

## Distribution and abundance of the intertidal saltmarsh beetle, *Bledius spectabilis*

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**ABSTRACT.** 1. The burrowing intertidal beetle *Bledius spectabilis* Kraatz (Coleoptera: Staphylinidae) occurs on all but the very youngest marshes on Scolt Head Island, Norfolk, U.K., and may reach densities of up to 4000 m<sup>-2</sup> (combined adult and larval densities).

2. The beetles are restricted to a narrow band about 1 m wide along the edges of creeks draining the low marsh areas of the island, and the vertical range is restricted to a zone between 0.8 and 1.55 m above Ordnance Datum. The majority of the aggregations and the highest densities are between 1.2 and 1.3 m O.D., that is between about 24 and 40 cm below MHWN (mean high water at neap tides).

3. Poor drainage, in particular the presence of long-standing pools of water over the soil surface, is important in restricting the beetles to well-drained edge regions.

4. Transplant experiments suggest that displacement by saltmarsh vegetation, in particular *Halimione portulacoides* (L.) Aell., sets the upper limit of the beetles' distribution.

5. The zonation of *B. spectabilis* fits well into the general scheme that has been proposed for the zonation of marine animals from rocky shores.

6. The beetles produce large (3–6 mm diameter), rapidly draining, abundant (up to 9% of soil volume) and persistent burrows. We suggest that these beetle aggregations may play an important role in the development of the saltmarsh.

**Key words.** Intertidal zonation, saltmarshes, beetles, Staphylinidae, *Bledius*, soil conditions.

### Introduction

The intertidal zone has proved to be an excellent environment in which to study the factors that control the local distribution of individual species. This is principally because of the domi-

nant influence of a single factor – the extent of tidal coverage. The zonation of marine organisms on rocky shores has been intensively studied (e.g. Lewis, 1964; Barnes & Hughes, 1982; Underwood & Denley, 1984; Moore & Seed, 1985), but the zonation of the terrestrial colonizers of the intertidal zone has received much less attention. The most extensive invasion of the intertidal zone by land organisms, at

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least in temperate regions, has occurred on saltmarshes, but although the zonation of saltmarsh plants has been studied in some detail (e.g. Chapman, 1977; Beefink, 1977), we know very little about the zonation of the animals that have invaded saltmarshes from the land (Foster & Treherne, 1976b; Long & Mason, 1983). Does the combination of physical and biological factors that has been shown to control the distribution of rocky shore animals also operate in an analogous way for these land animals on saltmarshes? The upper limit of many marine rocky shore animals is controlled by physical factors (e.g. Connell, 1972; Barnes & Hughes, 1982): is the lower limit of these intertidal land animals also controlled by physical factors? However, in saltmarshes local position may be more important than absolute tidal height. For example, it is known that the saltmarsh plant *Halimione portulacoides* (L.) Aell. (Chapman, 1950) and the root aphid *Pemphigus trehernei* Foster (Foster & Treherne, 1975) are both confined to edge and other well-drained regions of the marsh.

In an attempt to answer some of these questions, we investigated the distribution of the staphylinid beetle *Bledius spectabilis* Kraatz on the marshes of Scolt Head Island, Norfolk, U.K. *B. spectabilis* lives in burrows that it digs in the mud and banks of northern European saltmarshes (Larsen, 1936, 1952; Wohlenberg, 1937; van Wingerden *et al.*, 1981; Wyatt, 1984; Foster & Wyatt, 1985). For an insect it is unusual in two respects: it lives in the intertidal zone, and it shows elaborate parental care of eggs and young. The species has been used as an example of the evolution of parental care in a harsh environment (Wilson, 1971, 1975). The role of the female *B. spectabilis* in protecting her brood and the beetle's lifecycle have been described by Wyatt (1984). In summary, the female lays her eggs in individual chambers around the wine-bottle-shaped maternal burrow. When the eggs hatch, the larvae move into the main chamber where they feed on algae brought down from the mud surface by the female. When about 1 week old, the larvae leave the maternal burrow and dig their own individual burrows.

