the experiment were excluded from statistical analysis, since it is likely that individuals that are dying or shedding skin are showing differing behaviour. Infaunal biomasses were analyzed with paired *t*-test or Wilcoxon signed ranks test, when assumptions of normality and/or homogeneity of variances could not be met. All

Table 1
Summary table showing the experimental set-ups, treatments and densities

Experiment	Species	Treatment	Volume of aquaria l	n of ind replicate^{-1}	Abunbance ind m^{-2}	n of replicates[a]	Algal amount ww g repl^{-1}	Algal amount ww g ind^{-1}	Algal density ww g m^{-2}	Algal density dw g m^{-2}
1	*Enteromorpha* spp.	Control	0.75	–	–	6	3	–	300	28
	Nereis diversicolor	*Nereis*	0.75	3	300	4	3	1.0	300	28
	Saduria entomon	*Saduria*	0.75	1	100	4	3	3.0	300	28
	Nereis diversicolor	*Nereis* control	0.75	3	300	3	–	–	–	–
2	*Entermorpha* spp.	Control	3.0	–	–	5	5	–	170	20
	Nereis diversicolor	*Nereis* 35	3.0	1	35	5	5	5.0	170	20
	Nereis diversicolor	*Nereis* 105	3.0	3	105	5	5	1.5	170	20
	Nereis diversicolor	*Nereis* 210	3.0	6	210	5	5	0.8	170	20
	Nereis diversicolor	*Nereis* 345	3.0	10	345	5	5	0.5	170	20
3	*Cladophora glomerata*	Control	0.75	–	–	6	3	–	300	39
	Nereis diversicolor	*Nereis*	0.75	3	300	6	3	1.0	300	39
	Saduria entomon	*Saduria*	0.75	1	100	5	3	3.0	300	39
4	*Fucus vesiculosus*	Control	0.75	–	–	6	1.5	–	150	50
	Nereis diversicolor	*Nereis*	0.75	3	300	6	1.5	0.5	150	50
	Saduria entomon	*Saduria*	0.75	1	100	6	105	105	150	50

[a] The initial n of replicates were 6 in exp. 1 and 3 prior to exclusion of differing replicates due to low survival of or moulting in the animals.

values are presented as mean $\pm$ standard error. The carbon and nitrogen values represent percentage of sample.

3. Results

3.1. Experiment 1. The infaunal impact on the biomass of Enteromorpha spp.

During experiment 1 infauna died in two replicates belonging to both the *Nereis* treatment and the *Saduria* treatment. The number of replicates in these treatments was thus reduced to four as the differing replicates were excluded from analysis. The overall survival rate was $75.0\% \pm 11.7\%$. During the experiment, no significant changes occurred in individual weight for any of the infaunal species in algal treatments. However, in the *Nereis*-control containing only polychaetes and sediment, a highly significant reduction in the weight of the polychaetes was noted (Wilcoxon, $p < 0.001$).

When placed into the experimental aquaria, the infauna rapidly burrowed into the sediment. *N. diversicolor* responded quickly when filamentous algae were added to the aquaria and emerged at the sediment surface in order to pull algal filaments down into the burrows. *N. diversicolor* actively and consistently incorporated *Enteromorpha* into the sediment. The one-way ANOVA shows a clear difference in change in macroalgal biomass between the treatments (Table 2). The *Enteromorpha* biomass decreased significantly more in the *Nereis* treatment compared to the control (ANOVA, Bonferroni, $p = 0.001$) (Fig. 1). About one third of the *Enteromorpha* biomass remained in the *Nereis* treatment at the termination of the experiment, which constitutes a loss in biomass almost four times greater (360%) than in the control.

There was no significant decrease in *Enteromorpha* biomass in the presence of *S. entomon* even though the reduction was 140% greater compared to the control (Fig. 1). The infaunal treatments differed significantly from each other (ANOVA, Bonferroni, $p = 0.031$). Due to the burrowing activities of *S. entomon*, the sediment resuspended and covered the algae. The algae in infaunal treatments were thus in closer contact with the sediment than algae in the control. The sediment beneath the algae was darker, indicating oxygen consumption during a possible decomposition of the algae. Furthermore, the algae were noticeably more fragmented in presence of infauna.

