

# Predation of epipellic diatoms by the amphipod *Corophium volutator* and the polychaete *Nereis diversicolor*

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**ABSTRACT:** The effects of *Corophium volutator* (Pallas) and *Nereis diversicolor* (O. F. Muller) on the densities and specific compositions of epipellic diatom assemblages were investigated experimentally, in the laboratory and in an estuary. In laboratory experiments cores containing no macrofauna had significantly higher densities of diatoms than cores with *C. volutator* and cores with *N. diversicolor* after 8 d. In field experiments the densities of diatoms increased where *C. volutator* were removed, by spraying with insecticide, and where *N. diversicolor* were prevented from surface deposit feeding, by the insertion of porous mats under the surface. The mean daily rates of consumption of diatoms by individual *C. volutator* and *N. diversicolor* in the field were estimated to be 2150 to 3767 and 5476 to 12 184 cells respectively. In the laboratory the effects of *C. volutator* and *N. diversicolor* on the species composition of the diatom assemblage were similar. In the field the assemblages that developed where predation was reduced were different because of initial differences in diatom assemblage structure in the 2 experimental areas. The laboratory results showed that *C. volutator* and *N. diversicolor* may feed on the same species of diatoms when presented with the same diatom assemblage, indicating that interspecific competition for food may be important under some natural conditions.

**KEY WORDS:** *Corophium volutator* *Nereis diversicolor* Epipellic diatoms Predation

## INTRODUCTION

*Corophium volutator* and *Nereis diversicolor* are often very abundant in estuarine and coastal mudflats of northwestern Europe where densities greater than 100 000 m<sup>-2</sup> (Gerdol & Hughes 1993) and 50 000 m<sup>-2</sup> (Möller 1985) respectively have been reported. *C. volutator* live in U-shaped burrows up to 5 cm deep and are predominantly unselective deposit feeders (Gerdol & Hughes 1994a, b), although suspension feeding and epipsammic browsing may also occur. The amphipods scrape surface sediment into their burrow with their antennae (Meadows & Reid 1966). The sediment is drawn into the setal basket formed by the second

gnathopods, by the respiratory current produced by the beating pleopods, and sorted before food particles are passed to the mouth.

*Nereis diversicolor* also has 3 feeding methods: the worms may be scavengers/predators, suspension feeders or surface deposit feeders (Fauchald & Jumars 1979, Reise 1979, Riisgård 1991, Jensen & Andre 1993), of which the last 2 are the main methods (Pashley 1986, Esselink & Zwarts 1989). In suspension feeding a mucous funnel extends from the entrance of the burrow, which may be about 15 cm deep (Davey 1994), down to the worm which produces a current of water by undulating its body. Suspended food particles are trapped on the funnel which is then ingested (Harley 1950). In surface deposit feeding the worms partially emerge from their burrows, swallow some surface sediment by everting their proboscis, and retreat back into their burrows leaving furrows which radiate from the burrow opening. Suspension feeding cannot occur

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when no surface water remains during periods of low tide, and may be unprofitable in muddy estuaries (as in this study) because of the relatively low concentration of food particles among the high load of suspended inorganic material (Esselink & Zwarts 1989). Deposit feeding may be more profitable, but it increases the risk of predation by fish and birds. Esselink & Zwarts (1989) and Riisgård (1991) concluded that suspension feeding was the predominant feeding method. In contrast, Pashley (1986) considered that *N. diversicolor* was an opportunist that relied mainly on deposit feeding but changed to other, more energy-rich, food sources when they became available. In the estuaries of Essex (SE England) when the sediment is exposed by the tide there is often no overlying water, possibly because the burrows of *N. diversicolor* drain the surface sediment (Meadows & Tait 1989), and suspension feeding is not possible. The presence of radiating furrows indicates that deposit feeding occurs regularly, as has been observed often (Fig. 1).

The relationships between *Corophium volutator* and *Nereis diversicolor* have been studied extensively. Some authors have found that the 2 species coexist (Möller 1986, Flach 1992, Jensen & Andre 1993), while others, including Hughes & Gerdol (in press), who examined their distributions in 2 Essex estuaries, have recorded negative correlations between their densities. *N. diversicolor* may eat *C. volutator* (Rönn et al. 1988), deter recruitment of the amphipods, or cause their migration (Bornsdorff et al. 1986, Ólafsson & Persson 1986, Jensen 1988, Jensen & Andre 1993). Disturbance by the amphipods may prevent colonisation by small *N. diversicolor* but there is little evidence of this (see Hughes & Gerdol in press).