In this paper, we describe the detailed distribution of *Bledius spectabilis* in a Norfolk saltmarsh, offer experimental evidence of some of the factors that appear to control its distribution, and provide observations on the effects of its burrows on soil structure.

## Methods

Field observations and experiments were made at Scolt Head Island NNR and Brancaster Harbour on the North Norfolk coast, U.K. (grid ref. TK 815462) (see Foster & Treherne, 1975).

The distribution of *B. spectabilis* was measured along transects at three sites (Fig. 1). At 1 m intervals along the transect, five to seven cores were taken to a depth of 11 cm with an 8 cm diameter corer. The cores were carefully picked apart and the numbers of *Bledius* at different stages in the life cycle, separating the maternal and post-maternal phases (see Wyatt, 1984), were recorded. The drainage from holes the size of *B. spectabilis* burrows (5 mm diameter, 60 mm deep) was measured at each station by filling the holes ( $n=5-18$ ) with seawater, from a syringe via a catheter, and measuring at intervals the volume required to return the meniscus to the surface. The drainage measurements were made during a cycle of flooding tides, as Foster & Treherne (1976a) showed that soil drainage was impaired after covering tides – the conditions when *Bledius* burrows are at risk from flooding. The number of *Salicornia europaea* agg. L. plants was counted in five 20×20 cm quadrats at each station. The numbers of dead *Bledius* covered with the entomophagous fungus *Metarrhizium anisopliae* or in waterfilled burrows were also noted.

To study the effects of saltmarsh vegetation, ten sites were marked out at 2 m intervals within a large *Bledius* aggregation along the banks of a small creek in Missel Marsh. On 25 June 1981 a large fully grown bush of *Halimione*, covering more than 625 cm<sup>2</sup> in area, was transplanted into the centre of each of five sites, chosen from random number tables. The five other sites were kept as controls.

Soil air-space volume was measured by infilling five cores, 15 cm in diameter and 15 cm deep, with silicone resin under vacuum (Wyatt, 1986). When set, the resin was washed clean and sorted into current occupied *Bledius* burrows, old *Bledius* burrows, and other air spaces. This method fills all spaces larger than 0.1 mm in diameter. The resin casts were weighed and the volume calculated from the specific gravity of the resin (1.05).

The height of the marsh sites (in m O.D. (Newlyn)) was taken from survey measurements given by Foster (1974, 1975), and checked by

