ORIGINAL ARTICLE

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The effects of the polychaete *Nereis diversicolor* on the distribution and transplanting success of *Zostera noltii*

Abstract Loss of saltmarsh vegetation in south-east England is a significant problem for conservation and coastal defence. The losses of vegetation began in the 1930s with the loss of intertidal *Zostera marina* and have continued more recently. Some preliminary trials at re-establishing *Zostera* in some estuaries of Essex have not been successful. This paper addresses the hypothesis that the infauna, particularly the polychaete *Nereis diversicolor*, may restrict natural colonisation by *Zostera* and reduce the success of transplanting trials. In field experiments, *Z. noltii* were transplanted into areas where *Nereis* were common, close to an established seagrass bed and into two other estuaries. The transplants protected from the effects of the polychaetes by netting had a higher survival rate, lower index of root damage and greater biomass at the end of the experiments than those that were unprotected. In laboratory experiments, *Nereis* reduced the survival of *Z. noltii*. They were observed grasping the leaves and pulling them into their burrows. These results indicate that herbivory and disturbance by *N. diversicolor* is responsible, at least in part, for the restriction of the distribution of *Z. noltii* and may have been important in limiting the success of previous transplanting experiments. A hypothesis is proposed which states that there are two stable states on the upper mudflats. One state is dominated by plants, including *Zostera* spp., which prevent colonisation by burrowing infauna, and the other is dominated by infauna which prevent colonisation by plants. Managing these two states could be the key to re-establishing the early successional stages of saltmarsh development.

Key words Saltmarsh · Seagrass · *Zostera* · *Nereis* · Conservation

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Introduction

The estuaries of south-east England (Suffolk, Essex and north Kent) are internationally significant conservation areas, because of their importance for migrating and overwintering birds. Recent erosion of saltmarsh vegetation has been extensive, up to 44% was lost from some estuaries in the 15 years prior to 1988 (Burd 1992). The loss of saltmarsh has important consequences for coastal defence against rising sea level, as vegetation offers some protection to the sea walls that protect much of the coast of south-east England. The reasons for the loss of the vegetation are not known (see Hughes 1999), but may be exacerbated by the absence, or rarity, of intertidal *Zostera* spp., particularly *Z. marina* which declined as a consequence of the wasting disease that began in the 1930s. Little formal research has been conducted in these estuaries and data concerning the effects of the wasting disease on these habitats are lacking. In the seagrass beds that remain (see below) there is overlap in the vertical distribution of both intertidal *Zostera* species and the pioneering saltmarsh plants *Salicornia europaea* and *Spartina anglica*. It has been presumed, without direct evidence, that the seagrasses may help sediment accretion, by slowing water movement and binding sediment with their roots, and promote successional development of saltmarsh vegetation. Beardall et al. (1988) estimated that the loss of *Z. marina* led to a loss of 15 million m^3 of sediment from the River Stour and increased its tidal volume by 30%. There are informal accounts of some intertidal mud-flats being covered by eelgrass with blades in excess of 1 m in length (M. Dixon, personal communication). These accounts clearly refer to *Z. marina*, and not to the much smaller *Z. noltii*, which is now the more common species in these estuaries. An unknown effect of the loss of intertidal *Z. marina* has been of the loss of protection it afforded to the saltmarshes, which are now eroding rapidly. Further, these intertidal seagrasses were important as a food for brent geese (*Branta bernicla bernicla*), a protected species, which have become an increasing nuisance to some as they

now graze on autumn-sown cereal crops (McKay et al. 1996).

Small-scale experiments to transplant intertidal *Zostera* spp. as a possible precursor to larger-scale transplants to reduce erosion and to benefit the feeding by birds, have been unsuccessful (M. Dixon, personal communication, personal observation). One reason for these failures could be related to the activities of the macrofauna inhabiting the sediment. Hughes (1999) suggested that the activities of the infauna were responsible, at least in part, for the loss of the pioneer zone vegetation, through bioturbation and herbivory. This conclusion was based on the results of Gerdol and Hughes (1993), who showed that the amphipod *Corophium volutator* prevented colonisation of mud by the pioneer zone plant *Salicornia europaea*, and those of Smith et al. (1996), who showed that the amphipods and the polychaete *Nereis diversicolor* reduced the abundance of epipelic diatoms. Hughes (1999) extended these observations and demonstrated that *C. volutator* and *N. diversicolor*, also prevented colonisation of the mud by filamentous algae. These algae, together with epipelic diatoms, *Salicornia* and *Zostera* spp. should be the first plants to colonise mud in these estuaries, and should start the processes of successional development of vegetated marsh rarely seen in south-east England.