The different components of the experiment (*Enteromorpha*, *N. diversicolor*, sediment) were sampled for

Table 2
One-way ANOVA results from Experiment 1: the infaunal impact on the biomass of *Enteromorpha* spp.

	df	MS	F	p
Decrease in *Enteromorpha* spp. biomass				
Between groups	2	3.389	15.177	**0.001**
Within groups	11	0.224		
Total	13			
C:N				
Enteromorpha spp.$^{\diamond}$				
Between groups	2	0.022	5.663	**0.042**
Within groups	6	0.004		
Total	8			
N. diversicolor				
Between groups	1	0.027	0.822	0.517
Within groups	4	0.022		
Total	5			
Sediment				
Between groups	3	0.242	1.189	0.337
Within groups	8	0.294		
Total	11			
C				
Enteromorpha spp.				
Between groups	2	27.129	15.911	**0.004**
Within groups	6	1.705		
Total	8			
N. diversicolor				
Between groups	1	1.55	0.049	0.835
Within groups	4	31.373		
Total	5			
N				
Enteromorpha spp.				
Between groups	2	0.127	0.998	0.422
Within groups	6	0.127		
Total	8			
N. diversicolor				
Between groups	1	0.531	0.258	0.638
Within groups	4	2.056		
Total	5			

Significant values presented in bold.
$^{\diamond}$ = the values were transformed $\log(x + 1)$ in order to obtain homogenous variances.

measurement of carbon and nitrogen content. The initial value for *N. diversicolor* was omitted from statistical analysis due to complications during preparation of samples. The one-way ANOVA showed no significant difference in C:N-ratio for *N. diversicolor* between treatment and control at the termination of the experiment (Table 2, Fig. 2). No significant changes were noted from the initial values of the sediment or between treatment and control at the termination of the experiment. *Enteromorpha*, however, showed a significant decrease in C:N-ratio from the initial value of 17.65 ± 2.48 to 11.92 ± 0.77 in the treatment and 12.28 ± 0.33 in the control (ANOVA, $p = 0.042$). The post hoc analysis could not, however, reveal between which two treatments the difference occurred. On the
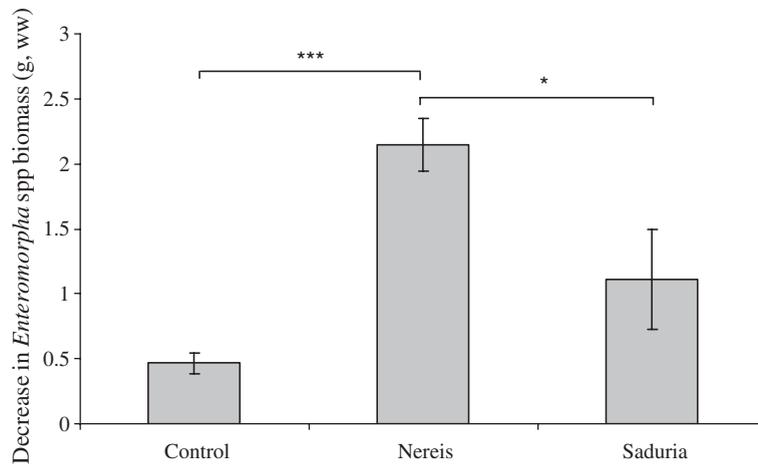
Fig. 1. Decrease in *Enteromorpha* biomass in the different treatments (mean ± SE). Significant differences occurred between treatments (ANOVA, Bonferroni, ***=$p \leq 0.001$, *=$p \leq 0.05$).

other hand, it is clear that the reduction is due to diminished carbon amounts (Table 2). While the nitrogen content of the algae remained at the same level throughout the experiment, the carbon content decreased significantly (ANOVA, Bonferroni, $p=0.008$) from the initial values.

