

Mark Emmerson

## Remedial habitat creation: does *Nereis diversicolor* play a confounding role in the colonisation and establishment of the pioneering saltmarsh plant, *Spartina anglica*?

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**Abstract** Increasing concerns over global warming and expected sea level rises have led to the adoption of new coastal management strategies around the south-east coast of England. This paper explores the role played by the estuarine invertebrate *Nereis diversicolor* in limiting the colonisation and establishment of the invasive pioneering salt marsh plant, *Spartina anglica*. The biology of *N. diversicolor* is briefly reviewed and data from field experiments are presented demonstrating significant negative effects of worm abundance on transplanted *S. anglica* biomass. Laboratory-based experiments demonstrated significant negative effects of *N. diversicolor* abundance on the survival of *S. anglica* seeds transplanted to sediment cores. The importance of estuarine invertebrates in engineering the mudflat habitat may confound the foreseen ecosystem services and function provided by saltmarsh management schemes.

**Key words** Community · Structure · Composition · Function

### Introduction

The ragworm *Nereis diversicolor* has a wide distribution ranging from the North Sea and western Baltic, through the English Channel and the Atlantic of north-western Europe to the Mediterranean (Hayward and Ryland 1995). *N. diversicolor* inhabits U-shaped or ramifying burrows in the sediment and has traditionally been described as a detritus and substrate feeder on the basis of gut content analysis (Goerke 1971; Fauchald and Jumars 1979). However, anecdotal observations and laboratory experiments carried out by Pashley (1985) suggest that *N. diversicolor* is an omnivore, feeding by carrion scavenging, deposit and filter

feeding, and active consumption of invertebrates, including conspecifics (Harley 1956; Goerke 1971; Fauchald and Jumars 1979; Reise 1979; Pashley 1985; Riisgård 1991; Riisgård et al. 1994). The combination of locally high densities, burrowing habit and ingestion of a range of particles of widely different types has led some authors to suggest that *N. diversicolor* may have major impacts on the stability of the sediment matrix and other infaunal species (Rönn et al. 1988). In the present paper, this functional role of *N. diversicolor* is examined with respect to the establishment and growth of the high-shore, pioneer saltmarsh grass, *Spartina anglica*. Previous studies have reported significant seed predation by *Corophium volutator* on another pioneer saltmarsh species, *Salicornia europaea* (Gerdol and Hughes 1993). An understanding of the effects of intertidal invertebrates on these species is important if proposed management strategies to allow the development of saltmarsh communities in areas of managed retreat (Dixon et al. 1998) are to be properly evaluated

### Methods

*Spartina anglica* is a hybrid cross resulting from the American *S. alterniflora* and the European *S. maritima*. On the saltmarsh it is present in the fertile tetraploid form and a sterile diploid form. The sterile hybrid is termed *S. townsendii* and the fertile hybrid *S. anglica*. Identification is complicated by the occurrence in some diploid individuals of fertile seeds.