The role of interspecific competition for food in determining the distribution and abundance of the 2 species has not been examined previously. Interspecific competition for food is possible since both species may feed on surface deposits and consume epipellic diatoms and detritus. Epipellic diatoms are often very abundant in the top few millimetres of intertidal mudflats (Underwood & Paterson 1993a). Gerdol & Hughes (1994b) have shown that predation by *Corophium volutator* reduces the abundance of epipellic diatoms, but there is no similar quantitative study on the effects of *Nereis diversicolor*.

This study examined the comparative effects of *Corophium volutator* and *Nereis diversicolor* on the abundance of epipellic diatoms, and on the specific composition of the diatom assemblage, in order to identify any differential resource utilisation. The approach was to use laboratory experiments, where both species were offered the same food under controlled conditions, and field exclusion experiments, which made use of natural areas where only one or the other species occurs.

## METHODS

**Laboratory experiments.** Fifteen corers, 14 cm diameter and 15 cm long, were used to collect cores of sediment 10 cm deep from a site at Battlesbridge (River Crouch, Essex, UK) where no macrofauna occur in the sediment (for unknown reasons). The cores of sediment were taken to the laboratory and placed in an artificial tidal regime of 3 h submergence every 12 h, using water of 30 salinity at 12°C and in 12 h light/12 h dark.



Fig. 1 A *Nereis diversicolor* which has emerged from its burrow to surface deposit feed. The furrows formed by the feeding by neighbouring worms are also visible

200 *Corophium volutator* (equivalent to 13 000 m<sup>-2</sup>) were added to each of 5 cores, 35 *Nereis diversicolor* (equivalent to 2300 m<sup>-2</sup>) were added to each of a further 5 cores, and 5 cores with no macrofauna were left as controls. Surface scrapings of a diatomaceous film from near the experimental field sites were mixed into a slurry with a little water and similar amounts spread evenly on the surface of each core to a depth of 0.5 cm. A length of plastic tube (5 mm diameter) was inserted through the sediment to facilitate drainage on emersion, and a mesh was placed over the top of each corer to retain the animals. After 8 d the diatoms in each core were sampled by taking 3 small sediment samples, 2 cm in diameter and 1 cm deep. These samples were placed in individual tubes containing 1% glutaraldehyde solution and kept at 9°C in the dark until used. Each core of sediment was sieved through a 0.354 mm sieve and the surviving macrofauna counted.

**Field experiments.** The field experiments were conducted in Clementsgreen Creek, a branch of the River Crouch approximately 15 km from the open sea (Fig. 2). The only macrofaunal species in the sediment in some troughs between residual mud mounds in a small bay off the creek was *Corophium volutator*, while approximately 200 m further up the creek the sediment contained only *Nereis diversicolor*.

Five *Corophium volutator* exclusion areas, each 25 cm × 25 cm, were established, each with a similar control area approximately 50 cm away. The exclusion areas were subjected to weekly applications of a pyrethrum-based insecticide (Bug Gun, ICI) from 12 October to 9 November 1993 to remove any amphipods (see Gerdol & Hughes 1993). Similarly, 5 *Nereis diversicolor* exclusion areas were established, each with a control area nearby. The deep burrowing worms are relatively unaffected by applications of insecticide and the worms could not be removed without sieving and disrupting the sediment. Instead in the exclusion areas surface deposit feeding by *N. diversicolor* was prevented by removing a slab of sediment 2 to 3 cm thick and inserting a mat of netting of 0.5 mm mesh size in

the hole before replacing the surface sediment. The control areas underwent the same treatment but without insertion of the mat. This experiment lasted 6 wk, from 19 October to 30 November 1993.

At the end of the field experiments diatoms were collected in 5 core samples, 2 cm diameter and 1 cm deep, from each exclusion and control area, and treated in the same way as the laboratory diatom samples. To sample the macrofauna 3 cores were taken from each control and exclusion area using a corer of 3.8 cm diameter. These cores were 10 cm deep in the *Corophium volutator* experiment, 15 cm deep in the *Nereis diversicolor* control areas, and down to the mats in the exclusion areas to capture any worms recruited during the experiment. These cores were sieved (mesh size 0.354 mm) and the macrofauna present were identified and counted.

**Treatment of diatom samples.** Each sample was sonicated (L & R, Ultrasonicator) for 7 min, which separates the diatoms from the sediment, but does not destroy them (Paterson et al. 1990). A constant volume (0.53 ml) of this suspension was added to a Lund chamber and the number of diatoms in half the chamber counted at a magnification of ×300. Two subsamples from each diatom sample were used to calculate the density of diatoms in the field and laboratory experiments.

