

Effect of the amphipod *Corophium volutator* on the colonisation of mud by the halophyte *Salicornia europaea*

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ABSTRACT: The upper limit of the distribution of *Corophium volutator* and the lower limit of the distribution of *Salicornia europaea* approximately correspond with mean high water of neap tide level (MHWNTL). Previous researchers concluded that the lower limit of *S. europaea* is determined by the higher frequency and duration of disturbance by tides and waves. At this site, moving water alone is not responsible for the absence of *S. europaea* below MHWNTL, the activities of *C. volutator* are important. Below MHWNTL there were fewer seeds, a greater proportion were buried and had failed to germinate than above MHWNTL. Some germinated seeds were present near the surface and the lack of established seedlings was attributed to disturbance by *C. volutator*. Seedlings transplanted to sediment sprayed with insecticide (to remove the amphipods) had a survivorship similar to those transplanted above MHWNTL, but twice those transplanted to unsprayed sediment. It was concluded that *C. volutator* prevent establishment of *S. europaea* partly by burial of seeds, but mostly by preventing establishment by seedlings, and in so doing reduce the stability of the sediment, increase erodability and lessen the prospects for successional development of salt marsh vegetation.

INTRODUCTION

There is concern over the stability of the mud flats and salt marshes of the southern North Sea because of isostatic rise in sea level, and any rise in sea level associated with global warming (Doody 1984, Boorman et al. 1989, Dijkema et al. 1990). Pioneering salt marsh plants like *Salicornia europaea* L. and *Spartina anglica* are often characteristic of the first stage in the successional development of salt marsh vegetation, because by colonising open mud they promote sedimentation by slowing local water movement, and reduce erosion by binding the sediment with their roots (Boorman et al. 1989, Dijkema et al. 1990). Therefore factors which affect the abundance and distribution of such plants may have important consequences for sediment stability and salt marsh development.

Salicornia europaea is an annual species widespread on the coastal salt marshes of northwestern Europe (Jefferies et al. 1981) and often grows as pure

stands on open mud flats, where densities may exceed 10000 m⁻² (Wiehe 1935, Ball & Brown 1970, Brereton 1971), or in disturbed areas in the perennial vegetation (Ellison 1987). The seeds germinate from March to May and plant growth occurs until late summer when flowering commences. The seeds reach maturity from about mid-September and are usually shed by falling from the dead or dying parent plant over the winter (Ball & Brown 1970). Most of the studies on the factors that limit the distribution of *S. europaea* have focused on the effects of moving water. Wiehe (1935), and Chapman (1960) working with Wiehe's data, concluded that *Salicornia* sp. was abundant only above mean high water of neap tide level (MHWNTL) because a threshold time of 2 or 3 d undisturbed by tides was necessary for the establishment of the seedlings. Below this level approximately twice daily tides remove the seedlings from the mud. Once plants become established daily submergence does not inhibit growth. The significance of moving

water and sediment mobility was also emphasised by Brereton (1971), Jensen & Jefferies (1984), Beeftink (1985) and Ellison (1987). Algal mats which rise from the sediment on the incoming tide may also pull the roots from their anchorage (Jefferies et al. 1983, Jensen & Jefferies 1984).

Corophium volutator (Pallas) is widespread in intertidal estuarine sediments of northern Europe and northeastern North America where it lives in U-shaped burrows. It occurs at densities of up to $100\,000\text{ m}^{-2}$ (Hughes 1988, Jensen & Kristensen 1990). *C. volutator* has been reported to be an unselective deposit feeder, which pulls surface sediment into its tube with its antennae (Meadows & Reid 1966, Fenchel et al. 1975, Icely & Nott 1985, Stuart et al. 1985, Murdoch et al. 1986), a suspension feeder (Fenchel et al. 1975) and an epipsammic browser (Nielsen & Kofoed 1982, Stuart et al. 1985). The feeding and burrowing activities of *C. volutator* may interfere with seed distribution, germination or seedling establishment of *Salicornia europaea* and the aim of this study was to investigate whether the colonisation of mud flats by *S. europaea* is affected by these amphipods.

METHODS

Identification within the *Salicornia europaea* agg. species complex is very difficult (Pirainen 1991) because the plants are largely cleistogamous, which has resulted in the development of small differences between adjacent populations (Ball & Tutin 1959, Dalby 1962, Jefferies et al. 1981, Ingrouille & Pearson 1987, Pirainen 1991). The plants were identified as *S. europaea* L. using the morphological characters recommended by Pirainen (1991).

Field observations

The field work was conducted in a semi-enclosed bay ($51^{\circ} 35' 12''\text{N}$, $0^{\circ} 48' 42''\text{E}$) on the northern shore of Wallasea Island on the River Crouch, Essex, UK (Fig. 1), where, as elsewhere in the area, the lower limit of *Salicornia europaea* abruptly terminates on the mud flat (Fig. 2).