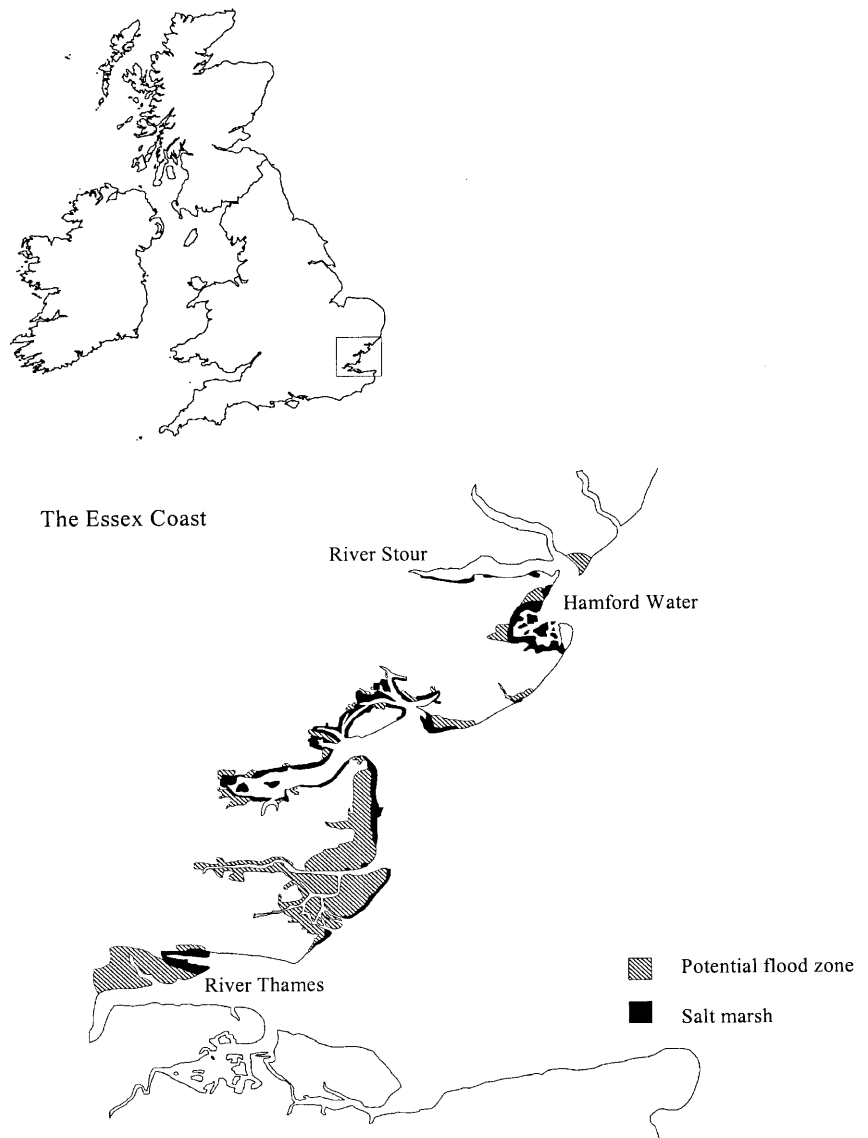
#### Field studies

The Essex coast, south-east England (Fig. 1) has been accorded considerable conservation status; it is considered to be one of the top five coastal wetlands in Britain in terms of value to bird, invertebrate and plant communities and is now one of 22 areas in England designated by the Ministry of Agriculture, Fisheries and Food (MAFF) under the Environmentally Sensitive Areas (ESA) scheme. The ESA is largely within the greater Thames Estuary Natural Area, designated as part of the UK Biodiversity Action Plan and a significant proportion is included within the mid-Essex Special Protection Area (SPA) in addition to being classified as a RAMSAR site, under the Convention on Wetlands of International Importance signed at Ramsar, Iran, in 1971. The adjoining mud-

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M. Emmerson (✉)  
Culterty Field Station, Department of Zoology,  
University of Aberdeen, Newburgh, Ellon, AB41 8RU, UK  
e-mail: m.emmerson@abdn.ac.uk

**Fig. 1** Essex coastline showing location of study site Hamford Water, and the extent of en-walled saltmarsh in Essex, with potential flood zones



flats, saltmarshes and estuaries are a proposed marine Special Area of Conservation (SAC) (MAFF 1998).

The field work was carried out in a region of Hamford Water known as the “wade” ( $1^{\circ}10'60''$  E  $51^{\circ}50'15''$  N). Hamford Water, found south of the river Stour estuary (Fig. 1) is an internationally important site for many migratory birds, such as brent geese (*Brenta bernicla*), redshank (*Tringla totanus*), wigeon (*Anas penelope*), oyster catchers (*Haematopus ostralegus*) and shelduck (*Tadorna tadorna*).

Boating activity in the western reaches of the estuary is limited by the presence of a causeway which runs across the mudflats to Horsey Island and which has been present historically since the seventeenth century. Located behind the seawall and formed when coastal defences were created is a “borrow dike”. This runs the length of the coastal defences at Hamford Water and at various points along the seawall is connected to the saltings on the seaward side by drains. This provides a source of fresh water to the marsh over most periods of the year. Beyond the “borrow dike”, the land use is dominated by agriculture and pasture.