The hydrographical conditions during experiment 1 (Table 3) did not differ significantly between treatments (ANOVA, $p>0.05$). At the beginning of the experiment, the following values were measured: total phosphorous 24.7 μg l^{-1}, total nitrogen 595.5 μg l^{-1} and chlorophyll-*a* 2.5 μg l^{-1}. At the termination of the experiment the corresponding values were 36.4, 369.3 and 4.9 μg l^{-1}.

3.2. Experiment 2. Density dependent impact of N. diversicolor on Enteromorpha spp.

All treatments had an infaunal survival rate of 100% and no replicates were excluded from the statistical analysis. According to the Wilcoxon signed ranks test, the polychaetes showed a significant increase in wet weight during the trial ($p=0.002$). When looking at the different treatments separately, however, the only significant increase to be found is in the treatment representing 210 ind m^{-2} ($p=0.043$). *N. diversicolor* redistributed *Enteromorpha* into the sediment as in the previous experiment. The maximum depth recorded was 4 cm. Clear differences emerged in macroalgal
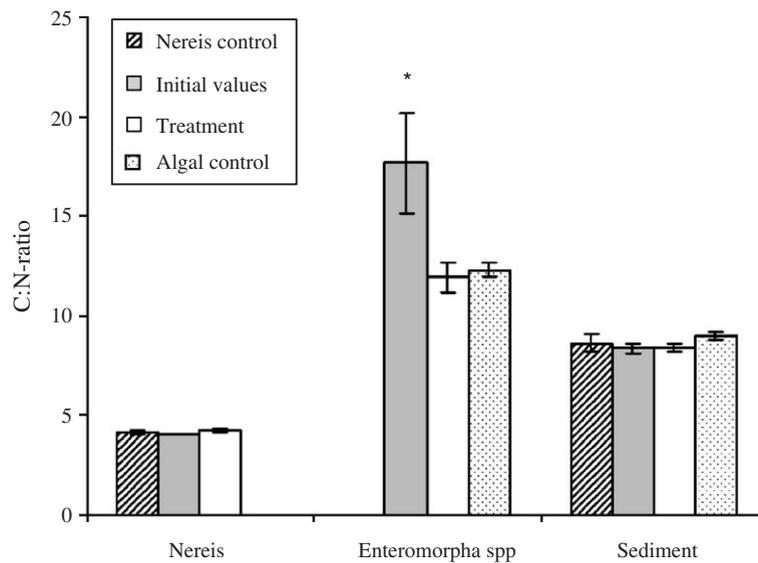

Fig. 2. C:N-ratio in *N. diversicolor*, *Enteromorpha* and the sediment (mean ± SE). The C:N-ratio of *Enteromorpha* decreased significantly from the initial value (ANOVA, Bonferroni, *=$p \leq 0.05$).

Table 3
Hydrographical conditions in experiment 1: the infaunal impact on the biomass of *Enteromorpha* spp.

	Control	*Nereis*	*Saduria*	*Nereis* control
Oxygen, %				
$x \pm SE$	82.0 ± 3.5	78.3 ± 2.2	76.5 ± 0.9	80.6 ± 3.1
min–max	$78.4 - 88.1$	$72.3 - 82.2$	$74.0 - 78.4$	$74.4 - 84.2$
Salinity, psu				
$x \pm SE$	5.25 ± 0.03	5.37 ± 0.06	5.22 ± 0.05	5.18 ± 0.05
min–max	$5.16 - 5.39$	$5.18 - 5.46$	$5.14 - 5.42$	$5.13 - 5.22$
pH				
$x \pm SE$	8.10 ± 0.03	8.00 ± 0.08	8.03 ± 0.02	8.10 ± 0.04
min–max	$8.01 - 8.15$	$7.91 - 8.08$	$8.01 - 8.06$	$8.03 - 8.14$
Temperature, °C				
$x \pm SE$	21.7 ± 0.6	22.0 ± 0.7	21.8 ± 0.7	21.7 ± 0.9
min–max	$20.0 - 23.0$	$20.0 - 23.0$	$20.0 - 23.0$	$20.0 - 23.0$