Transects. Four parallel transects of 2.4 m in length and 2 to 6 m apart were established across the lower limit of the *Salicornia europaea* zone in late April and early May 1991. In each transect 8 contiguous quadrats ($30 \times 30\text{ cm}$), designated A (the uppermost) to H (the lowermost) (see Fig. 3), were examined for emergent *S. europaea* seedlings which were counted. In each quadrat 2 cores of sediment (3.9 cm diameter, 5 cm deep) were collected and sieved through a 0.35 mm

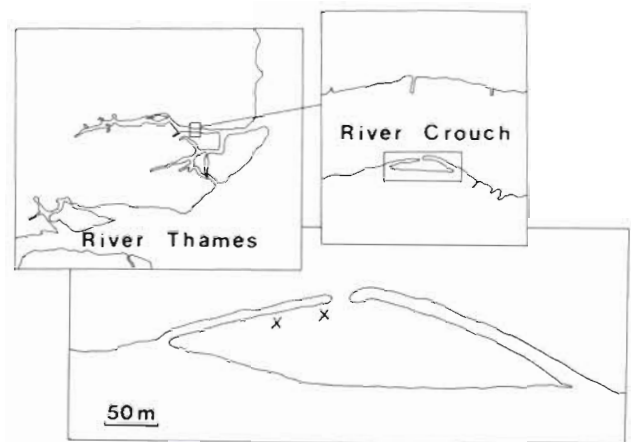


Fig. 1. Wallasea Island, River Crouch, Essex. Study area: inside the semi-enclosed bay between the 2 crosses

sieve to determine the abundance of seeds, buried seedlings, *Corophium volutator* and any other macrofauna. Previous work at this site had shown that *C. volutator* achieves mean densities between $6\,000\text{ m}^{-2}$ in February and $50\,000\text{ m}^{-2}$ in August and does not occur below a depth of 5 cm (pers. obs.). The relative height of the central point of each quadrat was measured using 2 rules and a spirit level. The heights of the quadrats above chart data were calculated from predicted tidal heights and by noting the time of immersion of one of the quadrats in each transect. This was done on 2 separate dates and the estimated heights were similar.

Core studies. In November 1991 and March 1992 the abundance and vertical distributions of *Salicornia europaea* seeds and seedlings and *Corophium volutator* were determined at 4 stations, A, D, E and H. These were at the same elevations as the corresponding quadrats in the previous transects; A and H at the upper and lower extremes of the transects, and D and E respectively immediately above and below the lower edge of the *S. europaea* zone. Four cores of sediment, similar to those described above, were taken from each station. The core of sediment was pushed up through the corer and as it emerged the top 3 cm was sliced with a blade into 1 cm thick sections. These sections and the remaining sediment, from a depth of 3 to 5 cm, were sieved separately through a 0.35 mm sieve and the seeds, seedlings and *C. volutator* in each layer counted.

Seedling transplant experiments. In May 1991, 50 *Salicornia europaea* seedlings (approximately 1.5 cm in total length – the smallest that were easily manipulable) were transplanted individually to each of 6 quadrats ($30 \times 30\text{ cm}$), 2 in the *S. europaea* zone at the same elevation as Quadrats A, and 4 in the open mud



Fig. 2. Photograph of the study area showing the *Salicornia europaea* zone and 3 turves of sediment bearing *S. europaea* transplanted to Stn H on the open mud

alongside Quadrats H. Two of the 4 open mud quadrats were sprayed with a pyrethrum-based insecticide (Bug Gun, ICI) at the beginning, and approximately once a week thereafter, to remove *Corophium volutator*. This method of removal of *C. volutator* was chosen in preference to sieving which disrupts the integrity of the sediment. The initial spraying caused the amphipods to leave their burrows and to lie on the surface where they either died or remained paralysed until the next tide washed them away. The subsequent sprayings were to remove any immigrant amphipods, but few were seen. The survival of the seedlings was recorded weekly for 7 wk after which 5 cores of sediment (3.9 cm diameter, 5 cm deep) were collected from each of the 3 treatments to determine the abundance of *C. volutator*.

In May 1992, 6 turves of sediment (16 × 16 × 5 cm deep) with *Salicornia europaea* seedlings were dug from the *S. europaea* zone and transplanted, 3 in the *S. europaea* zone at Stn A and 3 on the open mud at Stn H. The seedlings on each block were counted each month until October 1992 when the surviving plants were collected for determination of dry weight. Each turf in the *S. europaea* zone was marked with a small pole, but 1 pole was lost after 2 mo and thereafter this turf could not be located.

Laboratory experiments

Effect of *Corophium volutator* on seedling survival.