Nereis diversicolor (hereafter referred to as *Nereis*) is widespread and abundant in these estuaries (Hughes and Gerdol 1997). *Nereis* burrow to a depth of 10–40 cm and are predominantly surface deposit feeders (see Smith et al. 1996 for recent review). They partially emerge from their burrows to engulf sediment and larger particles, including plant material, before withdrawing into their burrows (Olivier et al. 1996). Hughes (1999) considered the possibility that *Nereis* has increased in abundance over the past few decades, as it has in the Wadden Sea (e.g. Beukema 1989; Jensen 1992), and consequently may have had, and may continue to have, an effect on the ecology of these systems, including the potential to reduce colonisation of mud by pioneering plants. This paper considers the possibility that the activities of *Nereis* reduce the potential for *Zostera* spp. to expand their range, and may explain some of the failure of the previous *Zostera* transplant experiments. The approach was to transplant *Z. noltii* into areas where *Nereis* were common, but to protect some of the plants from the effects of the polychaetes. These field experiments were complemented by laboratory experiments in which plant performance in the presence and absence of *Nereis* was compared.

Methods

Although *Z. noltii* is the more common of the two species in south-east England, it is found only in occasional small patches, with the exception of two extensive beds (Wyer et al. 1977). These two large beds are on Maplin Sands, which has no public access, and in the Leigh Marshes National Nature Reserve, immediately to the east of Two Tree Island (Grid ref. TQ836856, Fig. 1). In the *Z. noltii* beds at Leigh there are individual plants or occasional small patches of *Z. marina*. Leigh was the source of the *Z. noltii* plants used for transplants. The sites chosen to receive transplants were: (1) Clementsgreen Creek on the River Crouch, (2) Pitsea Creek, also on the northern shore of Thames estuary, and (3) patches of bare mud adjacent to, and within, the upper edge of the Leigh *Z. noltii* bed (Fig. 2). Three different techniques of transplanting the seagrasses were used to investigate the efficacy of the different methods. Transplants were either single shoots, groups of five shoots connected by rhizomes, or cores of mud 10–15 cm deep containing several shoots.

Field experiments

Clementsgreen Creek

In February 1993 *Zostera noltii* were transplanted to a site at Clementsgreen Creek where *Nereis* were abundant (see Smith et al. 1996 for map). Exclusion areas were established in which deposit feeding by *Nereis* was prevented by inserting a cotton mesh

Fig. 1 Map of the Thames estuary showing **A** the location of Two Tree Island and **B** the location of the *Zostera* spp. bed at Leigh (*shaded area*) with the location of the experimental area (*arrow*)
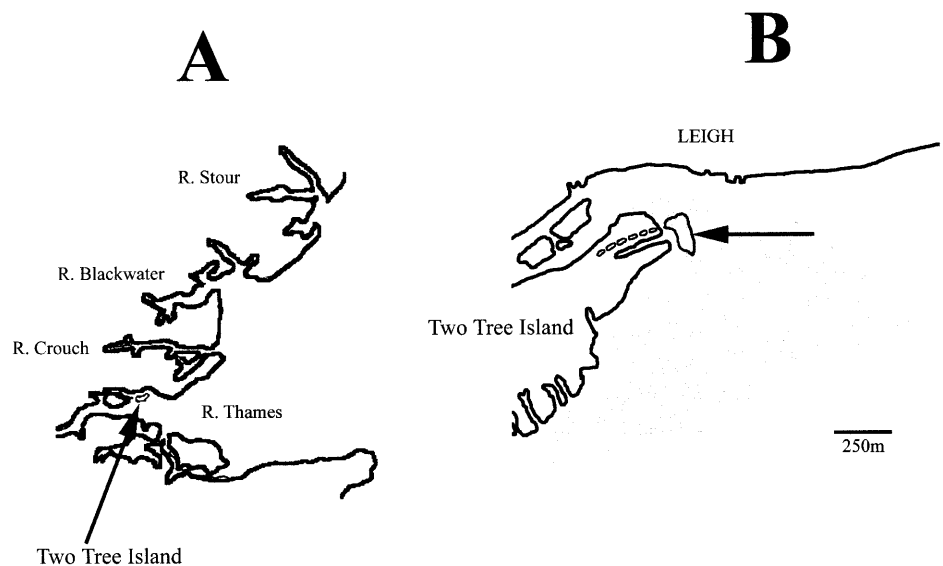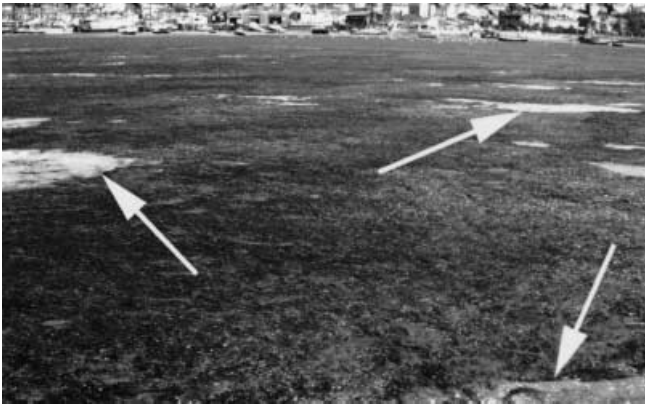
Fig. 2 Photograph of the upper part of the *Zostera* spp. bed at Leigh showing the bare patches of mud within the seagrasses which are colonised by *Nereis diversicolor*