The specific compositions of the diatom assemblages were determined at the same time as their densities. From each Lund chamber sample 50 randomly selected diatoms were identified to genus, and to species if possible, and given a code letter. Later, to confirm the species identities several samples of sediment were cleaned by washing with distilled water and then centrifuged at 7000 × *g* for 3 min. This procedure was repeated 4 times, removing the supernatant and replacing it with distilled water each time. The cleaned sample with some distilled water was added to an equal volume of nitric acid and placed on a hot plate until half the volume had evaporated. The solution was washed with distilled water and centrifuged a further 5 times. A small drop of this sample was placed on a

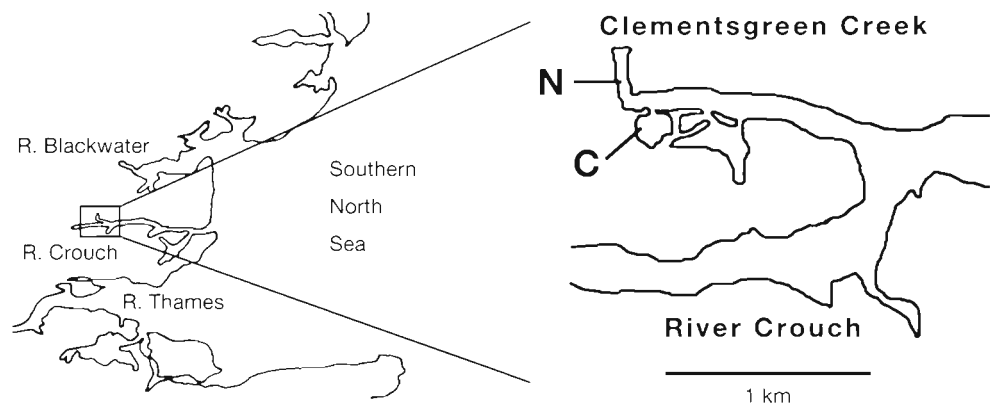


Fig. 2. The study area showing location of the *Corophium volutator* experiments (C) and the *Nereis diversicolor* experiments (N)

coverslip, dried and mounted in Naphrax. All the diatoms were identified to genus and, in most cases, to species. Cluster analyses of the diatom assemblages were performed using percentage similarity for sample comparisons and unweighted pair groups as the clustering method.

**Calculation of rates of predation.** These calculations were based on 2 assumptions: firstly, that the diatom densities in the control and exclusion areas at the start of the experiments were not different, and secondly that the higher diatom densities in the exclusion areas at the end of the experiments were due to reduced rates of predation, as any other extrinsic factor affected diatom abundance equally in the control and exclusion areas. On these assumptions, the mean daily rates of consumption of diatoms by individual worms and amphipods in the control areas in the field experiments were equal to the mean daily rates of increase in diatom densities in the exclusion areas.

The daily rates of increase in diatom densities were calculated in 2 ways. The first method presumed that there was a *constant rate of increase* of diatom densi-

ties in the exclusion areas relative to the control areas, while the second method presumed a *constant reproduction rate* (which would lead to an exponential rate of increase in densities). The first method use the following formula:

$$C = \frac{D_e - D_c}{(A_c - A_e) T}$$

where  $C$  is mean daily individual consumption (number of diatoms);  $D_e$  is the mean density of diatoms in the exclusion areas, and  $D_c$  the mean density in the control areas;  $A_c$  is the mean number of animals in the control areas, and  $A_e$  the mean number of animals in the exclusion areas;  $T$  is the duration of the experiment in days.

In the second method the rate of reproduction ( $R$ ) of the diatoms was calculated using the following formula:

$$R^T = \frac{D_e}{D_c}$$

This reproduction rate was used to calculate a daily rate of increase by multiplying the mean control density by  $R$ .

Table 1 Species of diatoms found, together with their sizes, based on Hendeny (1964), and Krammer & Lange-Bertalot (1986, 1988), and a code letter referred to in the text, figures and other tables