In May 1991, 10 cores of mud, 10.1 cm diameter and 8 cm deep, were collected in plastic tubes from an area of mud flat on Wallasea Island where previous surveys had determined that no macrofauna was present. The cores were placed in a laboratory tidal regime of 3 h submergence every 12 h. Water salinity was 30‰ and the temperature was 9°C. Fifteen *Salicornia europaea* seedlings, approximately 1.5 cm long, were planted in each core and 100 *C. volutator* were added to each of 4 cores on the same day to produce a density of 12500 m⁻². The natural density of *C. volutator* at this site in spring varies between 10000 and 20000 m⁻². The same number of amphipods were added to a further 3 cores 3 d later, while 3 cores were used as controls. The top of each tube was covered with a net of pore size 0.5 mm, 5 cm above the mud surface to prevent escape of *C. volutator*. Similar netting was placed under each core to facilitate drainage. The survival of the seedlings was monitored for 20 d after which the cores were sieved through a 0.35 mm sieve and the number of surviving *C. volutator* and seedlings recorded.

Effect of *Corophium volutator* on survival of seeds stimulated to germinate. In November 1991, 10 cores of mud, collected as described above, were placed in a laboratory tidal regime of 2 h submergence every 12 h. Water salinity was maintained at 33‰ and temperature at 9°C. Two hundred *C. volutator* (equivalent to 25000 m⁻²) were added to each of 5 of the cores, the other 5 were used as controls. Seeds of *Salicornia europaea* were kept in a moist environment at 10°C for 2 wk and placed in distilled water for 2 d at 5°C to promote germination (Ungar 1977). Fifty of these seeds were placed on the surface of each core and the tubes covered with net as described above. After 20 d the sediment in each core was sectioned into layers 1 cm thick, sieved through a 0.35 mm sieve and the number of *C. volutator*, seeds and seedlings in each section counted. A similar experiment was conducted in December 1992.

Effect of burial on survival of seeds stimulated to germinate. To establish the ability of germinating seeds to produce seedlings when buried, 14 cores of mud with no macrofauna, as described above, were collected. One hundred seeds in which germination had been stimulated were placed on the surface of 2 cores and in other pairs of cores were buried at depths of 1, 2, 3, 4, 5 and 6 cm. The tidal regime was 2 h submergence every 12 h, water salinity was 33‰ and the temperature 9°C. The emergence of the seedlings was recorded for 30 d, after which the sediment was divided into 1 cm thick layers, sieved and the number of seeds and seedlings in each section counted.

RESULTS

Field observations

Transect data

The contiguous Quadrats A to H along the transects covered a height range of only 15 cm (Fig. 3a). At this site mean high water of spring tide level (MHWSTL) is 5.2 m above, and MHWNTL 4.2 m above chart datum. Emergent *Salicornia europaea* seedlings were abundant in the quadrats above MHWNTL, and rare or absent below MHWNTL (Fig. 3B). *Corophium volutator* was present only in the quadrats below MHWNTL (Fig. 3C). There were relatively few buried or ungerminated seeds (Fig. 3D) and no significant difference in their abundance with height of quadrat. The propor-

tions of seeds in each quadrat from A to H that had germinated were 93, 75, 88, 56, 55, 15, 0 and 0% respectively.

Core data

The abundance and vertical distributions of *Corophium volutator* and *Salicornia europaea* seeds at Stns A, D, E & H in November and March are shown in Fig. 4. *C. volutator* was abundant only at Stns E & H, and rare at Stns A & D (Fig. 4A, C). In November *S. europaea* seeds were more abundant among the adult plants at Stns A & D, where 87% of seeds were found (Fig. 4B) than in the open mud of the lower 2 stations. In March the density of seeds (including seedlings) at Stn A was markedly reduced (Fig. 4D). A greater proportion (30%) of those found were in the lower 2 stations than in November (13%).