biomass loss between the treatments (Table 4, Fig. 3). A considerably greater diminution of *Enteromorpha* occurred in the treatments with higher densities of polychaetes than the treatment with the lowest density. The control differed significantly from the treatments representing densities of 210 and 345 ind m^{-2} (ANOVA, Scheffe, $p = 0.001$) as well as the treatment representing a density of 105 ind m^{-2} (ANOVA, Scheffe, $p = 0.002$). The treatment with the lowest density, 35 ind m^{-2}, did not, however, differ from the control, indicating a density dependent threshold at which the infaunal impact is noticeable. The lowest density treatment differed from the higher densities with an increasing significance (ANOVA, Scheffe, $p = 0.037$, $p = 0.002$, $p = 0.001$). No significant differences occurred between the treatments with highest densities (105–345 ind m^{-2}) and thus the infaunal impact seemed to level off at these densities. Nonetheless, *N. diversicolor* continued to increase the loss of biomass in these treatments by 50–60% compared to the control.

Differences in oxygen levels arose during the experiment (Table 5). The levels varied between 29.2% and 84.7% oxygen saturation. The lowest levels, 29.2% and 31.8%, were recorded in the treatment representing 105 ind m^{-2} and in the control. The other treatments showed at least 50% oxygen saturation. No significant differences in hydrography between treatments were noted. The measured levels of total phosphorous and total nitrogen were 39.3 and 776.3 µg l^{-1} at the beginning of the experiment, and 42.1 and 369.3 µg l^{-1} at the termination of the experiment.

3.3. Experiment 3. The infaunal impact on the biomass of C. glomerata

All organisms were recovered alive at the termination of the experiment. One *S. entomon*, however, had shed skin, and this replicate was excluded from the statistical analysis. No significant changes occurred in individual weight for any of the infaunal species during the experiment. The results from the experiment with *C. glomerata* are almost identical with those obtained from the first experiment with *Enteromorpha*. Again, the amount of remaining macroalgal material differed between the treatments (Table 6, Fig. 4) and the significantly largest decrease was observed in the *Nereis* treatment (ANOVA, Bonferroni, $p < 0.001$). The decrease of *C. glomerata* was 140% greater in the presence of *N. diversicolor* and 50% in the presence of *S. entomon*, though the change in the *Saduria* treatment was non-significant. As in the experiments with *Enteromorpha*, the polychaetes buried *C. glomerata* into the sediment, while the burrowing activities of *S. entomon* caused the sediment to resuspend and cover the algae.

The hydrographical conditions in the aquaria were relatively stable throughout the experiment (Table 7) and no statistical differences between treatments were observed. The following levels were recorded in the beginning of and at the termination of the experiment: total phosphorous, 34.0 and 31.7 µg l^{-1}; total nitrogen, 636.1 and 703.7 µg l^{-1}; and chlorophyll$-a$, 10.6 and 8.0 µg l^{-1}.

3.4. Experiment 4. The infaunal impact on the biomass of F. vesiculosus

All treatments showed an infaunal survival rate of 100%. While there was no change in *S. entomon* wet weight during the experiment, *N. diversicolor* showed a significant decrease in individual wet weight, from 241.1 ± 18.0 to 205.5 ± 15.3 mg ($p = 0.028$). No redistribution of *F. vesiculosus* into the sediment occurred during the experiment. Neither of the infaunal treatments revealed any significantly differing changes in biomass compared to the control. The only significant difference in macroalgal biomass occurred between the two infaunal treatments (ANOVA, Bonferroni, $p = 0.037$) (Table 8, Fig. 5). The results, however, indicate a

Table 4
One-way ANOVA results from experiment 2: density dependent impact of *N. diversicolor* on *Enteromorpha* spp.