Code	Species	Length ( $\mu\text{m}$ )	Width ( $\mu\text{m}$ )
A	<i>Navicula arenaria</i> Donkin	30–80	8–11
B	<i>Navicula crucicula</i> (W. Smith) Donkin	40–52	16
C	<i>Navicula halophila</i> (Grunow) Cleve	53	12
D	<i>Navicula phyllepta</i> Kützing	30–50	8
E	<i>Navicula ramosissima</i> (Agardh) Cleve	34–43	8
F	<i>Parlibellus berkeleyi</i> (Kützing) E. J. Cox	12–30	5–7
G	<i>Amphora coffeaeformis</i> (Agardh) Kützing	30–50	<25
H	<i>Nitzschia</i> sp. A		
I	<i>Nitzschia</i> sp. B		
J	<i>Nitzschia apiculata</i> (Gregory) Grunow	20–58	4.5–8.5
K	<i>Nitzschia bilobata</i> W. Smith	90–110	15–18
L	<i>Nitzschia closterium</i> (Ehrenberg) Kützing	50–80	<5
M	<i>Surirella</i> sp. A		
N	<i>Surirella gemma</i> (Ehrenberg) Kützing	72–140	53–56
O	<i>Surirella ovalis</i> Brébisson	45–80	12
P	<i>Diploneis elliptica</i> (Kützing) Cleve	20–130	10–60
Q	<i>Diploneis didyma</i> (Ehrenberg) Cleve	30–90	15–36
R	<i>Pleurosigma angulatum</i> (Quekett) W. Smith var. <i>angulatum</i>	150–360	30–60
S	<i>Pleurosigma angulatum</i> var. <i>undulatum</i> Grunow	Narrower than <i>angulatum</i>	
T	<i>Pleurosigma intermedium</i> W. Smith	126–194	17–18
U	<i>Gyrosigma balticum</i> (Ehrenberg) Cleve	236–300	28–32
V	<i>Gyrosigma hippocampus</i> (Ehrenberg) Hassell	142–180	22–26
W	<i>Gyrosigma littorale</i> (W. Smith) Cleve	100–160	22–35
X	<i>Gyrosigma obscurum</i> (W. Smith) Griggith & Henfrey	80–200	10–15
Y	<i>Gyrosigma wansbeckii</i> (Donkin) Cleve	100–190	13–15

## RESULTS

The diatom species recorded are listed in Table 1 with their approximate sizes and a code letter which is used to identify them in subsequent figures.

### Laboratory experiments

The mean densities of animals alive during the experiments, calculated as the mean of the initial densities and the final densities, were 9804 ( $\pm 145$  SE)  $\text{m}^{-2}$  for *Corophium volutator* and 2052 ( $\pm 51$  SE)  $\text{m}^{-2}$  for *Nereis diversicolor*. At the end of the experiments the mean density of diatoms in the control cores ( $35.1 \times 10^8 \text{ m}^{-2}$ ) was significantly higher than the densities in cores containing *C. volutator* ( $15.4 \times 10^8 \text{ m}^{-2}$ ) ( $p < 0.001$ , *t*-test) and those containing *N. diversicolor* ( $14.2 \times 10^8 \text{ m}^{-2}$ ) ( $p < 0.001$ , *t*-test). The densities of most diatom taxa were lower in the presence of *C. volutator* and *N. diversicolor* (Figs. 3 & 4). The exceptions were *Parlibellus berkeleyi* (F), and *Surirella* sp. A (M), whose densities did not differ significantly in either experiment; *Amphora coffeaeformis*

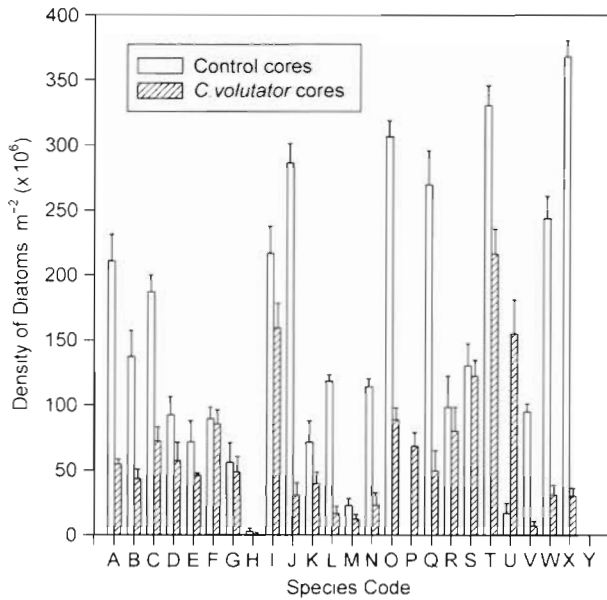


Fig. 3. Laboratory experiments. Mean density of the diatom taxa in control cores and in cores with *Corophium volutator*. Species codes are listed in Table 1

(G), *Nitzschia* sp. A (H) and the 2 *Pleurosigma angulatum* varieties (R and S), which showed no difference in the *C. volutator* experiment; and *Navicula ramosissima* (E) and *Nitzschia bilobata* (K), which showed no difference in the *N. diversicolor* experiment. *Diploneis elliptica* (P) and *Gyrosigma balticum* (U) had significantly higher densities in the presence of *C. volutator* and *N. diversicolor*.