#### *Spartina* transplant experiments

To assess the effects of *N. diversicolor* on the abundance and distribution of *S. anglica*, six replicate *N. diversicolor* exclusion ar-

reas were established in October 1994. The exclusion areas were situated approximately 60 m along and adjacent to the causeway to Horsey Island, at a site noted to have a particularly high abundance of *N. diversicolor* (approximately  $950\text{--}1,000\text{ m}^{-2}$ ). Because of the deep burrowing nature of *N. diversicolor*, the worms could not be removed without sieving and disrupting the sediment structure. To overcome this problem, a turf of mud  $30 \times 30$  cm and 5–7 cm thick was removed, a mat of netting 500  $\mu\text{m}$  mesh size was inserted beneath the mud and the turf returned to its original position. The surface of the exclusion site was then sprayed with a proprietary pyrethrum-based insecticide (Bug Gun, ICI) to remove any worms that remained. This procedure was repeated once, after 2 weeks. Each exclusion area had an appropriate control area located approximately 50 cm away. These control areas underwent the same treatment as exclusion areas but without insertion of the excluding mat and application of the pesticide to remove worms.

Specimens of *S. anglica* were collected, individually rinsed and wet weights recorded using an Aculab A639 J portable balance. Each plant was individually labelled using a piece of plastic and a small length of wire. Five plants were placed in each exclusion and control area and left for 28 days. Upon collection, plants were rinsed in seawater and taken to the laboratory where they were fixed in formalin.

Three cores (6.5 cm diameter) were taken from each exclusion and control area; these were returned to the laboratory and sieved

using a sieve of mesh size 500  $\mu\text{m}$ . Any *N. diversicolor* found were counted and stored live for later use in laboratory experiments. The maximum root and shoot lengths were measured and wet weights recorded. The plants were then dried to a constant weight at 60°C. The roots were then separated from shoots and rhizomes and weighed separately.

#### Laboratory studies

These experiments were carried out to determine any effect *N. diversicolor* might be having on the colonisation of mud-flats by *S. anglica* through seed propagation.

#### Seed transplants to tidal simulation

In January 1995, 20 corers, 10 cm diameter and 11 cm long, were used to collect cores of sediment from a site at the "wade", Hamford Water, Essex, UK. The cores of sediment were taken to the laboratory and stored until used in an artificial tidal regime of 3 h submergence every 12 h, using water  $34.5 \pm 1.54$  (psu) at 10°C and in 12 h light/12 h dark. Exclusion cores had *N. diversicolor* excluded from the surface by placing a circular disc of netting (500  $\mu\text{m}$  mesh size) within the sediment at a depth of 2 cm. Control cores had seven *N. diversicolor* added to each (equivalent to 900  $\text{m}^2$ ).

*S. anglica* seeds were collected in late October 1994. The seed heads were collected from the plants and returned to the laboratory, where seeds were removed. All seeds were washed in a 5% solution of sodium hypochlorite after Marks and Truscott (1974) and then rinsed in distilled water and stored in petri dishes with dampened discs of filter paper at 10°C for later use.

#### *S. anglica* seed transplant experiment 1

Dehusked seeds of *S. anglica* were germinated at 26°C after being pierced with a needle and exposed to 24 h light. These were then transplanted to the tidal system. Ten *S. anglica* seeds were transplanted to each of five exclusion and five control cores. These were left in the tidal simulation for 14 days. At the end of this period those seeds which were recoverable from the sediment surface were counted. Many of the seeds were not immediately recoverable due in part to their small size and the bioturbatory activities of *N. diversicolor* in control cores. To determine to what extent the seeds had been grazed (eaten) or buried, each core was sectioned in 0.5 cm slices to a depth of 3 cm in control cores and to the depth of the netting in exclusion cores. Each section was sieved using a sieve of mesh size 500  $\mu\text{m}$  and the depth at which seeds were found in the sediment column were noted. The remaining sediment was sieved (mesh size 500  $\mu\text{m}$ ) to determine the number of individual worms in each core.

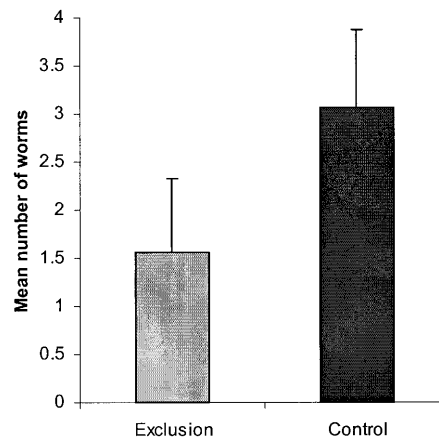
#### *S. anglica* seed transplant experiment 2

Dehusked intact seeds were treated with gibberellic acid. This initiated abnormal levels of growth in the seeds relative to untreated seeds. These oversized precocious seedlings were transplanted to five control and five exclusion mud cores to allow for easy recovery and quantification of worm-caused damage. Five seeds were placed in each core. These were left in the tidal simulation for a period of 14 days at the end of which time the procedures detailed in transplant experiment 1 for the recovery and quantification of seeds were repeated.