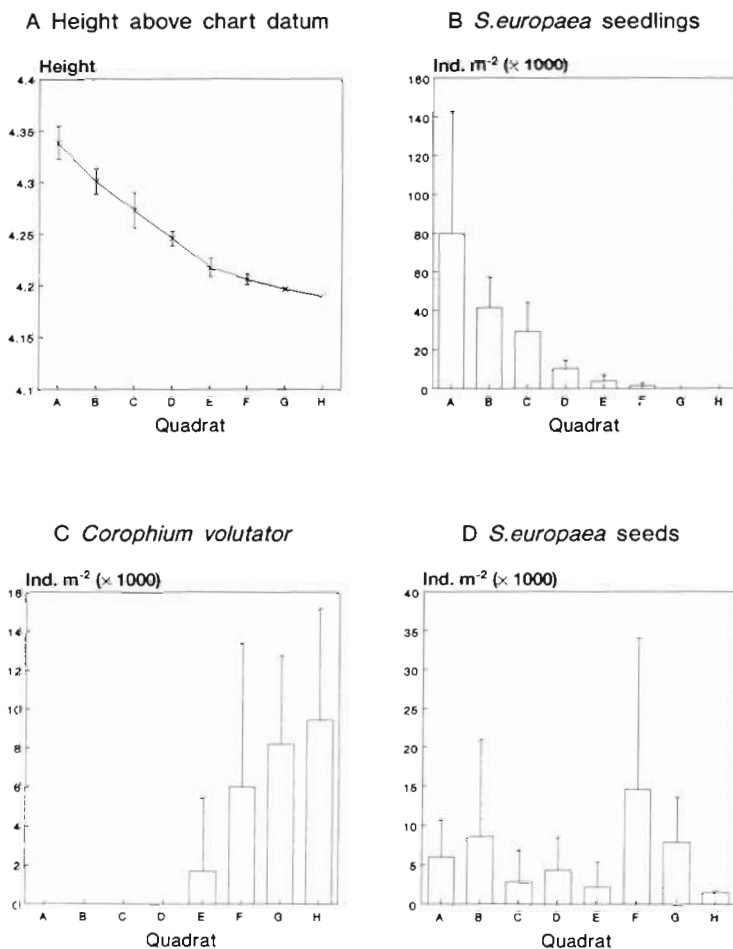


Fig. 3. Data from the 8 contiguous quadrats in the 4 transects (April–May 1991). Quadrats A to H: (A) mean (\pm SD) heights above chart data; (B) mean (\pm SD) abundance of emergent *Salicornia europaea* seedlings; (C) mean (\pm SD) abundance of *Corophium volutator*; (D) mean (\pm SD) abundance of *S. europaea* seeds

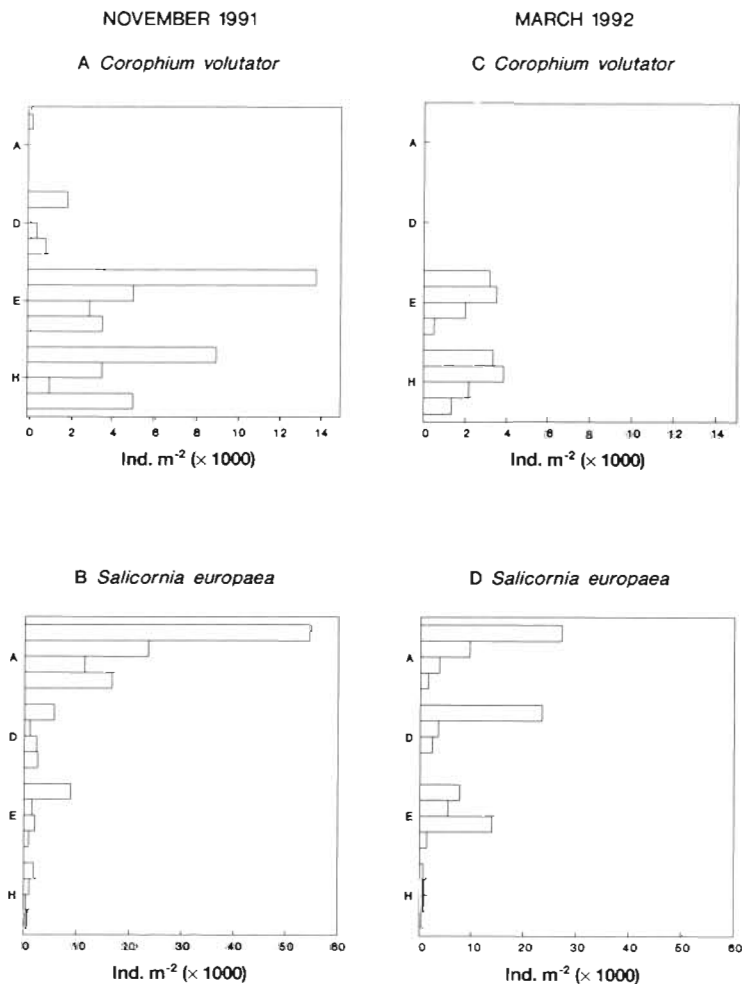


Fig. 4. Mean densities of *Corophium volutator* and *Salicornia europaea* seeds at depths of 0 to 1, 1 to 2, 2 to 3 and 3 to 5 cm at Stns A, D, E & H on 28 November 1991 and 5 March 1992. Data are from 1 core per station from each of 4 transects

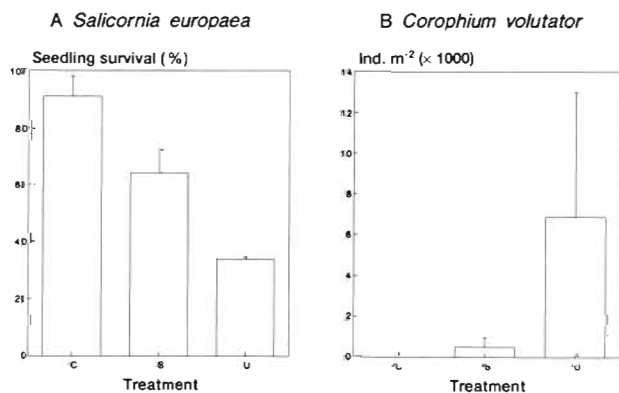


Fig. 5. (A) *Salicornia europaea*. Mean number (+SD) of surviving seedlings transplanted individually to the control site among natural seedlings above MHWNTL (C), and to insecticide-sprayed sediment (S) and unsprayed sediment (U) below MHWNTL. (B) *Corophium volutator*. Mean number (+SD) of amphipods at the same sites