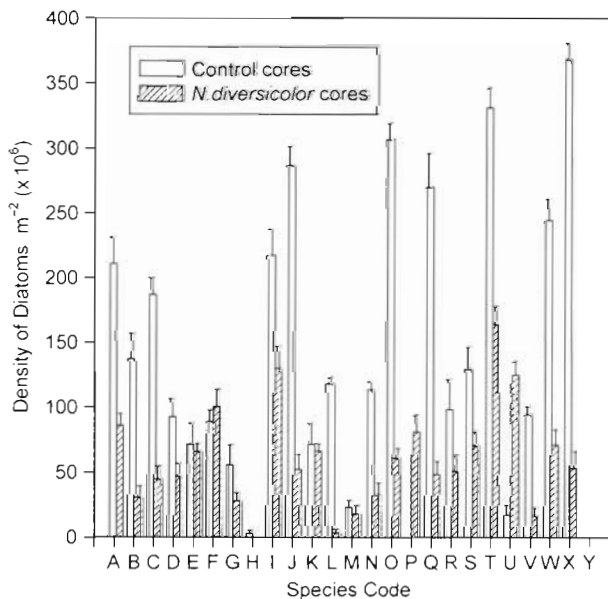


Fig. 4. Laboratory experiments. Mean density of the diatom taxa in control cores and in cores with *Nereis diversicolor*. Species codes are listed in Table 1

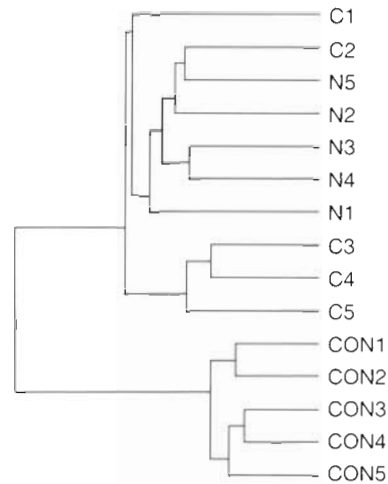


Fig. 5. Laboratory experiments. Dendrogram showing the clustering of the diatom assemblages in the cores with *Corophium volutator* (C), *Nereis diversicolor* (N), and the control cores (CON)

The specific compositions of the diatom samples from each core are available from R. G. Hughes. Cluster analysis revealed 2 distinct groups, one group containing only the control cores and the other containing the cores with animals (Fig. 5). These groups were separated largely because in the control cores there was a higher relative abundance of *Nitzschia apiculata* (J), *N. closterium* (L), *Surirella ovalis* (O), *Diploneis didyma* (Q), *Gyrosigma hippocampus* (V), *G. littorale* (W), and *G. obscurum* (X), a lower relative abundance of *Nitzschia* sp. B (I), *Pleurosigma angulatum* var. *undulata* (S), and *G. balticum* (U), and no *Diploneis elliptica* (P).

### Field experiments

One of the *Corophium volutator* exclusion areas and its control was damaged and the results from only the remaining 4 pairs of areas are presented. The mean densities of *C. volutator*, *Nereis diversicolor* and the diatoms in the exclusion and control areas of both experiments are shown in Fig. 6. The insecticide treatment removed all the amphipods from the exclusion areas, and the sub-surface mats reduced the density of surface deposit feeding worms by approximately 80%. The mean densities of diatoms increased by a factor of 2.9 in the *C. volutator* exclusion areas and by a factor of 4.3 in the *N. diversicolor* exclusion areas. The calculated daily rate of predation by individual *C. volutator* was 3767 diatoms, assuming a constant rate of diatom increase, and 2150 diatoms, assuming a constant rate of reproduction. The respective figures for *N. diversicolor* were 12 184 and 5476 diatoms  $d^{-1}$ .

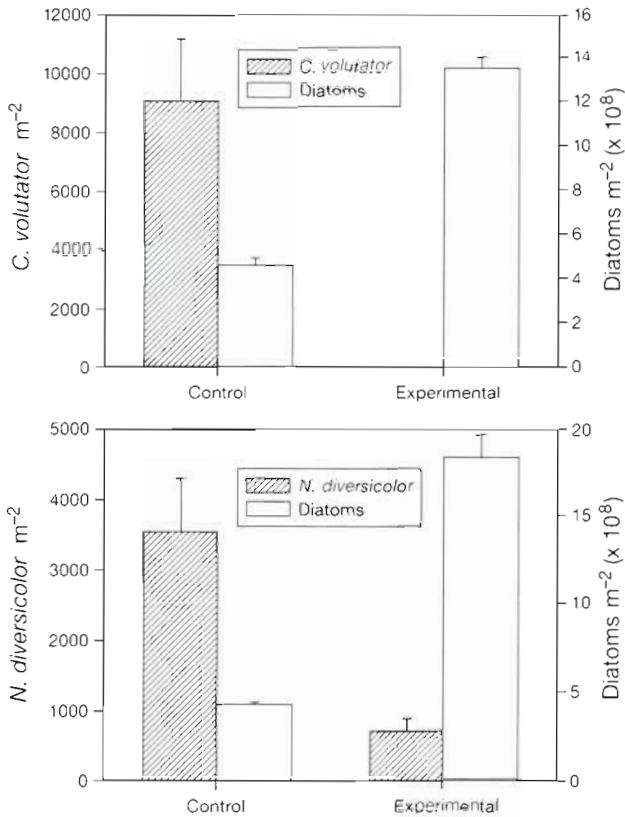


Fig. 6. Field experiments. Mean densities of the macrofauna and diatoms in control areas and experimental exclusion areas in both field experiments