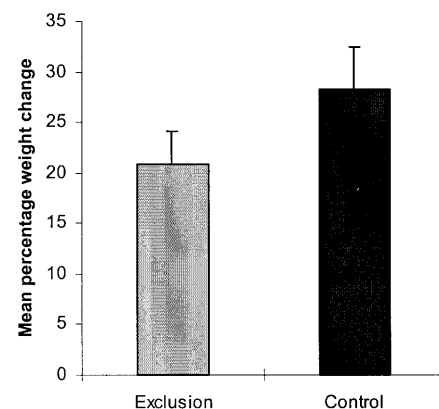
## Results

### *Spartina* transplant experiments

There were significantly more worms in control areas ( $P < 0.05$ , unpaired *t*-test; Fig. 2). Weight loss in *S. ang-*

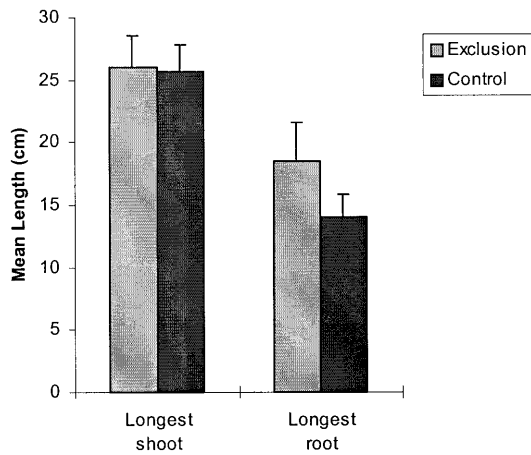


**Fig. 2** Field experiments: there were significantly more worms in control areas compared to the treatment sites ( $P < 0.05$ , unpaired *t*-test)

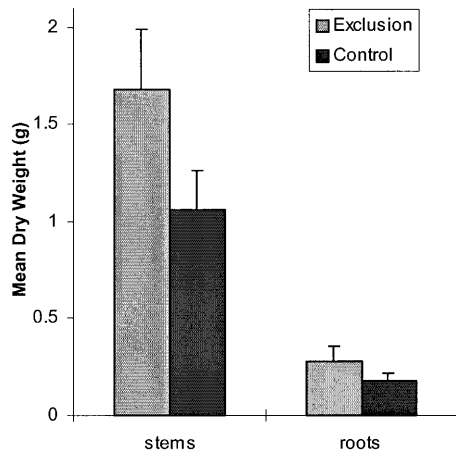


**Fig. 3** Field experiments: mean percentage change in weight over duration of experiment was significantly different ( $P < 0.007$ , unpaired *t*-test)

*lica* plants from both *N. diversicolor* exclusion and control areas was significant over the duration of the experiment ( $P < 0.000$  and  $P < 0.000$ , respectively, paired *t*-test). The mean percentage change in weight of *S. anglica* from control areas containing *N. diversicolor* was significantly greater (Fig. 3) than in those specimens of *S. anglica* transplanted to sites in which *N. diversicolor* had been excluded ( $P < 0.007$ , unpaired *t*-test). There was no significant difference between the mean maximum shoot length of *S. anglica* from control and *N. diversicolor* exclusion areas (Fig. 4). However, the roots of *S. anglica* plants transplanted to control areas and exposed to significantly higher densities of *N. diversicolor* ( $P < 0.05$ , unpaired *t*-test; Fig. 2), were significantly shorter (Fig. 4) than the roots of plants transplanted to *N. diversicolor* exclusion areas ( $P < 0.02$ , unpaired *t*-test). There was a significant difference (Fig. 5) between the mean dry weight fraction of stems/rhizomes and roots from control and *N. diversicolor* excluded areas ( $P < 0.01$ , unpaired *t*-test and  $P < 0.05$ , unpaired *t*-test, respectively).