Some burial of seeds had occurred at Stns E & H over the winter because the vertical distribution of seeds at these stations in March was significantly deeper than at Stns A & D (2-way ANOVA, $p < 0.05$). The proportion of seeds that had germinated was related to their depth in the sediment. In the surface 1 cm, 31 % of seeds had germinated, 4 % in the layer 1 to 2 cm deep, 5 % in the layer 2 to 3 cm deep and 1 % in the layer 3 to 5 cm deep. Of the seeds in the surface 1 cm, 39 % from Stns A & D had germinated but only 11 % from Stns E & H.

Transplant experiments

Seedlings planted individually in the *Salicornia europaea* zone had a 91 % survivorship after 17 d (Fig. 5). This was not significantly different from the 64 % seedling survival in the sprayed sediment, where the abundance of *Corophium volutator* was significantly reduced (unpaired t -test; $p > 0.05$) (Fig. 5). However, the survival of the seedlings transplanted to untreated sediment containing *C. volutator* (Fig. 5B) was approximately half that of the sprayed sediment, a difference that was significant (unpaired t -test; $p < 0.05$).

The survivorship curves of seedlings transplanted in turves of sediment to the open mud and to the *Salicornia europaea* zone were not significantly different (2-way ANOVA on arcsine-transformed data) (Fig. 6). Both curves were Type III with a high initial mortality rate that declined after about 80 d. Over the period 14 May to 14 October the mortality rate was $>80\%$. The mean biomass of the plants transplanted below MHWNTL was 0.82 g, significantly higher (ANOVA, $p < 0.05$) than the 0.53 g of those transplanted to the *S. europaea* zone.

Laboratory experiments

Effect of *Corophium volutator* on seedling survival

The survival of seedlings in cores with no *Corophium volutator* was significantly higher than in those with the amphipods added (Fig. 7) (z-test on slopes of fitted regression lines; $p < 0.05$). The survival of seedlings that had 3 d in which to establish before the addition of *C. volutator* had a higher survival than those added at the same time ($p < 0.05$).

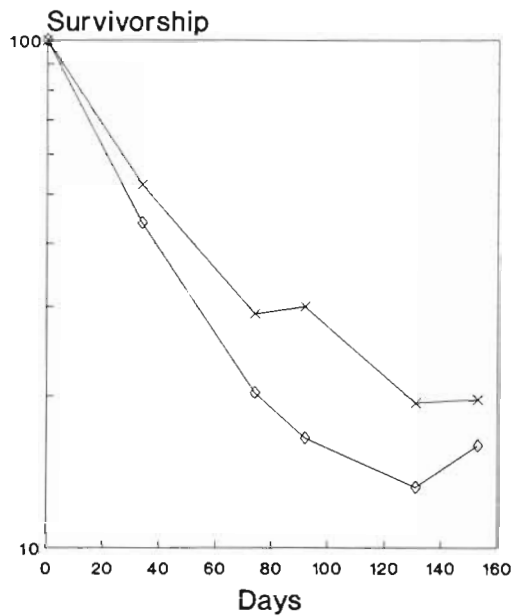


Fig. 6. Survivorship curves (logarithmic scale) of seedlings transplanted in cores above (x) and below (◊) MHWNTL

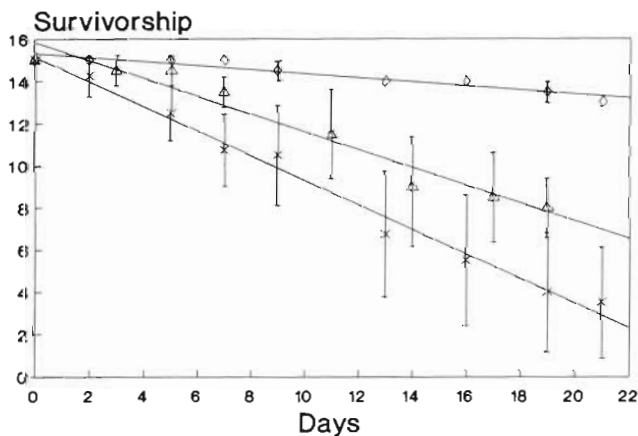


Fig. 7. Survivorship curves (arithmetic scale, means, \pm SD) of seedlings transplanted individually to cores containing *Corophium volutator* (x: seedlings introduced with the amphipods; \triangle : seedlings introduced 3 d before the amphipods) and to control cores with no amphipods (◊)