(0.5 mm mesh size) under a slice of mud, 25×25 cm and 5 cm deep, which was raised using a spade and replaced after the insertion of the mesh. Control areas were treated in the same way but without inserting the mesh. Six *Z. noltii* plants, each consisting of a small core of mud and one shoot, were transplanted into each of the six exclusion areas and six control areas. One week later the remaining plants were recovered and taken to the laboratory where their fresh weight was determined. Six cores of mud were taken from the exclusion areas and six from the control areas to determine the abundance of *Nereis*.

Pitsea Creek

In October 1995 a turf of *Z. noltii* with a depth of 7 cm was taken from Leigh to an upper shore mud-flat at Pitsea Creek where *Nereis* were abundant. On the previous day six *Nereis* exclusion areas and six control areas had been established, as described above. Into each of the 12 areas, four *Zostera* plants, each with five shoots, excised from the turf, were placed into the mud and held in place with a metal staple, as described by Kenworthy and
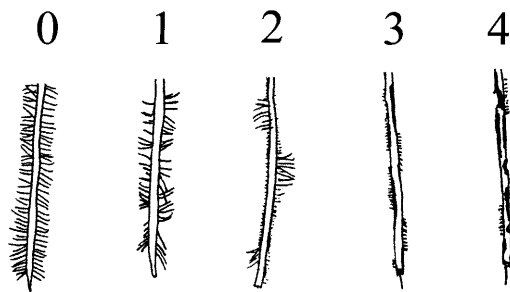

Fig. 3 The five-point scale devised as an index of root damage experienced by *Zostera noltii*:

0=<10% damage. Roots were a pale colour and damage was difficult to detect. The hairs gave a fluffy appearance to the roots

1=10–30% damage. Roots had a yellow colour, some damage to the root was visible, some hairs (in clumps) were missing

2=30–50% damage. Roots were light brown in colour, hairs were more sparse and often reduced in length, but patches of intact hairs present

3=50–70% damage. Brown colour with a few patches of stunted hairs. Some damage to the root was detected

4=>70% damage. Roots had a dark brown colour, surfaces were rough and indented and hairs, if present, were short

Fonseca (1992). After 1 week the remaining plants were removed carefully, placed in separate labelled bags and taken to the laboratory.

In the laboratory the plants were washed free of mud and the fresh and dry weights of each plant were determined. In addition, the condition of the roots was observed under a stereomicroscope and the extent of root damage within each group of five plants was estimated using a five-point scale (Fig. 3).

Leigh

In June 1994 and in October 1996, 30 cores of mud were collected randomly from within the upper seagrass bed and 30 from the adjacent areas of bare mud to estimate the abundance of the macrofauna. The cores were 8 cm in diameter and 15–20 cm deep, the depth of the underlying hard clay, into which the corer could not be pushed. The top 5 cm of each core was sieved through a 0.5 mm mesh to retain the small animals, and the remaining sediment was broken up and carefully sorted by hand to reveal the larger deeper burrowing invertebrates. All the invertebrates were identified and counted.

In November 1996, ten cores of *Z. noltii* (8 cm in diameter and 15 cm deep) were taken randomly from within the *Z. noltii* bed and transplanted almost immediately to adjacent areas of bare mud. The seagrass cores were placed in holes formed by the removal of similar cores of sediment using the same corer. Five cores were placed into bags of 0.5 mm cotton mesh before insertion into the holes so that the surface of the transplanted cores was flush with the surface of the surrounding sediment, and five were placed in the holes without mesh. These cores are referred to as bagged and unbagged. Ten similar cores were transplanted back into the *Zostera* bed to act as a control for the method. After 32 days the transplanted cores were recovered, by use of the bags or by re-coring the unbagged cores, and taken to the laboratory where the number of leaves on each shoot was counted and the length of each leaf was measured. The sediment in the cores from the bare mud patches was washed through a 1-mm sieve to capture any macrofauna, which were identified and counted.