In both experiments the mean densities of all diatom taxa in the control areas were significantly lower than in the exclusion areas, with only 5 exceptions (Figs. 7 & 8). These were *Nitzschia* sp. B (I), *N. bilobata* (K), and *Gyrosigma wansbeckii* (Y) in the *Corophium volutator* experiment, and *Surirella* sp. A (M) and *Pleurosigma intermedium* (T) in the *Nereis diversicolor* experiment.

The specific compositions of the diatom samples from the *Corophium volutator* experiment and the *Nereis diversicolor* experiment are available from R. G. Hughes. The samples had a high equitability (evenness) which means that the differences that led to the formation of the clusters in the dendrogram, shown in Fig. 9, cannot be attributed easily to a small number of species. Rather the clustering is due to cumulative small differences in abundance of many taxa. The samples form 2 major clusters, one for the *C. volutator* experiment and the other for the *N. diversicolor* experiment. This separation is due mainly to the higher relative abundance of *Navicula crucicula* (B), *Surirella gemma* (N), *Diploneis didyma* (Q), and *Gyrosigma hippocampus* (V), in the *C. volutator* area compared to the *N. diversicolor* area, where there was a higher relative abundance of both *Pleurosigma angulatum* varieties (R and S) and *G. obscurum* (X).

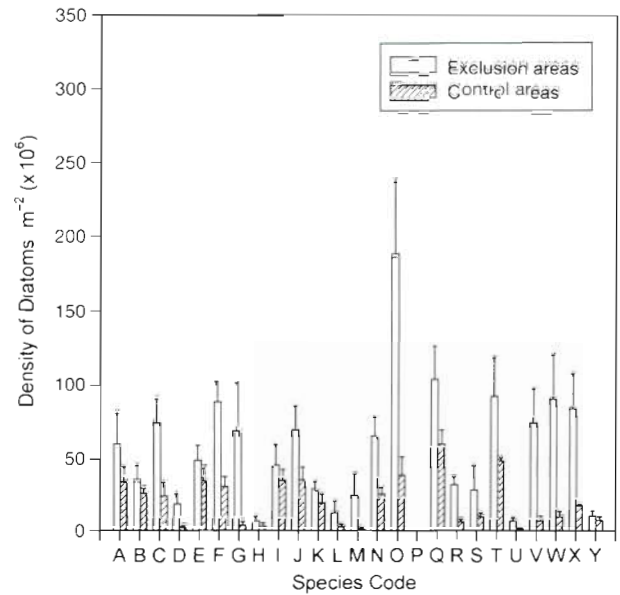


Fig. 7. Field experiments. Mean density of the diatom taxa in control areas and in *Corophium volutator* exclusion areas. Species codes are listed in Table 1

Within the cluster from the *Nereis diversicolor* experiment the samples separate into a group comprising the control areas and another consisting of the exclusion areas, with exclusion area N4 as an outlier. The 2 groups are formed largely because there were relatively low abundances of *Pleurosigma intermedium* (T), and relatively high abundances of *Gyrosigma obscurum* (X), in the exclusion areas.

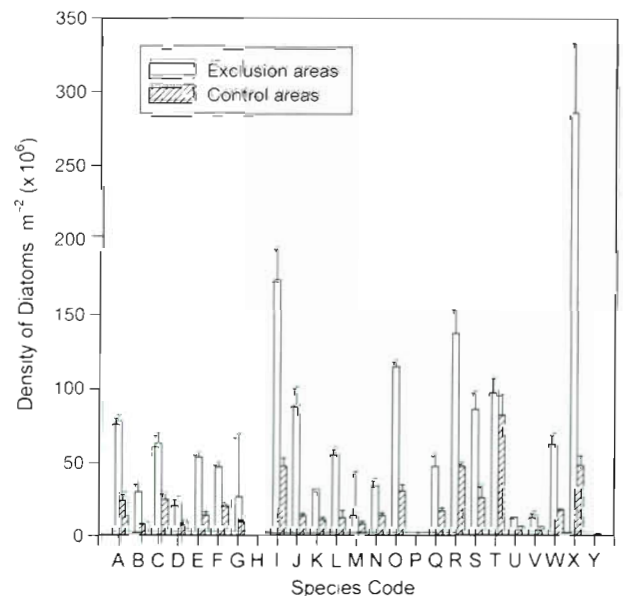


Fig. 8. Field experiments. Mean density of the diatom taxa in control areas and in *Nereis diversicolor* exclusion areas. Species codes are listed in Table 1