Effect of *Corophium volutator* on survival of seeds stimulated to germinate

There was some indication from the first experiment that after 30 d the germinating seeds in the cores containing *Corophium volutator* had been buried to a greater extent than those in control cores (Table 1a) but the differences in vertical distribution were not significant (Kruskal-Wallis test, $H = 1.30$). The results from the second experiment were different to the first

Table 1. Effect of *Corophium volutator* on the burial of *Salicornia europaea* seeds

(a) Experiment 1		
Depth (cm)	Seeds recovered (%)	
	Control	<i>C. volutator</i> added
1	94.12	79.84
2	5.04	10.89
3	0	7.26
4	0.84	2.02
(b) Experiment 2		
<i>S. europaea</i>	Control	<i>C. volutator</i> added
Total recovered (%)	94.4	64.4
Seeds (%)	21.6	8.8
Germinated seeds (%)	72.4	55.6
Emerged seedlings (%)	12.4	0
Remained on surface (%)	48	0

because the amphipods did not burrow below a depth of 1 cm and no seeds were found beneath this level. Nevertheless, in the control cores 94 % of the seeds were recovered, 48 % were still on the surface and 12 % were emergent seedlings (Table 1b). In the cores containing *C. volutator* only 64 % were recovered, no seeds remained on the surface and no emergent seedlings were produced (Table 1b).

Effect of burial on survival of seeds stimulated to germinate

Of the seeds in which germination had been stimulated and laid on the surface or buried at different depths, only 33 % of those on the surface produced seedlings. No seedlings were produced from buried seeds.

DISCUSSION

On Wallasea Island the lower limit of the distribution of *Salicornia europaea* approximately corresponds to MHWNTL (Fig. 3), below which usually 2 tides flood and ebb over the mud flat every day. This could simply reflect the susceptibility of seedlings to disturbance associated with moving water, mobile sediment or algal mats, which may prevent the seedlings establishing a sufficiently strong anchorage (Wiehe 1935, Chapman 1960, Brereton 1971, Jefferies et al. 1981, Jefferies et al. 1983, Jensen & Jefferies 1984, Beeftink 1985, Ellison 1987). Above this level there are some days when the tide does not reach the seedlings, which have more time to establish before

the next tide reaches them. However, the data presented here indicate that, at this site, moving water alone is not responsible for the downshore limit of *S. europaea*, and that the activities of *Corophium volutator* are important.

Most seeds were found in the upper 2 stations, among the dying plants in November and the dead plants in March (Fig. 4). These observations confirm some previous conclusions that seeds remain close to the parent plant (Jefferies et al. 1983, Jensen & Jefferies 1984, Watkinson & Davy 1985). However seed dispersal may vary between sites of different exposure to water movement, for while Ellison (1987) reported that more than 50 % of seeds landed within 20 cm of the parent plant, Brereton (1971) found that the distribution of seeds was related to neither the parents nor plants in the following season.

There was some downshore dispersal of seeds over winter (Fig. 4) and the absence of plants below MHWNTL cannot be attributed to an absence of seeds. However, a lower proportion of seeds in the lower 2 stations had germinated than in the upper 2. This may be partly attributable to the burial of seeds which occurred during the winter (Fig. 4) since the field data indicate that germination rate declines with depth. In the laboratory seeds in which germination had been stimulated, but once buried did not produce emergent seedlings, only some of those placed on the surface of the sediment did so (Table 1). These observations confirm the similar results of Jensen & Jefferies (1984) and Ellison (1987) that burial of seedlings causes their death because they are unable to reach the surface. In deposit feeding the amphipods scrape surface sediment into 1 opening of their U-shaped burrows with their antennae (Meadows & Reid 1966) and redeposit it by expelling it from the other opening (Icely & Nott 1985). This disturbance of the sediment may be responsible for the burial of seeds, which either do not germinate or cannot produce emergent seedlings, and reduces the potential for colonisation by *Salicornia europaea*. Although there was no evidence from the 2 laboratory experiments that *Corophium volutator* buried the seeds, this may be due to their relatively short duration and the fact that the amphipods did not burrow deeper than 1 cm in the second experiment. In some areas *S. europaea* seeds are able to remain dormant and germinate later when the conditions are appropriate (Ungar et al. 1979, Ungar 1987) and Beeftink (1985) recorded viable seeds in sulphide-rich sediment. Seed banks have been reported for populations of *S. europaea* on an inland salt flat (Ungar et al. 1979, Philipupillai & Ungar 1984) and in Hudson Bay (Jefferies et al. 1983), but in temperate coastal populations in England (Jefferies et al. 1981, Davy et al.

1990), Denmark (Jensen & Jefferies 1984) and The Netherlands (Beeftink 1985) there is apparently no permanent seed bank.