Laboratory experiments

The effects of Nereis *on* Z. noltii

In November 1993, ten cylindrical corers (14 cm diameter and 15 cm deep) containing mud free of macrofauna were established in a laboratory tidal aquarium where the sediment surface was immersed for 3 h twice per day. This degree of immersion was similar to that experienced by *Zostera* at Leigh and at the other transplant sites. The salinity of the water was maintained at 33 and the temperature at 20°C. Thirty-five *Nereis* were added to each of five cores and five cores were left as controls. After 8 days, five *Z. noltii* plants, consisting of a small core of sediment and one shoot were planted in each of the ten cores and their fate was monitored for 9 days. This experiment was repeated for 8 days in February 1994.

In November 1994, 20 corers containing mud with *Nereis* from Pitsea were placed in the laboratory tidal aquarium. Ten cores were left as controls and ten had a cotton mesh, similar to that used in the field experiments, inserted at a depth of 5 cm to exclude *Nereis* from the surface. Ten *Z. noltii* shoots with a small core of sediment around the roots were planted individually into each core. After 3 weeks the remaining plants were counted.

The effects of Nereis *on seeds*

An intended investigation of the effects of *Nereis* on the survival and the burial of seeds of *Z. noltii* and *Z. marina* was not possible. The production of seeds by *Z. noltii* during the period of this study was low and intermittent and insufficient could be collected for the experiments. Since *Z. marina* were relatively rare, and proba-

bly annual plants depending on seeds for continued survival, it was deemed inappropriate to take seeds for experiments. Instead, to assess the potential impact of *Nereis* on seeds, the seeds of *Spartina anglica* were used as surrogates for *Zostera* seeds. Although *Spartina* seeds are larger than those of the two *Zostera* species they were readily available. In November 1993 ten cores were established in the laboratory, as described above, five with no macrofauna and five with 35 *Nereis* added to each. The cores were placed in the tidal regime for 2 days to allow the animals to acclimatise, after which 20 *Spartina* seeds, with the husks removed, were placed on the surface of the sediment in each core. The fate of the seeds was monitored for 8 days, after which each core of mud was divided into 1-cm-thick sections to determine the vertical distribution of the remaining seeds. This experiment was repeated in February 1994.

Throughout, the data were transformed (log $n+1$) where necessary before performing parametric statistical tests and the sample units were cores or exclusion areas to avoid pseudoreplication.

Results

Field experiments

Clementsgreen Creek

Significantly more *Z. noltii* were recovered from the *Nereis* exclusion areas (4.83=81%) than from the control areas (1.17=19%) (unpaired *t*-test, $t=5.431$; $P<0.0005$). There were significantly more *Nereis* in the control areas (1,940m^{-2}±76 SE) than in the exclusion areas (250m^{-2}±49 SE) (unpaired *t*-test, $t=6.421$; $P<0.005$), where mainly small *Nereis* were found in the mud above the mesh.

Pitsea Creek

The differences in the dry weight, root condition and survival of *Z. noltii* from *Nereis* exclusion areas and from control areas, where the mean abundance of *Nereis* was 1,200m^{-2}, are shown in Fig. 4 (A, B and C, respectively). The mean dry weight of plants recovered from the exclusion areas was significantly higher than that of the plants from the control areas. The mean index of root damage for plants exposed to *Nereis* in the control areas was significantly higher than the mean index of root damage recorded from the exclusion areas. A mean of 4.4 shoots per transplanted plant were recovered from the control areas, compared with 4.9 from the exclusion areas. Mortality, recorded as the complete absence of leaves from any of the five shoots in each trial, was significantly higher in the control areas than in the exclusion areas (unpaired *t*-test, $t=2.1$; $P<0.05$).