**Fig. 4** Field experiments: mean longest shoot lengths of *S. anglica* were not significantly different, but the mean longest root lengths of plants exposed to *N. diversicolor* were significantly shorter ( $P < 0.05$ , unpaired *t*-test)



**Fig. 5** Field experiments: *S. anglica* from control areas weighed significantly less than *S. anglica* plants that had not been exposed to *N. diversicolor*, for both the stem/rhizome and root fractions ( $P < 0.01$  and  $P < 0.05$ , respectively, unpaired *t*-test)

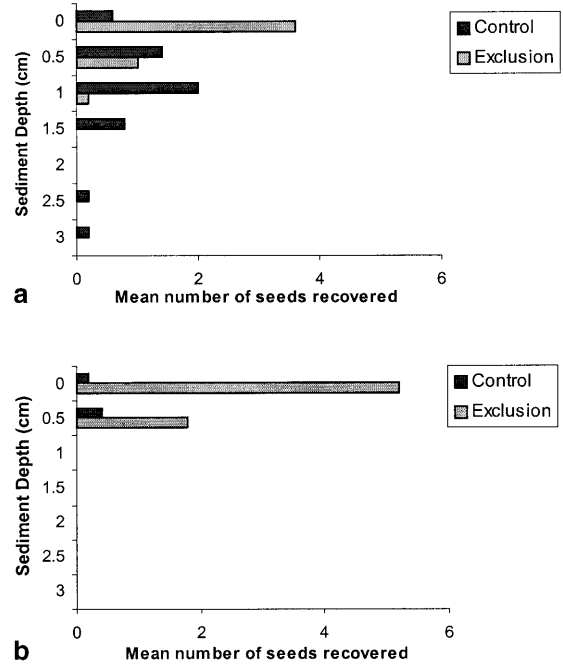
#### Laboratory studies

##### *S. anglica* seed transplant experiment 1

The depth distribution of seeds from control and exclusion cores were significantly different ( $P < 0.01$ ,  $\chi^2$ ). More seeds were found on the sediment surface (0 cm) in *N. diversicolor*-excluded mud cores than in control cores and more seeds were found at depth in cores containing *N. diversicolor* (Fig. 6a).

##### *S. anglica* seed transplant experiment 2

The depth distribution of seeds from control and exclusion cores were not significantly different when compared using  $\chi^2$ . However, the mean number of seeds



**Fig. 6a,b** Laboratory experiments. **a** Seed transplant experiment 1: the depth at which *S. anglica* seeds were recovered from the sediment was significantly different ( $P < 0.01$ ,  $\chi^2$ ), fewer seeds were recovered from cores containing *N. diversicolor*. **b** Seed transplant experiment 2: the depth distribution of seeds recovered from control and *N. diversicolor* treatment cores was not significantly different, but mean number of seeds on sediment surface differed significantly ( $P < 0.006$ , unpaired *t*-test)

found at the sediment surface (0 cm) was significantly different in control and exclusion cores ( $P < 0.006$ , unpaired *t*-test), with more seeds present at the surface in cores from which *N. diversicolor* had been effectively removed (Fig. 6b).

## Discussion

### Field studies

The significant loss in weight of *S. anglica* from both control and exclusion areas can be accounted for by the autumn senescence of *S. anglica* leaves, also reported for *S. alterniflora* by Levinton and Stewart (1988). This can in turn be correlated with seasonal increases in sediment microbial productivity (Ruble 1982), ultimately benefiting deposit-feeding communities. In the presence of *N. diversicolor*, *S. anglica* plants lost a significantly higher proportion of their weight over the course of the experiment compared with plants in plots from which *N. diversicolor* had been excluded. Specimens of *S. anglica* from control plots containing *N. diversicolor* had significantly shorter mean maximum root lengths than specimens from plots, again, from which *N. diversicolor* had been removed. The reduced mean maximum root lengths of *S. anglica* when exposed to *N. diversicolor* might infer some form of grazing pressure on *S. anglica*, although