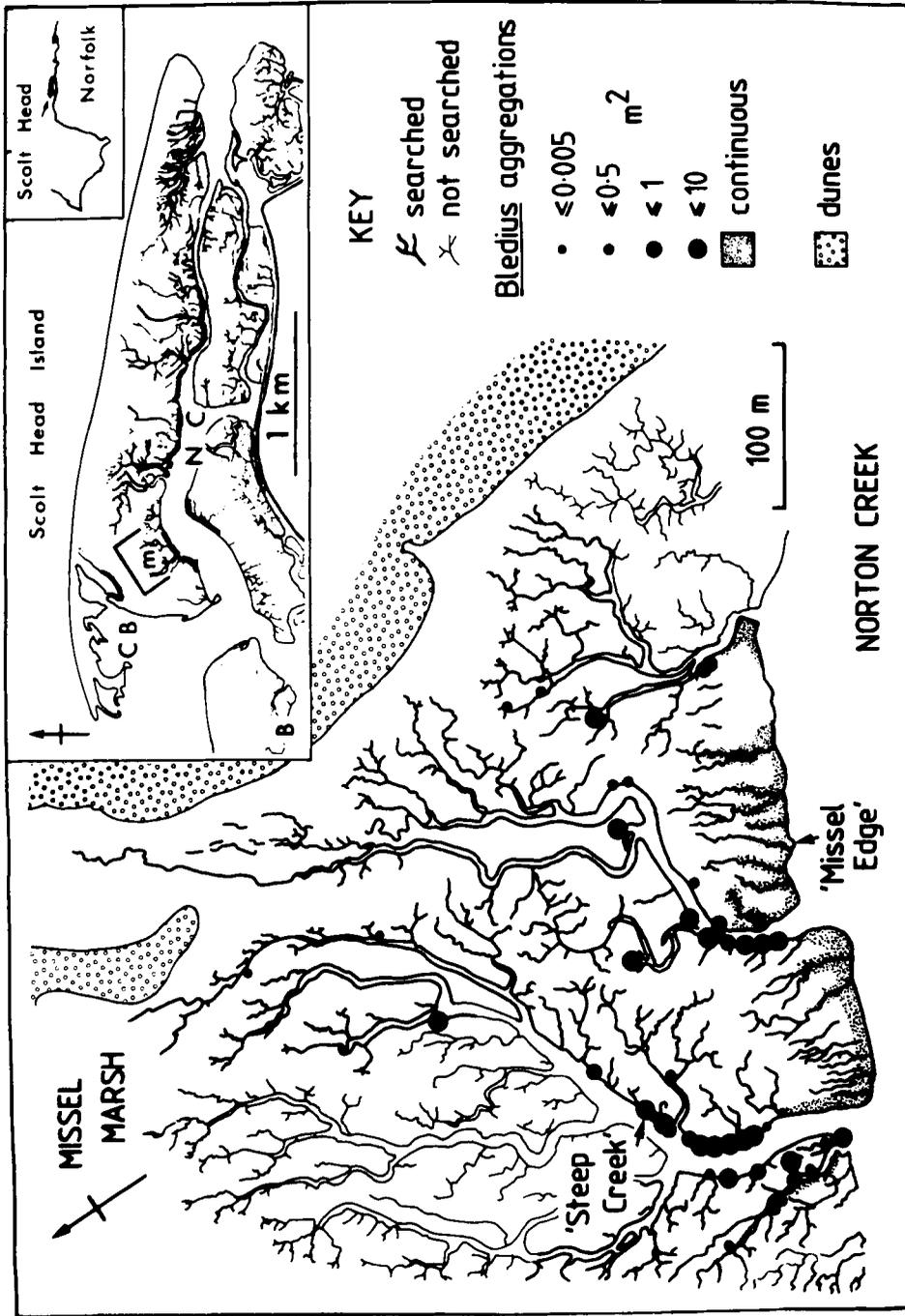


FIG. 1. Map of Scoll Head Island, Norfolk, U.K., showing the distribution of *Bledius spectabilis* aggregations of different sizes (based on surveys made on foot August 1981) and the transect sites in Missel Marsh. The large inset shows the whole island with NC (Norton Creek), m (Missel Marsh), B (Brancaster Harbour transect), CB (Cockle Bright), with major *B. spectabilis* aggregations marked in solid black along Norton Creek. Outlines of marsh topography drawn from aerial photographs.