Leigh

In July 1994 the only invertebrate found in the bare mud was *Nereis*, with a mean density of 430m^{-2}, but no worms were found in the cores from within the *Zostera* bed. In October 1996 only *Nereis* was found in the bare
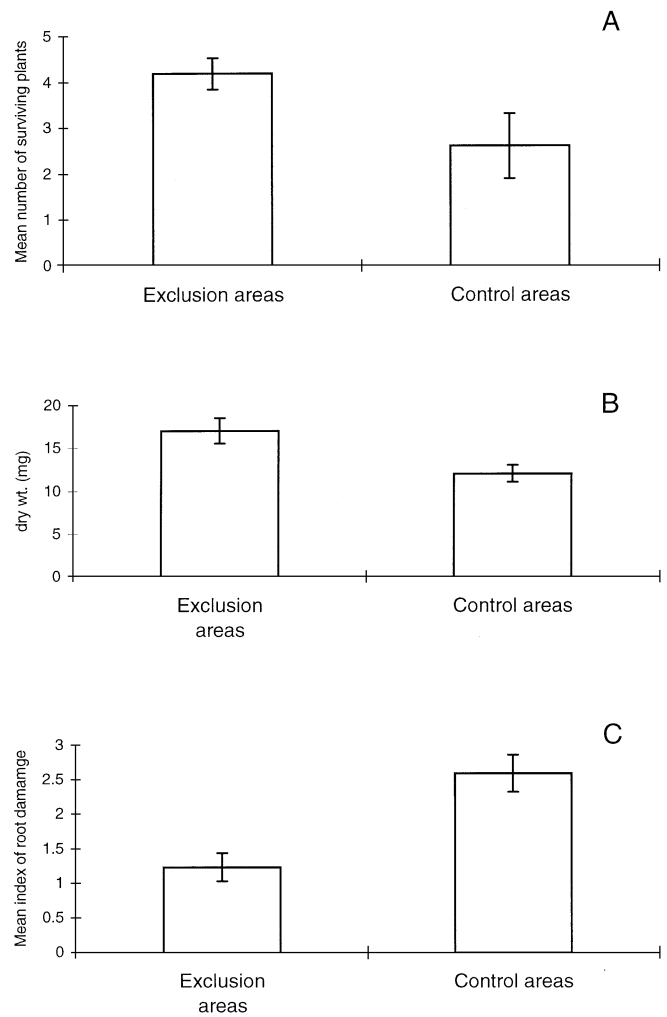

Fig. 4 The mean number of surviving plants (**A**), the mean dry weight of the plants (**B**) and the mean index of root damage (**C**) of the *Zostera noltii* transplanted to exclusion areas and control areas in Pitsea Creek

mud patches, with a mean density of 718m^{-2}, and none were found in the *Zostera* bed. The macrofauna within the *Zostera* bed included *Littorina littorea* and *Hydrobia ulvae*, which were found on the seagrasses and the mud surface, and three species of burrowing bivalves, *Cerastoderma edule*, *Scrobicularia plana* and *Mya arenaria*.

There was no significant difference in either the number of leaves or in the length of the leaves in the plants from the bagged and unbagged cores transplanted back into the seagrass bed. However, the *Z. noltii* transplanted to the bare mud in mesh bags had a significantly greater number of leaves and total length of leaves, than those in the unbagged cores (Fig. 5). On recovery the unbagged cores contained a mean of six *Nereis* and the bagged cores a mean of one.
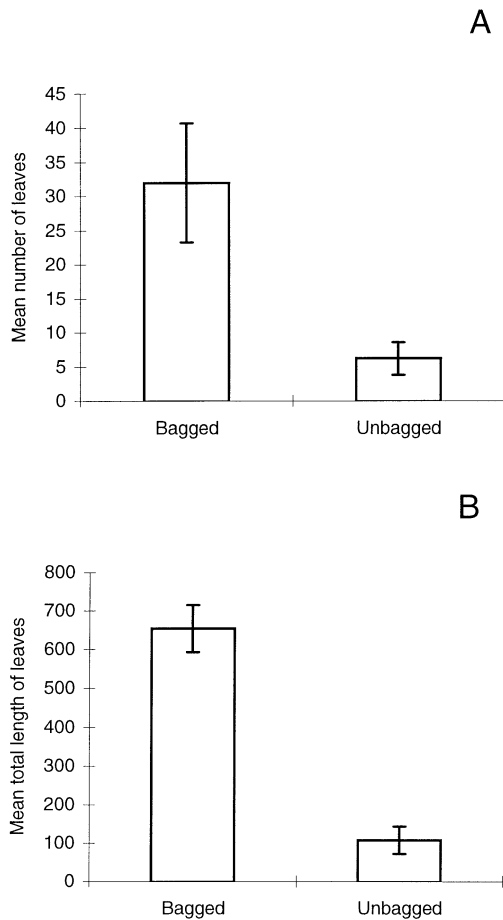
A