none has been previously reported. If grazing were to have occurred, it may have been an active process (the worms actively sought the roots) or a passive process (the worms unselectively grazed everything in the vicinity of their burrows). Worms forage for a short distance immediately around their burrows, extending short distances (typically 1.5 cm) in a straight line, whilst taking bites from the sediment surface with their jaws and proboscis, the jaws being used as rakes to aid the collection of surface material by the everted proboscis (Goerke 1971). This second conclusion is more likely, given Pashley's (1985) conclusions regarding the unselective feeding nature of *N. diversicolor*. Alternatively, the physical burrowing activities of *N. diversicolor* might in some way impair root growth if in close proximity to *S. anglica*. *N. diversicolor* inhabits U-shaped or ramifying burrows in the sediment, most burrows typically being approximately 10 cm deep (Harley 1956), although deeper burrows have been described, to a depth of 30 cm in summer (Schäfer 1972) and up to 60 cm in winter (Muus 1967; cited in Pashley 1985). The mean root length of plants from *N. diversicolor*-exclusion areas were significantly longer than in control plants despite the presence of an excluding mat at a depth of 5–7 cm in the sediment. It was noted whilst collecting plants from each area that the roots of *S. anglica* had in fact penetrated the excluding mesh to a depth of 10–15 cm in some instances.

#### Laboratory studies

These experiments have demonstrated the overall trend of the loss and disappearance of seeds from control mud cores containing high densities of *N. diversicolor* equal to 900 m<sup>-2</sup>. Jensen (1992) reported densities ranging from 2,000 to 3,800 individuals m<sup>-2</sup> in the Skallingen area of the Danish Wadden sea, whilst Riisgård (1991) reports densities of 2,400 individuals m<sup>-2</sup> from Odense Fjord, Denmark, a 2- to 4-fold increase in the densities used in these experiments. It is assumed that those worms present grazed any seeds that were not recovered. This "grazing" is most likely a passive process, involving shredding of *S. anglica* seeds into smaller unrecognisable fragments, which subsequently form the basis for detritus as they are progressively decomposed by bacteria. Groenendijk (1986) described the loss of transplanted seeds from sediments, through erosion/accretion processes and the rapid deterioration of implanted seeds in the sediment, which caused a serious reduction in potential population size. The combined bioturbatory effects of *N. diversicolor* and *C. volutator*, being dominant members of the deposit-feeding community, could also conceivably account for such losses. This is a factor which at the time may have been overlooked.

In south-east England the development of historical coastal defences has contributed to a reduction in the area of intertidal habitats by fixing the limit of their landward migration; this effect is often referred to as "coastal

squeeze" (MAFF 1995). This has led to the adoption of some novel management strategies at a number of localities around the Essex coast. These schemes known variously as "coastal realignment" and "managed retreat" strategies have involved removal or breaching, of certain existing, but deteriorated, seawalls and make use of enhanced low level counterwalls to limit the extent of saline flooding. The philosophy behind this approach has been "to allow natural processes to work, with as little human engineering and interference as possible" (Dixon et al. 1998).

British and other Northern European saltmarshes are found in the region above the lowest neap high tide. Within this region, saltmarsh plants are not covered by the tide daily but are covered periodically by spring high tides. Saltmarshes demonstrate a clear zonation and successional sequence from low to high elevations (McLusky 1989). Much attention has been given to the relationship between saltmarsh development and factors such as length of the tidal immersion (Ranwell et al. 1964) wave action at the seaward edge (Morley 1973) and erosion/accretion processes limiting the distribution and viability of seeds and seedlings (van Eerd 1985; Groenendijk 1986). The relationship between saltmarsh development and benthic deposit-feeding macrofaunal communities has largely been ignored. Gerdol and Hughes (1993) demonstrated significant negative effects of the amphipod *Corophium volutator* (a prominent member of mudflat communities occurring at densities of up to 140,000 m<sup>2</sup>) on the colonisation of mud by *S. europaea* and postulated that the bioturbatory feeding habit of *C. volutator* might be responsible for the loss and lower limit of pioneer zone vegetation. The plants most typical of this pioneer zone are *Salicornia europaea* and the invasive *S. anglica*.

Seed setting and the resulting germination is not the main form of propagation in seagrasses and cord grasses, but vegetative expansion is (Kenworthy and Fonseca 1977; Groenendijk 1986; Hartman 1988; Goubin and Loqués 1991). If this is the case then the results of the experiments detailed here imply that *S. anglica*'s vegetative and propagative expansion may be slowed or halted by *N. diversicolor* in areas where both are common. Gerdol and Hughes (1993) demonstrated that *Salicornia europaea* seedlings were able to survive beyond the pioneering zone when the bioturbatory effects of the amphipod *C. volutator* were removed.