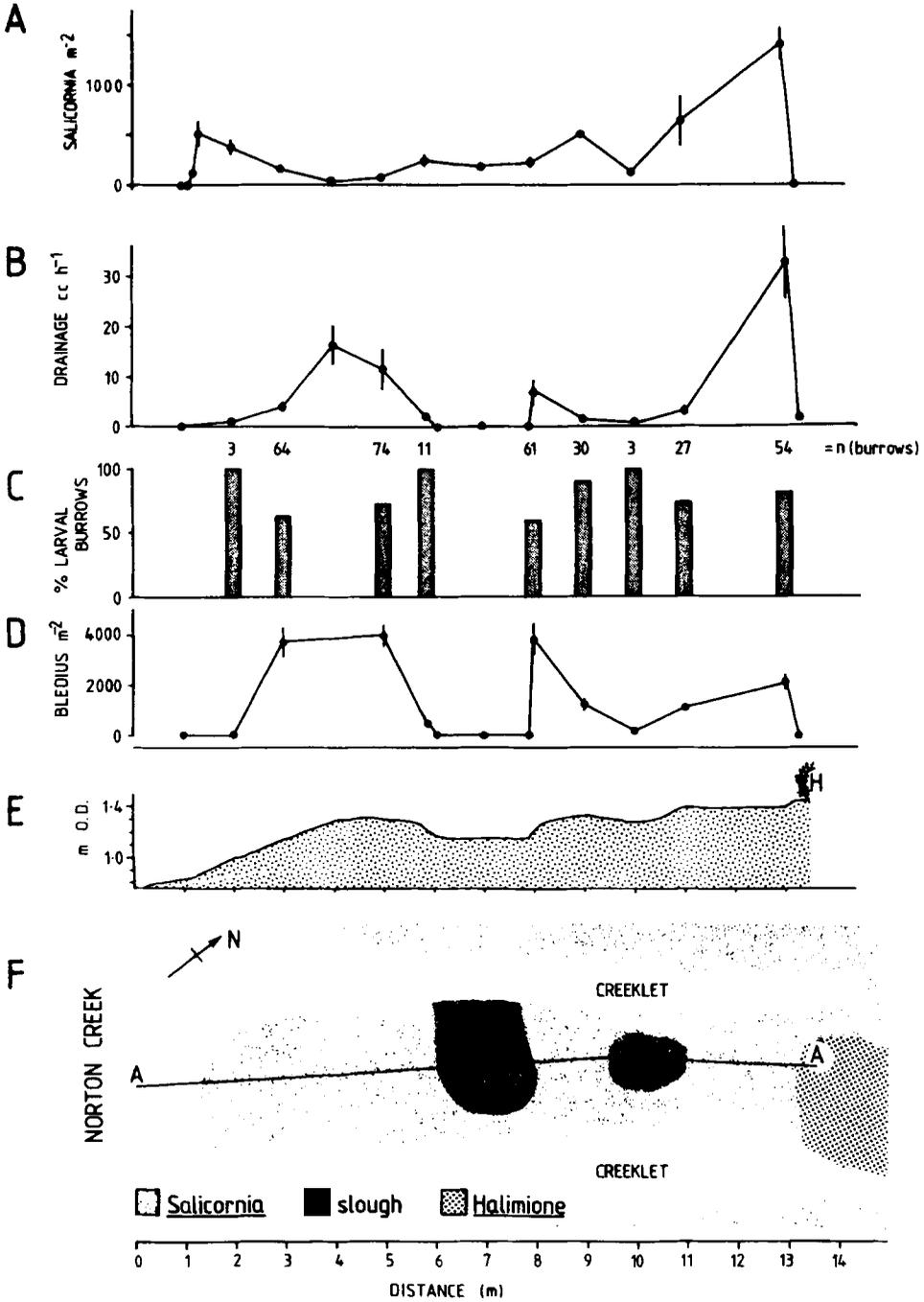


FIG. 2. Distribution of *B. spectabilis* at the Missel Edge site, 9 July 1981, along a transect A-A. (A) Density of *Salicornia* plants; (B) soil drainage ( $n=20$ ); (C) percentage of the beetle burrows that contain post-maternal phase larvae; (D) mean numbers of *B. spectabilis* (adults and larvae) ( $n=5$  or 7 soil cores); (E) profile of transect, H marks *Halimione* cover (see F); (F) plan view of the transect. Mean values are given  $\pm 1 \times$  SEM).

observations of the coverage of several tides in relation to the values given in the Admiralty Tide Tables.

Except where otherwise stated, all values are given as means  $\pm 1 \times \text{SEM}$  ( $n$ ).