November 1993

B

February 1994

Fig. 6 Survivorship curves for *Zostera noltii* planted in cores in the laboratory where *Nereis diversicolor* had access to the plants (*diamonds*) and in control cores (*squares*)

Fig. 5 The mean number of leaves (**A**) and the mean total length of leaves (**B**) of the *Zostera noltii* transplanted in mesh bags and without mesh bags into bare sediment adjacent to the seagrass bed at Leigh

Laboratory experiments

The effects of Nereis on Z. noltii plants

In November 1993 and February 1994 no *Z. noltii* shoots survived beyond 9 days in cores where *Nereis* were present (Fig. 6). In the control cores all the shoots survived. In November 1994 the mortality of *Z. noltii* was significantly higher in control cores than in the cores where *Nereis* were present but prevented from reaching the surface by the mesh. After 21 days the mean number surviving in control cores (6.0) was significantly lower (unpaired *t*-test, $t=3.7$; $P<0.05$) than the mean of 8.6 retrieved from the exclusion cores. Subsequently, observations were made of captive *Nereis*. The worms were fed with fish flake and pieces of plants, including excised leaves of *Z. marina* and *Z. noltii*. The worms were seen to partly emerge from their burrows, grasp the seagrass leaves and drag them down into their burrows.
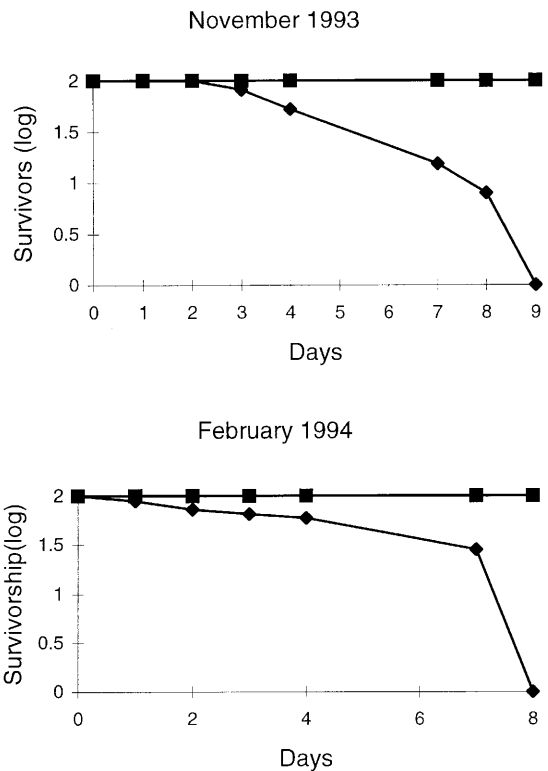
The effects of Nereis on seeds

The proportion of *Spartina* seeds visible on the surface in the two experiments is shown in Fig. 7. In both experiments significantly more seeds remained on the surface of the control cores than in the cores containing *Nereis* (unpaired *t*-tests, $t=4.9$, $P<0.005$ and $t=5.8$, $P<0.005$, respectively). On sectioning the cores, it became apparent that the seeds had been buried by the activities of the polychaetes. In the control cores 93% of the seeds were visible on the surface or in the surface 1 cm slice, and the remainder were found at a depth of 1–2 cm. In the cores containing *Nereis* some seeds were found at depths below 2 cm in both experiments, and in the first experiment some seeds were found below 4 cm deep (Fig. 8). Subsequent observations have shown that *Nereis* will grasp *Spartina* seeds and drag them into their burrows.

Discussion

The results of all the field experiments indicate that *Nereis* has a negative effect on the success of *Z. noltii* transplants, as in each experiment the protected transplants were more successful than the unprotected ones. There are two mechanisms by which *Nereis* can have these effects. Firstly, *Nereis* are capable of grasping
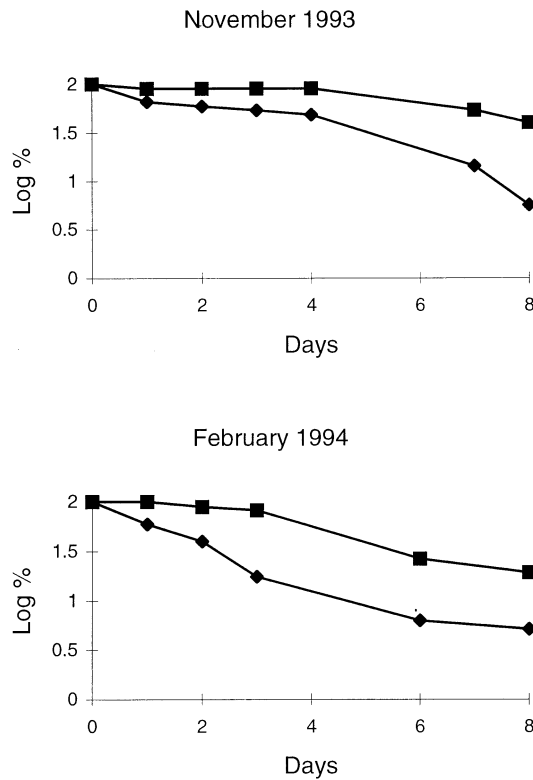
November 1993