Corophium volutator may also prevent establishment of seedlings other than by burial, since germinated seeds were present close to the surface of the sediment below MHWNTL (transect data). In the laboratory no seedlings were produced from germinating seeds placed on the surface of the cores containing *C. volutator*, in contrast to the control cores with no *C. volutator* (Table 1b). This effect was not caused by burial, but may have been a consequence of disturbance by the feeding amphipods of the surface sediment which may prevent the seedlings from achieving root anchorage.

The data from the laboratory and field transplant experiments support the hypothesis that *Corophium volutator* may also prevent colonisation by disturbance of seedlings. In the laboratory, seedlings planted in cores 3 d before the introduction of the amphipods had a higher survivorship than those planted when the amphipods were introduced (Fig. 7). The seedlings transplanted below MHWNTL in turves had a survivorship similar to those transplanted to the *Salicornia europaea* zone (Fig. 6), indicating that factors associated with frequency and duration of immersion are not responsible for a significant mortality of plants below MHWNTL. The higher biomass of plants transplanted below MHWNTL than those transplanted in the *S. europaea* zone is further evidence that the physico-chemical environment is not stressful. (The difference may reflect intraspecific competition with plants surrounding the turves transplanted in the *S. europaea* zone.) Moreover, the seedlings transplanted individually to insecticide-treated sediment below MHWNTL also had a survivorship similar to those transplanted above MHWNTL but approximately twice that of seedlings transplanted to adjacent sediment containing *C. volutator* (Fig. 5). This indicates that disturbance to seedlings by the amphipods, perhaps acting synergistically with moving water which is more frequent and longer lasting below MHWNTL, is a significant cause of mortality.

Corophium volutator may affect *Salicornia europaea* by changing the soil aeration. Meadows & Tait (1989) found that the burrows of *C. volutator* decreased the permeability of sediment, which could help water retention at low tide. Halophytes like *S. europaea* have a requirement for well-aerated sediment (Armstrong et al. 1985) that may not be satisfied in the presence of *C. volutator*. However this effect is not considered important since the small areas of sprayed mud, in which seedling survival was enhanced, was, for the relatively short duration of the experiment, apparently not differently saturated to the surrounding sediment. This may

have been because the burrows were still intact or there was movement of water from the surrounding saturated mud. In addition, the subsurface water in the sprayed areas may have contained less oxygen than where the amphipods were present and circulate water through their burrows.

The conclusion that seedling establishment is a critical stage in the life cycle of *Salicornia europaea* agrees with those of previous researchers, but for different reasons. Jefferies et al. (1981) and Jensen & Jefferies (1984) found that filamentous algae markedly influenced the survival of *S. europaea* seedlings, which were uprooted as algal mats floated on the incoming tide, and suffered by being covered by the mats so that the seedlings became etiolated. Ungar et al. (1979) and Jefferies et al. (1981) found that seedlings were particularly susceptible to drought but their data were from inland salt pans and high shore populations respectively and are not strictly comparable with this study. The several previous researchers (Wiehe 1935, Chapman 1960, Brereton 1971, Jensen & Jefferies 1984, Beeftink 1985, Ellison 1987) that concluded that *S. europaea* was unable to colonize habitats that were flooded every day by tides did not consider any effect of the infauna on sediment mobility. The inhibition of *S. europaea* colonisation of mud by *Corophium volutator* is perhaps one way in which the infauna of mud flats may have an indirect but important effect in reducing sediment stability, increasing the rates of erosion and lessening the potential for successional development of salt marsh vegetation.