## Results

### 1. Distribution of *Bledius* on the Scolt Head marshes

*Bledius spectabilis* occurs on all the Scolt Head marshes apart from the youngest and lowest marsh, Cockle Bight. Detailed and careful searches of the main Cockle Bight marsh in 1981 and 1986 revealed no *Bledius* colonies, but there were large numbers of brooding females of *Heterocerus fossor* Kiesenwetter in burrows in the mud banks where *Salicornia* was starting to establish itself. The densest (up to 4000 beetles  $\text{m}^{-2}$  (adults and larvae combined)) and most extensive *Bledius* colonies were on Missel Marsh; on the more mature marshes towards the east of the island (see Pethick, 1980), for example Plantago and Plover marshes, the beetle aggregations were restricted to the very edge of the saltings cliffs bordering Norton Creek and in isolated aggregations up the small creeks (Fig. 1). Detailed transects from three different, characteristic beetle aggregations are given below, together with observations on beetle distribution in depressions and salt pans.

(i) *Extensive aggregations: Missel Edge.* There were many large aggregations of *B. spectabilis*, sometimes more than  $10 \text{ m}^2$  in area, along the edge of Missel Marsh bordering Norton Creek (Fig. 1). The saltmarsh soil sloped gently towards the creek. The *Bledius* aggregations stretched back up the marsh away from the main creek for up to 7 m from the lower edge of the saltmarsh marked by the lower limit of *Salicornia*. However, no part of the aggregations here or elsewhere was more than about 1 m from an edge of a large or small creek. The extensive aggregations were dissected by creeklets 30–50 cm deep. Surface drainage was rapid.

A transect was taken along the centre of a 2 m wide spur between two small creeklets 50 cm deep (Fig. 2F). The vegetation was dominated by *Salicornia europaea* agg. (Fig. 2A) but also included *Aster tripolium* L., *Suaeda maritima* (L.) Dum., *Limonium humile* Mill., and *Limonium vulgare* Mill. Away from Norton

Creek the transect ended with 100% cover of *Halimione*. Below 0.9 m O.D. (Ordnance Datum), the lower limit of *Salicornia*, the slope merged into mud-flats filled with *Nereis* holes and covered with a thick layer of fine filamentous algae. The density of *B. spectabilis* increased gradually up the slope facing Norton Creek, but it dropped sharply in even slight depressions, for example at 7 and 10 m, along the transect (Fig. 2D, E), although these areas were at a higher level than other areas with greater densities of *Bledius*. Maternal burrows were restricted to areas of high *Bledius* density, whereas *Bledius* larvae in independent burrows occurred lower on the marsh and penetrated the edges of the sloughs. In these marginal areas, almost all the burrows were those of larvae (Fig. 2C). Higher densities of adults and larvae occurred in the better draining areas along the transect (Fig. 2B, D).

(ii) *Limited aggregations: Steep Creek Bank.* Small, isolated *B. spectabilis* aggregations occurred on the sides of creeks cutting into higher, more mature areas of marsh. For example, aggregations of this kind occurred on Missel Marsh on the edges of creeks up to 500 m from their confluence with Norton Creek. The area covered by these aggregations ranged from a few  $\text{m}^2$  to less than  $0.1 \text{ m}^2$ . The distance between colonies was, in some cases, more than 30 m along the creek.

A transect was taken through a typical example of one of these limited aggregations on the bank of a creek cutting into Missel Marsh 150 m from its confluence with Norton Creek (Fig. 3). Between a thick layer of algae which covered the lower end of the transect and dense *Halimione* that covered the top of the creek bank, the transect was mostly bare mud. At this and other similar sites, the *B. spectabilis* aggregations extended upwards until the *Halimione* was reached.

These aggregations were not only smaller but also half the maximum density of the main aggregations along the edge of Norton Creek. The vertical range of *B. spectabilis* at the Steep Creek Bank site was greater and the distribution also markedly different from that of the main aggregations (Fig. 4). *Bledius* of all stages occurred much lower down the transect; maternal burrows were even found among *Nereis* burrows in the anoxic mud underneath the algal mat (0.85 m O.D.).