February 1994

Fig. 7 The proportion (%) (on a logarithmic scale) of the *Spartina* seeds remaining on the surface of cores with *Nereis diversicolor* (*diamonds*) and control cores with no worms (*squares*)

December 1993

February 1994

Fig. 8 The mean proportion (±SE) of the *Spartina* seeds recovered from different depths in cores containing *Nereis diversicolor*

seagrass leaves that lie on the surface of the sediment, breaking or damaging them, and pulling fragments into their burrows. This behaviour has been observed in the laboratory. The second mechanism is the potential effect of the burrowing worms on the roots of the seagrasses. The higher degree of damage of roots in plants exposed to *Nereis* in the experiments at Pitsea may be an artefact of the experimental procedure, as the plants were placed above *Nereis* that were already present. The damage may have been caused simply by the animals burrowing upwards through the transplanted *Zostera* to re-establish access to the surface. The same may also be true of the Leigh experiment where *Nereis* under, or to the side of, the unprotected *Zostera* cores burrowed up through them to the surface; more *Nereis* were found in these cores than in the bagged cores. Nevertheless, the experiments demonstrate that *Nereis* may restrict the natural extension by vegetative growth of plants over established *Nereis* burrows. This may explain the continued existence of distinct patches of bare mud containing *Nereis* within the Leigh seagrass bed. Further, *Nereis* may interfere with established plants if under natural conditions the worms create new burrows or make their existing burrows more complex. Little is known of the behaviour of *Nereis* in sediments but Davey (1994) demonstrated under laboratory conditions that the structure of new *Nereis* burrows becomes more complex with time as the
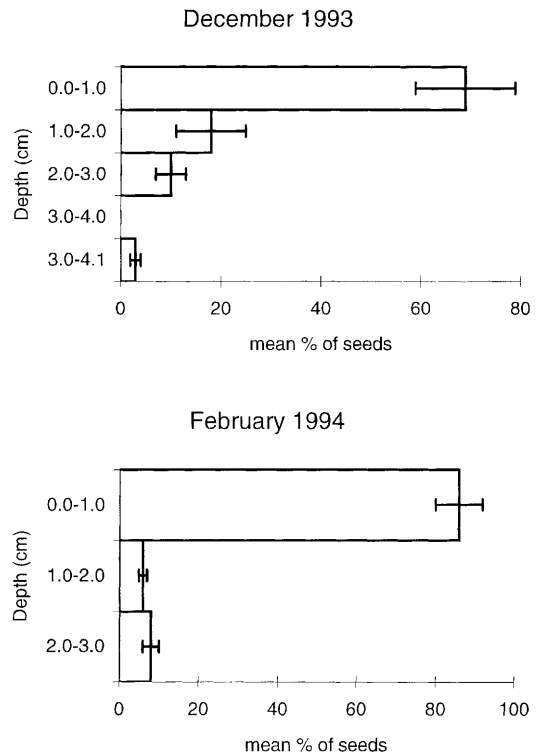
worms create more openings to the surface. If this behaviour occurs in situ, elaboration of burrows could interfere with established plants nearby, although Davey (1994) found that the casts of in situ burrows were less elaborate, possibly because of restrictions imposed by intraspecific interactions.

The experiments on the effect of *Nereis* on *Spartina* seeds, indicate that these polychaetes may prevent colonisation by seeds too, by burying them. Consumption of seeds was not apparent in the experiments on *Spartina* seeds, but *Nereis* have been observed to eat the smaller *Z. noltii* seeds (personal observation). *Nereis* may eat a variety of seedlings too (Paramor and Hughes, in preparation) and, like *Corophium volutator*, can prevent seedling establishment by physically disturbing the surface of the sediment. Seed burial may reduce germination success if light, reduced salinity or relatively high temperatures are needed to break seed dormancy. Harrison (1991) detected no effect of light or temperature on breaking the physiological dormancy of *Z. marina* seeds, in contrast to previous workers, but recorded more successful germination in reduced salinity. Hootsmans et al. (1987) had reported previously that germination of *Z. marina* was promoted by higher temperatures in the range of 10–30°C. For *Z. noltii*, Loques et al. (1990) noted that in experiments germination was increased by low salinity (1–10), with no germination at salinities above 20, and that temperature had no effect. Burial may re-

duce the survival of seedlings if they, or the seeds, were buried deep enough to prevent access to the surface.