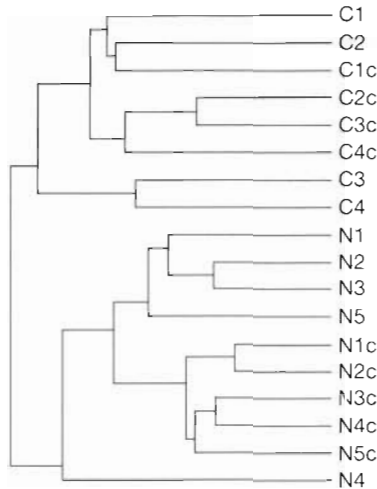


Fig. 9. Field experiments. Dendrogram showing the clustering of the diatom assemblages in the *Corophium volutator* exclusion areas (Cn), the *C. volutator* control areas (Cnc), the *Nereis diversicolor* exclusion areas (Nn), and the *N. diversicolor* control areas (Nnc)

The samples from the *Corophium volutator* experiment form 3 groups. One group, consisting of control areas 2, 3 and 4, was characterised by relatively high abundances of *Navicula ramosissima* (E), *Nitzschia* sp. B (I) and *Diploneis didyma* (Q), and a relatively low abundance of *Gyrosigma hippocampus* (V). Control area 1 is separated from the other control areas and clusters with exclusion areas 1 and 2, largely because of a relatively high abundance of *Navicula arenaria* (A) and *Nitzschia closterium* (L), and a low relative abundance of *Navicula ramosissima* (E). Exclusion areas 3 and 4 cluster because of their relatively low abundance of *Navicula arenaria* (A), *Nitzschia apiculata* (J), *Diploneis didyma* (Q), but a relatively high abundance of *Navicula halophila* (C), *Amphora coffeaeformis* (G) and *G. hippocampus* (V).

## DISCUSSION

The results from the laboratory and field experiments demonstrate that both *Corophium volutator* and *Nereis diversicolor* markedly reduce the abundance of epipellic diatoms. The results for *C. volutator* confirm those of Gerdol & Hughes (1994b), who demonstrated that the amphipods caused significant decreases in the abundance of epipellic diatoms, due to their feeding rather than bioturbation. In this study the effects of *N. diversicolor*, in the laboratory at least, were also a result of their feeding, since as the animals had already burrowed no bioturbation occurred other than that associated with feeding. The presence of feeding tracks on the mudflats also points to sur-

face deposit feeding as the major cause of decreased diatom abundance in the estuary.

The daily rates of predation calculated from the field experiments indicate that the mean daily consumption rate of an individual *Nereis diversicolor* is 4 to 5 times that of an individual *Corophium volutator*, an expected result as the worms are larger. The total number of diatoms consumed by these populations during the field experiments were estimated to be  $18.0$  to  $31.5 \times 10^6 \text{ m}^{-2} \text{ d}^{-1}$  for *C. volutator* (at  $8375 \text{ m}^{-2}$ ), and  $19.3$  to  $42.9 \times 10^6 \text{ m}^{-2} \text{ d}^{-1}$  for *N. diversicolor* (at  $3562 \text{ m}^{-2}$ ). These are the first such estimates of this kind to be calculated.

Despite these apparently high rates of consumption the calculated constant daily reproduction rates of the diatoms in the *Corophium volutator* and *Nereis diversicolor* exclusion areas were very similar, but low, at 1.038 and 1.035 respectively. These figures indicate a doubling time of approximately 20 d, much lower than that achieved in the laboratory where doubling times of fractions of a day to a few days have been obtained in experiments with unialgal cultures (e.g. Cox 1993, 1994). Small diatoms tend to divide more rapidly than large ones. For example, *Amphora coffeaeformis* divided several times a day ( $k > 3$ ) (in 50% seawater,  $20^\circ\text{C}$  and 14 h light/10 h dark), while under similar conditions *Nitzschia scalpelliformis* only divided once a day, and the much larger *Pinnularia viridis* took 3 to 5 d per division. G. Reid (Natural History Museum; unpubl.) observed that doubling times in *Gyrosigma* spp. varied between 1 and 3 d according to temperature, light and salinity regime.

The relatively low rates of reproduction calculated in the field experiments may indicate that there were other environmental limitations on diatom densities. These include predation by meiofaunal organisms, particularly nematodes which are abundant in these estuaries. Predation by meiofauna on the smaller diatoms may also explain why these species in particular did not have a more marked increase in abundance.