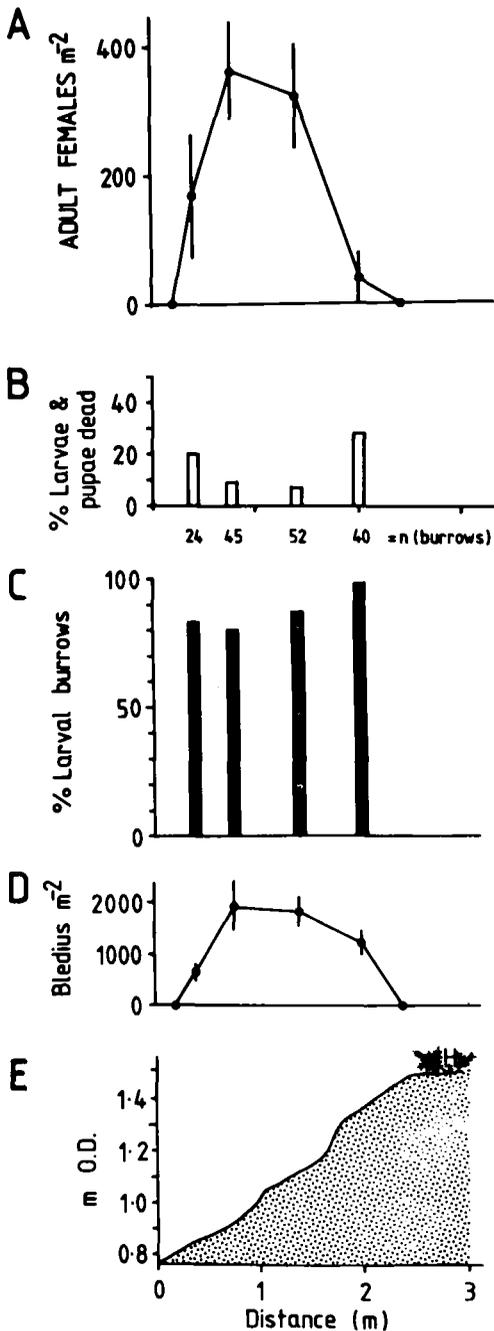


FIG. 3. Distribution of *B. spectabilis* on the Steep Creek transect, 2 August 1981. (A) Density of brooding adult *Bledius*; (B) percentage of larvae and pupae that were dead (in the upper stations, most of the dead individuals were infected with *Metarrhizium anisopliae*) (numbers given in Table 1); (C) percentage of the beetle burrows that contain post-maternal phase larvae; (D) mean density of *Bledius* ( $n=5$  or 7 cores); (E) profile of the transect. Mean values  $\pm 1 \times$  SEM.

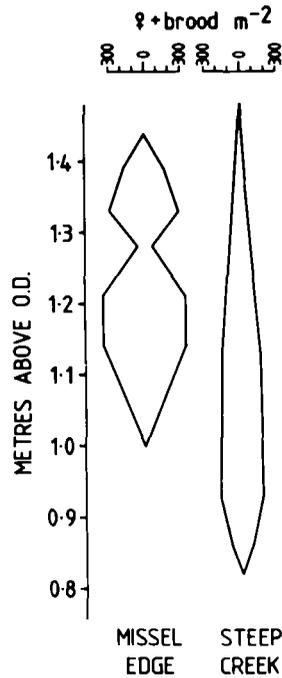


FIG. 4. The distribution of brooding female *Bledius spectabilis* at the Missel Edge and Steep Creek transects plotted against height above Ordnance Datum (m). The low density of *Bledius* at about 1.28 m O.D. along the Missel Edge transect marks the position of a poorly draining area.

Larval and pupal mortality was greater at the extreme ends of the transect (Fig. 3B; Table 1) than in the centre. The majority of the dead larvae and pupae in the top sampling station were covered with the fungus *Metarrhizium anisopliae* (Metchnikoff) Sorokin, but the dead larvae in the lowest sampling station appeared to have died from anoxia or drowning; many of the dead larvae were in blue-walled burrows and some were in burrows full of water.