There is some evidence which indicates that *N. diversicolor* has become more abundant around the southern North Sea in the past few decades, particularly in the Wadden Sea (e.g. Beukema 1989; Jensen 1992), but also in the estuaries of south-east England (Hughes 1999). Hughes and Gerdol (1997) found *Nereis* in 93% of the sites examined in the estuaries of the Crouch and the Blackwater. Their widespread distributions and abundance, combined with their effects on plants, identified in these, and previous, experiments, indicate that these polychaetes may have major effects on these estuarine ecosystems, particularly in reducing the potential for colonisation by plants. Hughes (1999) suggested that *Nereis*, together with *Corophium volutator*, could be responsible for the lack of development of pioneer zone vegetation, and the erosion of established saltmarsh vegetation, by making the sediment within the creeks of the marsh more erodable. The results of this study support this hypothesis, for it is clear that *Nereis* can restrict the colonisation of mud by *Zostera*.

At Leigh there is an almost complete separation of *Nereis* and *Zostera.* There is the possibility that on the upper mud-flats of the estuaries of south-east England there are two stable states. One state is domination by plants, in this case *Zostera*, which prevent colonisation by burrowing animals, in this case *Nereis,* and the other state is domination by *Nereis*, and possibly other animals to a lesser extent, which prevent colonisation by plants. The restriction of the distribution by some plants by the infauna in these estuaries has been demonstrated (Gerdol and Hughes 1993; Smith et al. 1996; Hughes 1999, this study). That there are very few *Nereis* within the sediment in the seagrass bed may indicate a reciprocal interaction, where the dense root systems of the seagrasses may prevent burrowing by the polychaetes. That vascular plants restrict colonisation of sediment by *Nereis* has been demonstrated (in preparation). Harrison (1987) identified a similar interaction between *Zostera* spp. and a burrowing decapod, *Callianassa californiensis*. The decapods decreased in abundance when the seagrasses colonised the substrata, usually in the spring, and Harrison concluded that this may have been caused by the seagrasses preventing burrowing by the crustaceans. Experimental removal of the seagrasses allowed *Callianassa,* and some tubeworms, to recolonise the sediment. Experimental additions of shoots of *Z. japonica* caused temporary decreases in decapod abundance, but established populations of *Callianassa* eventually destroyed the transplanted seagrasses, usually in the summer when the animals were most active. Philippart (1994) also recorded spatially distinct distributions of *Z. noltii* and a polychaete, in this case *Arenicola marina*. Following reciprocal transplant experiments she concluded that the worms restricted colonisation by seagrass, due to their bioturbatory activities. However, the restriction on the distribution of the worms was not due to the seagrasses preventing burrowing, but was due to the presence of underlying clay, which restricted burrow forma-

tion. Philippart concluded that an increase in lugworm density in the Dutch Wadden Sea may have contributed to the decline of the area covered by *Z. noltii* over the last 20 years. Short and Wyllie-Echeverria (1996) in their review of all disturbances on seagrasses, referred to a similar example in San Francisco Bay where patches of *Z. marina* are surrounded by worms that may prevent extension of the seagrass.

It is possible, therefore, that the loss of *Z. marina* due to wasting disease from the 1930s may have allowed an expansion in the range of burrowing animals, including *Nereis*, and these now are important in preventing any expansion in the range of intertidal *Zostera* and other plants. The distributions of the two *Zostera* species overlap and although *Z. noltii* was less affected by the wasting disease than *Z. marina* (Vergeer and Den Hartog 1991), any potential for significant expansion in its range following the demise of its congener has not been realised, possibly because of the effects of *Nereis*.

Previous transplants of *Z. noltii* and *Z. marina* in some East Anglian estuaries used larger "turfs" cut from the seagrass bed and moved to other estuaries (Ranwell et al. 1974). These were more successful than transplanting individual shoots (turions). The different techniques for transplanting the seagrasses in this study gave somewhat different results. Planting individual plants was the least successful, with a high mortality recorded within 1 week. Transplanting cores of *Z. noltii* was the most successful, with no apparent mortality after 32 days, and will be used in forthcoming larger-scale trials.

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