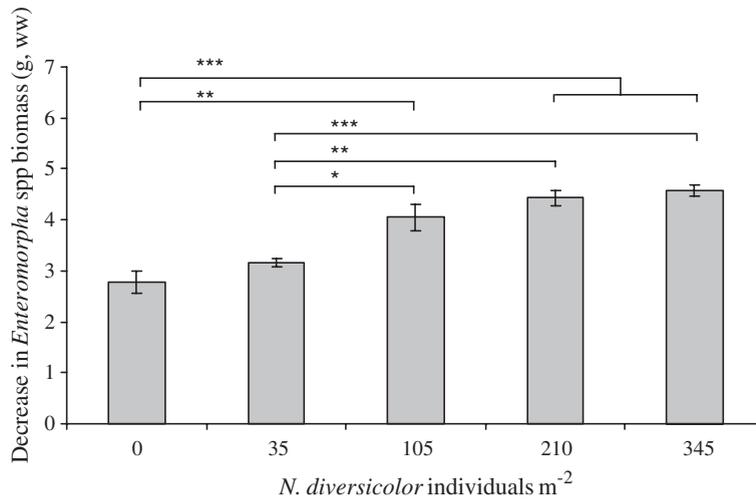|	df	MS	F	p
Decrease in *Eteromorpha* spp. biomass during density dependency experiment				
Between groups	4	3.121	20.013	**<0.001**
Within groups	20	0.156		
Total	24			

Significant value presented in bold.

Fig. 3. Decrease in *Enteromorpha* biomass in the different treatments (mean ± SE). Significant differences occurred between treatments (ANOVA, Scheffe, ***=$p \leq 0.001$, **=$p \leq 0.01$, *=$p \leq 0.05$).

possible effect of the polychaetes, even though it was not statistically detectable.

The hydrographical data reveals variations in oxygen content of the water during the experiment (Table 9). Low oxygen levels, around 55%, were registered at the termination of the experiment, while the levels in the beginning of the experiment were about 75%. The experimental aquaria, however, always showed oxygen levels similar to those recorded in the incoming water. It is thus reasonable to assume that the cause for the drop in oxygen concentration is to be located in the incoming water and not in the actual experimental system. The oxygen conditions as well as the other hydrographical parameters were similar in all treatments (ANOVA, $p > 0.05$). The amounts of total phosphorous, total nitrogen and chlorophyll-a were 48.5, 760.3 and 12.6 μg l^{-1} prior to the trial, and 126.6, 1283.8 and 7.2 μg l^{-1} when it ended.

4. Discussion

4.1. N. diversicolor actively redistributes filamentous green algae

N. diversicolor proved to be able to contribute to the redistribution and biomass loss of macroalgae on marine soft bottoms. The filamentous green algae experienced a significant diminution in biomass in the presence of the polychaetes, which is in accordance with the findings of Raffaelli (2000) and Hughes (1999). The decrease in C:N-ratio of *Enteromorpha* was due to leakage and mineralization of the carbon (Robinson et al., 1982; Best et al., 1990) as no changes in nitrogen percentages occurred. The second experiment indicated a threshold between 35 and 105 ind m^{-2}, and when the polychaete density exceeded this value, the algal biomass decreased significantly. The impact

Table 5

Hydrographical conditions in experiment 2: density dependent impact of *N. diversicolor* on the biomass of *Enteromorpha* spp.

	Control	35 ind m^{-2}	105 ind m^{-2}	210 ind m^{-2}	345 ind m^{-2}
Oxygen, %					
$x \pm$ SE	73.5 ± 4.0	75.8 ± 1.4	65.4 ± 4.6	70.7 ± 1.8	68.2 ± 2.4
min–max	$31.8 - 82.8$	$67.7 - 84.4$	$29.2 - 84.2$	$56.0 - 77.7$	$50.1 - 76.9$
Salinity, psu					
$x \pm$ SE	5.36 ± 0.02	5.38 ± 0.02	5.38 ± 0.03	5.34 ± 0.04	5.37 ± 0.04
min–max	$5.27 - 5.42$	$5.30 - 5.49$	$5.24 - 5.46$	$5.14 - 5.42$	$5.14 - 5.60$
pH					
$x \pm$ SE	7.70 ± 0.05	7.61 ± 0.05	7.50 ± 0.09	7.58 ± 0.04	7.64 ± 0.04
min–max	$7.56 - 7.88$	$7.35 - 7.82$	$6.94 - 7.70$	$7.38 - 7.72$	$7.47 - 7.81$
Temperature, °C					
$x \pm$ SE	14.8 ± 0.1	14.8 ± 0.1	14.8 ± 0.1	14.8 ± 0.1	14.8 ± 0.1
min–max	$14.5 - 15.5$	$14.5 - 15.5$	$14.5 - 15.5$	$14.5 - 15.5$	$14.5 - 15.5$

Table 6
One-way ANOVA results from experiment 3: the infaunal impact on the biomass of *Cladophora glomerata*

	df	MS	F	p
Decrease in *C. glomerata* biomass				
Between groups	2	0.967	38.761	**<0.001**
Within groups	14	0.018		
Total	16			

Significant value presented in bold.