(iii) *Ribbon aggregations: Brancaster Harbour*. Small mud cliffs occur commonly on saltmarshes (e.g. Long & Mason, 1983). The distribution of *B. spectabilis* across such a cliff was studied at the Northern Edge of Brancaster Harbour ('B' inset, Fig. 1). The cliff was about 20 cm high, plunging sheer into poorly drained mud-flats inhabited by *Nereis*. The height of the marsh edge was not measured, but judging by the vegetation it was similar to the height of the main Missel Marsh Edge aggregations, i.e. about 1.3–1.4 m O.D. The beetles were confined to a very narrow band 0.4 m wide along the top

TABLE 1. The density of live and dead *Bledius spectabilis* larvae and pupae at different heights along the Steep Creek bank transect and at the Missel Edge site (4-7 August 1981). A higher proportion of larvae and pupae were dead at the lower and upper extremes of the Steep Creek transect ( $\chi^2=9.1$ ,  $df=3$ ,  $P<0.03$ ). The mortality at the middle stations on the Steep Creek transect was similar to that in the main aggregations at the Missel Edge site, which were at about the same height above O.D. Data on bottom line are from Wyatt (1984); mean from twenty 15 cm diameter samples.

Site	Height (m O.D.)	No. of cores	Total live larvae and pupae	Total dead larvae and pupae	Dead (%)	Equivalent density $m^{-2}$ (live larvae and pupae)
Steep Creek	0.2	6	16	4	20	533
	0.9	5	33	3	8	1320
	1.1	5	42	3	7	1620
	1.4	5	29	11	28	1154
Missel Edge	1.2				6	2473

edge of the cliff. The aggregations were small, rarely covering an area of more than  $0.6 m^2$  and the adult beetle density within the aggregations was low ( $276 \pm 92 m^{-2}$  ( $n=8$ )). The cliff was undercut by wave action in many places and holed by numerous crab burrows. Such ribbon aggregations were common along saltings cliffs that plunged directly into poorly drained, low-level mud.

(iv) *Depressions and saltpans.* *B. spectabilis* adults were absent from depressions and the floors of saltpans (Fig. 2C). However, some dispersing *B. spectabilis* larvae walked from the main aggregations into these marginal areas. During neap tides, when the marsh surface is not covered by the tide, the saltpans and depressions dry out. Dispersing first instar larvae walked into the pans and dug burrows in the floor. The majority of the burrows were near the edge of the pan: in one survey on Missel Marsh on 23 June 1980 in two pans, the mean distance of larval burrows from the edge of the pan was  $14 \pm 1$  cm ( $n=46$ ). The dried pan floor had a rich algal cover but the fine mud below was anoxic and the tailings produced by the larvae were blue-grey in colour. Although the habitat seemed ideal during neap tides, a heavy mortality occurred on the return of the covering tides. Four days after the first covering tide following a period of neap tides, samples were taken from within 20 cm of the edge of a newly flooded saltpan on Missel Marsh (28 June 1980). The total density of *Bledius* larvae was  $840 \pm 130 m^{-2}$  ( $n=5$ ) and of these larvae 43% ( $n=24$ ) were dead in their burrows. The burrows of some dead larvae were flooded, others were dry but anaerobic.

## 2. Factors influencing the distribution of *Bledius*

(i) *Drainage.* Measurements of the rate of drainage along the Missel Edge transect (Fig. 2B) showed that there was a significant positive correlation between the density of *B. spectabilis* and the rate of drainage (Fig. 5) (Spearman's rank,  $r_s=0.85$ ,  $n=13$ ,  $P<0.005$ ). The percentage of independent post-maternal larvae was negatively correlated with drainage ( $r_s=-0.68$ ,  $n=13$ ,  $P<0.05$ ); maternal burrows were found almost entirely in the better-draining areas (Fig. 2C).

The poorly draining areas remained covered with water long after the tide had gone out. For example, the depression centred on 10 m along the Missel Edge transect was still full of water more than 2 h after the freely draining parts of the transect had dried out.