In the laboratory experiments the estimated mean daily consumption rates were approximately 10 times higher than those from the field experiments, at 25 000 diatoms for *Corophium volutator* and 125 000 for *Nereis diversicolor* (assuming a constant rate of diatom depletion over the 8 d). The laboratory results were obtained under conditions where the animals were at relatively low densities, the diatoms at relatively high densities, and where no food in suspension was available. However, they indicate that potential food consumption by both species is much higher than that achieved *in situ* where food may be limiting.

Intraspecific competition may reduce consumption rates by *Corophium volutator* at high densities (see Jensen & Kristensen 1990) and food supply may limit *C. volutator* growth rate and abundance at certain

times of the year. Stuart et al. (1985) concluded that diatoms offer a superior food source during the summer but are less important in spring and autumn. Gerdol & Hughes (1993) reported densities of *C. volutator* greater than  $100\,000\text{ m}^{-2}$ , and densities of *Nereis diversicolor* of over  $50\,000\text{ m}^{-2}$  were recorded by Möller (1985), but at these high densities the animals are probably smaller than those used in this study, and presumably had lower individual food requirements and consumption rates.

Epipellic diatoms are important in estuarine ecosystems; they may contribute up to one-third of the fixed carbon of an estuary (Underwood & Paterson 1993a), and increase the resistance of the sediment to erosion by the production of mucopolysaccharides during their short vertical migrations (Holland et al. 1974, Paterson et al. 1990, Round et al. 1990, Underwood & Paterson 1993a, b). Predation on epipellic diatoms by *Corophium volutator* and *Nereis diversicolor* may, therefore, have several important consequences for the functioning of the estuarine ecosystem by reducing primary production, facilitating energy transfer from primary producers to secondary consumers, including birds and fish, and increasing sediment erosion. Gerdol & Hughes (1994b) demonstrated that *C. volutator* made the sediment more susceptible to erosion by eating diatoms. More studies are required to quantify more accurately the effects of predation, on primary and secondary production, and to investigate seasonal differences.

*Corophium volutator* and *Nereis diversicolor* may alter the specific composition of epipellic diatom assemblages. When offered samples from the same diatom assemblage in the laboratory, the 2 species had similar effects on the relative abundance of the diatom taxa. This observation, together with the indication that food may be limiting (see above), leads to the conclusion that under some natural conditions where both species coexist interspecific competition may be an important factor in determining their abundances.

Most diatom species had lower densities in the cores containing animals than in the control cores. Predation had no significant effect on the density of some species, while *Diploneis elliptica* (P) and *Gyrosigma balticum* (U) densities increased in the presence of animals in both experiments. The reasons why different species are affected differently need further investigation but may include one or more of the following: both *Corophium volutator* and *Nereis diversicolor* consume preferentially certain diatom species; consumption is unselective but some species become relatively more abundant because they have higher reproductive rates; some diatom species are better adapted to the different interspecific competitive environment or to the different chemical environment created by the animals activities.

Increases in the density of *Diploneis elliptica* (P) and *Gyrosigma balticum* (U) in the presence of the animals in the laboratory experiments may be related to their large robust cells; *D. elliptica* is highly silicified and *G. balticum* has the largest cells in this assemblage. Gerdol & Hughes (1994a) concluded that diatoms were crushed by the mandibles of *Corophium volutator*, since no diatom frustules were found in the guts of amphipods that had consumed large numbers. This indicates that diatoms may be manipulated individually introducing an opportunity for selection, perhaps by size, shape or hardness. Selectivity would not be expected of *Nereis diversicolor* as they ingest relatively large volumes of surface sediment. The diatom species whose relative abundance decreased show a wide range of sizes and shapes, indicating that selective feeding by the animals may not be important.

In the field experiments a similar comparison of the effects of *Corophium volutator* and *Nereis diversicolor* on diatom species abundances could not be made, for the diatom assemblages differed between the 2 sites. This probably reflected the contrasting physical environments of the 2 sites; the *C. volutator* site was more sheltered than the creek where the *N. diversicolor* experiments were conducted. Colijn & Dijkema (1981) reported that the species composition of epipellic diatoms may vary along an exposure gradient.

That *Corophium volutator* and *Nereis diversicolor* differentially reduce the abundance of diatom species may have consequences for sediment stability, for Holland et al. (1974) found interspecific differences in the ability of epipellic diatoms to stabilise sediment with their secretions. Madsen et al. (1993) recorded an increase in sediment stability corresponded with an increase in the volume of *Navicula*, *Amphora*, and *Nitzschia* species, as well as the larger sigmoid genera *Gyrosigma* and *Pleurosigma*. It is perhaps significant that species of these 5 genera increased both in relative abundance and absolute density in the field exclusion areas. Predation may, therefore, reduce sediment stability, not only by reducing overall diatom densities, but also by reducing particularly the densities of those diatoms best able to stabilise sediments with their secretions.

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