Table 7
Hydrographical conditions in experiment 3: the infaunal impact on the biomass of *Cladophora glomerata*

	Control	*Nereis*	*Saduria*
Oxygen, %			
$x \pm SE$	79.0 ± 1.3	77.8 ± 1.3	74.8 ± 1.1
min–max	$75.1 – 82.2$	$74.3 – 81.9$	$71.9 – 77.9$
Salinity, psu			
$x \pm SE$	5.33 ± 0.05	5.26 ± 0.06	5.22 ± 0.04
min–max	$5.18 – 5.46$	$5.02 – 5.42$	$5.10 – 5.30$
pH			
$x \pm SE$	7.95 ± 0.02	7.93 ± 0.03	7.91 ± 0.03
min–max	$7.86 – 8.00$	$7.81 – 8.02$	$7.78 – 7.97$
Temperature, °C			
$x \pm SE$	17.3 ± 0.2	17.3 ± 0.2	17.3 ± 0.2
min–max	$17.0 – 18.0$	$17.0 – 18.0$	$17.0 – 18.0$

seemed to level off at the higher densities, probably due to increased intraspecific competition (Esnault et al., 1990), and thus, this observed density dependent process resembles a type III functional response (Mattila and Bonsdorff, 1998; Boström, 2002). *S. entomon* enhanced the biomass loss of the algae, albeit non-significantly.

The observed decrease in algal biomass is most likely not only due to the direct consumption of the infauna, but also a result of the vertical redistribution as algae in contact with the sediment are degraded faster than algae in the water column (Salovius and Bonsdorff, 2004). Polychaetes, such as *N. diversicolor* and *Arenicola marina* L., have been shown to relocate a variety of organic material into the sediment, such as leaves of *Zostera noltii* Hornemann and *Zostera marina* L. (Hughes et al., 2000), seeds of *Spartina anglica* C.E. Hubbard (Emmerson, 2000; Hughes et al., 2000), and macroalgae (Reise, 1985; Raffaelli, 2000; Kristensen and Mikkelsen, 2003). Several of these studies report occurrences of organic material down to 4 or 5 cm in the sediment, and are in concordance with this investigation. The anchorage of algae by *A. marina* is regarded as unintended by the polychaete (Reise,

1985), in contrast to the behaviour of *N. diversicolor* observed here. Throughout the study, *N. diversicolor* was consistently redistributing *Enteromorpha* and *C. glomerata* down into the burrows. This is probably a result of anti-predatory (Esselink and Zwarts, 1989) or "gardening" behaviour (Hylleberg, 1975; Reise, 1985; Olivier et al., 1995). While no active relocation of algal material was observed in the *Saduria* treatments, the burrowing activities of the isopod caused the sediment to resuspend, which increased the contact between algae and sediment.

Infauna may accelerate the degradation of algal material by enhancing the contact between algae and the microbial community in the sediment (Salovius and Bonsdorff, 2004), as well as by fragmenting the algae (Andersen and Kristensen, 1991). It is well known that bioturbating macrofauna affects physical, chemical and biological characteristics and increases the metabolism
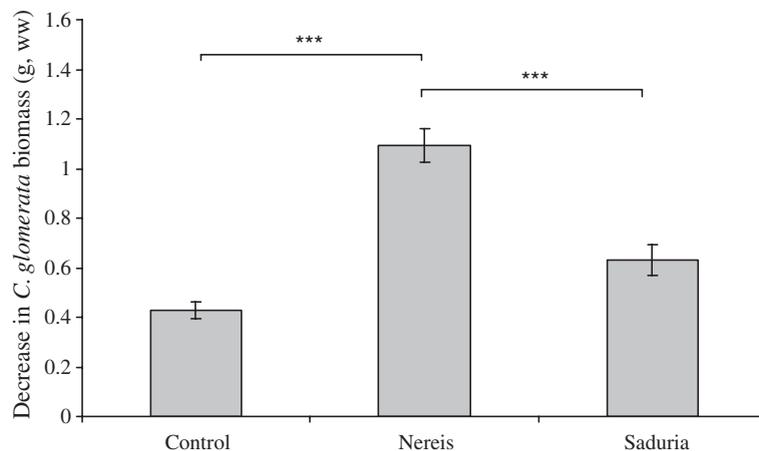