LITERATURE CITED

- Armstrong, W., Wright, E. J., Lythe, S., Gaynard, J. T. (1985). Plant zonation and the effects of the spring-neap tidal cycle on soil aeration in a Humber salt marsh. *J. Ecol.* 73: 323–339
- Ball, P. W., Brown, K. G. (1970). A biosystematic and ecological study of *Salicornia* in the Dee Estuary. *Watsonia* 8: 27–40
- Ball, P. W., Tutin, T. G. (1959). Notes on annual species of *Salicornia* in Britain. *Watsonia* 4: 109–113
- Beeftink, W. G. (1985). Population dynamics of annual *Salicornia* species in the tidal salt marshes of the Oosterschelde, The Netherlands. *Vegetatio* 61: 127–136
- Boorman, L. A., Goss-Custard, J. D., McGrorty, S. (1989). Climatic change, rising sea level and the British Coast. NERC: ITE research publication 1, HMSO, London
- Brereton, A. J. (1971). The structure of the species populations in the initial stages of salt marsh succession. *J. Ecol.* 59: 321–338
- Chapman, V. J. (1960). Salt marshes and salt deserts of the world. Leonard Hill Ltd, London
- Dalby, D. H. (1962). Chromosome number, morphology and breeding behaviour in the British *Salicorniae*. *Watsonia* 5: 150–162
- Davy, A. J., Noble, S. M., Oliver, R. P. (1990). Genetic variation and adaptation to flooding in plants. *Aquat. Bot.* 38(1): 91–108
- Dijkema, K. S., Bossinade, J. H., Bouwsema, P., De Glopper, R. J. (1990). Salt marshes in the Netherlands Wadden sea: rising high-tide levels and accretion enhancement. In: Beukema, J. J., Wolff, W. J., Brouns, J. J. W. M. (eds.) Expected effects of climatic change on marine coastal ecosystems. Kluwer Academic Press, Dordrecht, p. 173–188
- Doody, J. P. (1984). Great Britain and Ireland. In: Dijkema, K. S. (ed.) Salt marshes in Europe. European Committee for the Conservation of Nature and Natural Resources, Council of Europe, Strasbourg, p. 103–119
- Ellison, A. M. (1987). Effects of competition, disturbance and herbivory on *Salicornia europaea*. *Ecology* 68: 576–586
- Fenchel, T., Kofoed, L. H., Lappalainen, A. (1975). Particle size-selection of two deposit feeders: the amphipod *Corophium volutator* and the prosobranch *Hydrobia ulvae*. *Mar. Biol.* 30: 119–128
- Hughes, R. G. (1988). Dispersal by benthic invertebrates: the *in situ* swimming behaviour of the amphipod *Corophium volutator*. *J. mar. biol. Ass. U.K.* 68: 565–579
- Icely, J. D., Nott, J. A. (1985). Feeding and digestion in *Corophium volutator* (Crustacea: Amphipoda). *Mar. Biol.* 89: 183–195
- Ingrouille, M. J., Pearson, J. (1987). The pattern of morphological variation in the *Salicornia europaea* L. aggregate (Chenopodiaceae). *Watsonia* 16: 269–281
- Jefferies, R. L., Davy, A. J., Rudmik, T. (1981). Population biology of the salt marsh annual *Salicornia europaea* agg. *J. Ecol.* 69: 17–31
- Jefferies, R. L., Jensen, A., Bazely, D. (1983). The biology of the annual *Salicornia europaea* agg. at the limits of its range in Hudson Bay. *Can. J. Bot.* 61: 762–773
- Jensen, A., Jefferies, R. L. (1984). Fecundity and mortality in populations of *Salicornia europaea* agg. at Skallingen, Denmark. *Holarct. Ecol.* 7: 399–412
- Jensen, K. T., Kristensen, L. D. (1990). A field experiment on competition between *Corophium volutator* (Pallas) and *Corophium arenarium* Crawford (Crustacea, Amphipoda): effects on survival, reproduction and recruitment. *J. exp. mar. Biol. Ecol.* 137: 1–24
- Meadows, P. S., Reid, A. (1966). The behaviour of *Corophium volutator* (Crustacea: Amphipoda). *J. Zool., Lond.* 150: 387–399
- Meadows, P. S., Tait, J. (1989). Modification of sediment permeability and shear strength by two burrowing invertebrates. *Mar. Biol.* 101: 75–82
- Murdoch, M. H., Barlocher, F., Laltoo, M. L. (1986). Population dynamics and nutrition of *Corophium volutator* (Pallas) in the Cumberland Basin (Bay of Fundy). *J. exp. mar. Biol. Ecol.* 103: 235–249
- Nielsen, M. V., Kofoed, L. H. (1982). Selective feeding and epipsammic browsing by the deposit feeding amphipod *Corophium volutator*. *Mar. Ecol. Prog. Ser.* 10: 81–88
- Philupillai, Y., Ungar, I. A. (1984). The effect of seed dimorphism on the germination and survival of *Salicornia europaea* L. populations. *Am. J. Bot.* 71: 542–549
- Piirainen, M. (1991). Flora nordica notes. I. *Salicornia* (Chenopodiaceae) in northern Europe: typification and taxonomic notes. *Ann. Bot. Fenn.* 28: 81–85
- Stuart, V., Head, E. J. H., Mann, K. H. (1985). Seasonal changes in the digestive enzyme levels of the amphipod *Corophium volutator* (Pallas) in relation to diet. *J. exp. mar. Biol. Ecol.* 88: 243–256
- Ungar, I. A. (1977). Salinity, temperature, and growth regulator effects on seed germination of *Salicornia europaea* L. *Aquat. Biol.* 3: 329–335

-
- Ungar, I. A. (1987). Population ecology of halophyte seeds. Bot. Rev. 53: 301–334
- Ungar, I. A., Benner, D. K., McGraw, D. C. (1979). The distribution and growth of *Salicornia europaea* on an inland salt pan. Ecology 60: 329–336
- Watkinson, A. R., Davy, A. J. (1985). Population biology of salt marsh and sand dune annuals. Vegetatio 62: 487–497
- Wiehe, P. O. (1935). A quantitative study of the influence of the tide upon populations of *Salicornia europaea*. J. Ecol. 23: 323–333

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