Seaward of the pioneering zone, mudflats in the UK were formerly dominated by the seagrass *Zostera marina* with its associated infauna. These beds of *Z. marina* along with those on most of the North Sea coast of north-western Europe, were decimated during the *Z. marina* "wasting disease" epidemic of the early 1930s. In the absence of *Z. marina*, benthic communities of deposit-feeding invertebrates dominate the mudflat. Deposit feeders can be strong habitat fabric interactors, altering the structural nature of marine soft sediments (Nowell et al. 1981). Levinton (1995) argues that strongly interacting species may affect an ecosystem through two distinct

routes. Firstly, species might be biological interactors and affect other species by being predators, grazers or competitors. Within some marine ecosystems, predators may often exert strong effects on prey species (Paine 1966, 1974; Harrold and Reed 1985) to the point where the ecosystem is directed into distinct and stable states. In marine and estuarine soft sediment systems, these interactions have been well documented and in most cases there is no difficulty in categorising them, e.g. predation (Commito 1982; Highsmith 1982; Peterson 1982; Ambrose 1984; Smith et al. 1996), competition (Peterson and Andre 1980; Levin 1982; Race 1982; Wilson 1983; Flach 1992; Flach and De Bruin 1994). The presence of both predators and competitors can have important consequences for the relative abundance of different plant and animal species and hence community structure. Secondly, Levinton (1995) argues that species may be habitat fabric interactors, altering and engineering the physical habitat itself. The burrowing and feeding activity of deposit-feeding infaunal marine invertebrates alters the fabric of the sediment, which in turn alters the environment for the deposit feeder, and other constituents of the infaunal community. In this sense deposit feeders are therefore engineers, *sensu* Lawton and Jones (1995) and Jones et al. (1994) and affect the habitat fabric of the ecosystem (Levinton 1995).

Evidence exists to suggest an increase (doubling) in *N. diversicolor* abundance in the Wadden Sea area (Beukema 1989; Reise et al. 1989; Jensen 1992) which was accompanied there by increased algal blooms on the mudflats. These have similarly doubled their primary production and biomass in localised areas. This is mainly related to increased eutrophication. Similar algal mat blooms have been experienced along the east coast of Great Britain (Raffaelli 2000) and may have been accompanied there by similar increases in *N. diversicolor* abundance. No historical data are available for the site at Hamford Water in the present study, but it is tentatively suggested that increases in *N. diversicolor* abundance around the south-east coast of England and those countries bordering the southern North Sea are not unlikely.

The suggestion by Dixon et al. (1998) that “managed retreat” or “coastal realignment” schemes represent a minimalist approach and provide a cost-effective solution to the problem of seawall maintenance through a process of sustainable natural development that ensures evolution towards a natural system, may well be true. However, evidence from the present study detailing the effects of *N. diversicolor* on *S. anglica*, and other studies (Gerdol and Hughes 1993) detailing the negative effects of *C. volutator* on *Salicornia europaea* distribution, contribute to a growing body of evidence that indicates the importance of bioturbating infaunal invertebrates in limiting the distribution of pioneering saltmarsh plants and hence saltmarsh development. Levinton (1995) argues that deposit feeders occupy space within, and may monopolise the environment, thus excluding other species. Often single species regulate the composition of sediment community assemblages both by modifying

sediment chemistry and physical structure, and by displacing other species. Regarding this, it is not clear whether other species might refer to plants or animals; both could potentially compete for the same resource-space within the sediment. Dixon et al. (1998) report some preliminary results as being earlier than expected colonisation by halophytic plants and rapid take-up by marine invertebrates. Marine bioturbators are major controllers of sediment ecosystems, their impact on human attempts at ecosystem engineering and manipulations of the “natural environment” towards some desired end state should be considered carefully.

In conclusion, coastal realignment schemes could develop into desired areas of new saltmarsh habitat serving the purpose for which they were conceived (economic coastal defence). It is also tentatively suggested that coastal realignment schemes could simply develop into new areas of mud-flat dominated by infaunal communities, with major detrimental impacts on the desired ecosystem service that these newly created habitats were perceived to serve. Although the present study concentrates on *N. diversicolor* it contributes to the growing body of evidence indicating the importance of bioturbating infaunal invertebrates in regulating mud-flat community structure. It is apparent that the effects of infaunal invertebrates on pioneering saltmarsh plants are worthy of further investigation, if the UK government is to pursue an extensive policy of “coastal realignment” or “managed retreat” in the face of economic concerns over global sea level rise.

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