Fig. 4. Decrease in *Cladophora glomerata* biomass in the different treatments (mean ± SE). Significant differences occurred between treatments (ANOVA, Bonferroni, *** = $p \leq 0.001$).

Table 8
One-way ANOVA results from experiment 4: the infaunal impact on the biomass of *Fucus vesiculosus*

	df	MS	F	p
Decrease in *F. vesiculosus* biomass				
Between groups	2	0.010	4.383	<**0.032**
Within groups	15	0.002		
Total	17			

Significant value presented in bold.

in the sediment (Andersen and Kristensen, 1991, 1992; Aller et al., 2001; Emmerson et al., 2001; Kristensen and Mikkelsen, 2003). Several studies have proven the ability of *N. diversicolor* to contribute to the breakdown of organic material, such as micro- and macroalgae, in marine sediments (Andersen and Kristensen, 1992; Hansen and Kristensen, 1998; Kristensen and Mikkelsen, 2003). However, most of these studies have concentrated on enrichment of the sediment with homogenized fine organic material, in contrary to the present investigation.

4.2. Differential relocation of and decrease in algal biomass

The experimental set-up of the present study does not allow a statistical analysis to compare the impact between the different algal species. However, the material implies a difference in susceptibility between the algae as the following sequence: *Enteromorpha* > *C. glomerata* > *F. vesiculosus*. One possible explanation for the difference between the green algae is that *C. glomerata* may be more difficult to break down than *Enteromorpha*, as the former contains much cellulose

Table 9
Hydrographical conditions in experiment 4: the infaunal impact on the biomass of *Fucus vesiculosus*

	Control	*Nereis*	*Saduria*
Oxygen, %			
$x \pm SE$	71.1 ± 3.4	68.3 ± 4.3	70.2 ± 3.7
min–max	61.2 – 80.7	54.8 – 77.2	60.0 – 79.1
Salinity, psu			
$x \pm SE$	5.22 ± 0.02	5.21 ± 0.01	5.23 ± 0.02
min–max	5.18 – 5.31	5.17 – 5.26	5.16 – 5.30
pH			
$x \pm SE$	7.73 ± 0.05	7.65 ± 0.05	7.70 ± 0.05
min–max	7.57 – 7.87	7.49 – 7.74	7.50 – 7.83
Temperature, °C			
$x \pm SE$	13.7 ± 0.8	13.7 ± 0.8	13.7 ± 0.8
min–max	12.0 – 16.0	12.0 – 16.0	12.0 – 16.0

(van den Hoek et al., 1995). The most notable difference, however, lies between the filamentous green algae and *F. vesiculosus*, with the latter not being affected as much by the presence of the infauna. The results from the statistical analysis on change in individual wet weight of the infauna confirm the assumption of *F. vesiculosus* being the least palatable among the algae. The polychaetes cannot have profited from the presence of *F. vesiculosus*, as their weight actually decreased during the trial, similarly to the *Nereis*-control in the first experiment. The polychaete wet weight remained constant or even increased during the filamentous algae experiments. Algae characteristic of later successional stages, like *F. vesiculosus*, have complex chemical and structural defence mechanisms to reduce their attractiveness to herbivores (Littler and Littler, 1980; Duffy and Hay, 1990). Opportunistic, annual macroalgal species, on the other hand, protect themselves through
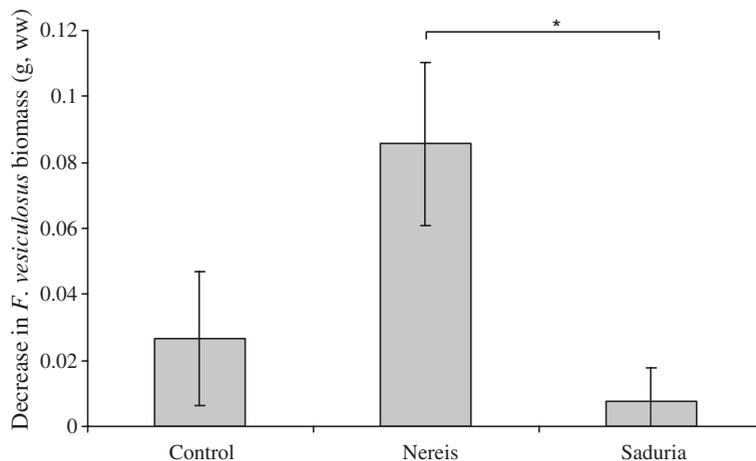

Fig. 5. Decrease in *Fucus vesiculosus* biomass in the different treatments (mean ± SE). Significant differences occurred between treatments (ANOVA, Bonferroni, *=$p \leq 0.05$).

rapid growth and unpredictable spatial and temporal occurrence as they lack the defences typical of perennial species, and are often considered more attractive as food for grazers (Littler and Littler, 1980; Duffy and Hay, 1990). In contrast to the results from this study, Kristensen and Mikkelsen (2003) found redistribution, as well as an increased degradation, of *Fucus serratus* L. in the presence of *N. diversicolor*. It should be noted that in their study, Kristensen and Mikkelsen (2003) used homogenized algal material, which may be more accessible to the polychaetes than the intact pieces of algal thalli used in this investigation. *Fucus* thalli of the size used in the experiments are frequently found as a part of drifting algal mats (pers. obs.) and by using intact pieces, the fragmenting effect of the infauna was included. It is however, possible that the level of fragmentation of the algae affects the impact the infauna has on the material. The infaunal impact has been suggested to be of significant importance at low algal biomasses (Raffaelli, 2000), like the ones used in this study, as density blooms are highly likely to result in primarily negative effects on the infauna, which has been established on several occasions (Raffaelli et al., 1998 and references therein).

N. diversicolor is omnivorous, as well as opportunistic, and can thereby utilize the food source of best quality or the one that is occurring the most abundantly at the moment (Olivier et al., 1995). Even though the water entering the aquaria was filtered, there was always phytoplankton present in the experimental system, as shown by the amounts of chlorophyll-*a*. The facultatively filter-feeding *N. diversicolor* may have fed on the available phytoplankton as the polychaete begins filtrating when chlorophyll-*a* levels of 1–3 µg l^{-1} are present in the ambient water (Vedel et al., 1994). The infaunal weight analysis, however, suggests that the polychaetes did not feed on other food sources, besides the filamentous algae, in sufficient amounts to sustain polychaete wet weight. Whether or not filtering has occurred during the experiments, the significant impact on macroalgal degradation remains. Alternative food sources may, however, influence the extent to which macroalgal material is utilized. The feeding preferences of the polychaete depend on season and local conditions, such as primary productivity (Vedel et al., 1994). Searching for food at the sediment surface is regarded as the main feeding behaviour (Esnault et al., 1990).

5. Conclusion

When annual, filamentous macroalgae increase at the expense of perennial species, the transformation of carbon through the web is accelerated (Valiela et al., 1997). A detritus pool consisting of easily degraded macroalgae leads to increases in the mineralization rates and metabolism in the sediment (Buchsbaum et al., 1991). As the carbon and nutrient dynamics of soft bottoms change, macroalgal proliferation may be promoted by the released nutrients (Hansen and Kristensen, 1997; Sundbäck et al., 2003) though the infauna is believed to be able to affect the system towards a more pristine state (Hansen and Kristensen, 1997). In conclusion, it is clear that soft bottom macroinvertebrates can show large potential to process and redistribute drifting macroalgal material.

Acknowledgments

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