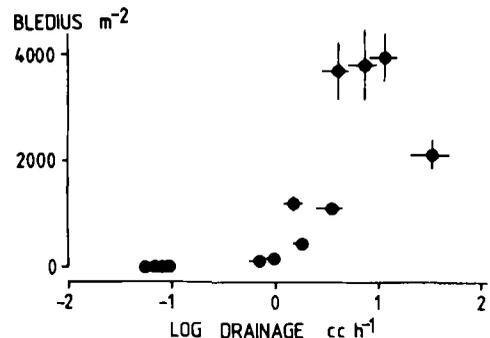


FIG. 5. The density of *B. spectabilis* (larvae and adults) ( $n=5$  or 7 cores) plotted against the log of the drainage rate from holes the size of *Bledius* burrows ( $n=5-18$  holes) at the same stations along the Missel Edge transect (see Fig. 2). Mean values  $\pm 1 \times SEM$ .

(ii) *Halimione portulacoides*. *Halimione* bushes formed the upper boundary of many *B.spectabilis* aggregations in Missel Marsh and there were numerous old *Bledius* burrows under some bushes. The hypothesis that shading by plants might cause the disappearance of *Bledius* was tested experimentally by transplanting *Halimione* bushes into randomly chosen sites within established *Bledius* aggregations. The density of *B.spectabilis* adults in these sites was initially  $764.0 \pm 141.2 \text{ m}^{-2}$  ( $n=4$ ). Three months later, the number of *Bledius* under the transplanted bushes was found to be significantly lower than in control areas within the same *Bledius* aggregations (under *Halimione*:  $99.5 \pm 67.8 \text{ m}^{-2}$  ( $n=10$  cores), control:  $875.3 \pm 223.2 \text{ m}^{-2}$  ( $n=5$  cores);  $t=4.25$ ,  $df=13$ ,  $P<0.001$ ). The mean beetle density under the bushes was only 11% of that in the control areas. The death of *Salicornia* under the transplanted *Halimione* was also noticeable within a few weeks of the start of the experiment.

(iii) *Zonal position in the saltmarsh*. To test whether *B.spectabilis* could rear broods in lower regions of the marsh, females were moved to holes at 0.8 m O.D., 40 cm below the majority of the *B.spectabilis* aggregations on the Missel Marsh Edge site. Each female was placed in a hole 50 mm deep and 5 mm in diameter and the top was closed over with mud. The move was made during a period of neap tides so the beetles would have time to modify (see Wyatt, 1986) the holes before the next covering tide. This lower site was very similar in general appearance to the

bottom station (0.85 m O.D.) on the Steep Creek transect (Fig. 3). The mud was covered with a thick layer of algae and, although firm, was anaerobic in parts. The drainage from the burrow-sized holes was  $0.7 \pm 0.1 \text{ cm}^{-3} \text{ h}^{-1}$  ( $n=15$ ); an average maternal burrow would therefore empty in about 100 min (T. D. Wyatt, unpublished observations).

One month later, the transplanted females were disinterred: of the ten females that had remained in the new burrows, nine had resumed egg-laying after the move. The eggs were in perfect condition, the burrows were in good condition, and the larvae in the maternal burrows were healthy.

### 3. Effects of *Bledius spectabilis* on saltmarsh soil

Fig. 6 indicates that soil macropores (>1 mm diameter) are much more abundant in beetle aggregations than in uncolonized areas, and that these pores persist in regions (for example under *Halimione* bushes) long after the beetles themselves have died. The old burrows are preserved because their necks are blocked with debris as soon as they are not continuously maintained by the beetles.

In these examples (Fig. 6), the cross-sectional area occupied by the macropores was 8.5% (living *B.spectabilis* area) and 6.8% (soil under *Halimione* with old beetle burrows). Another technique, resin-infilling, showed that within the top 8 cm of soil, the maximum depth of *Bledius* burrows, the total macropore volume was 3% of

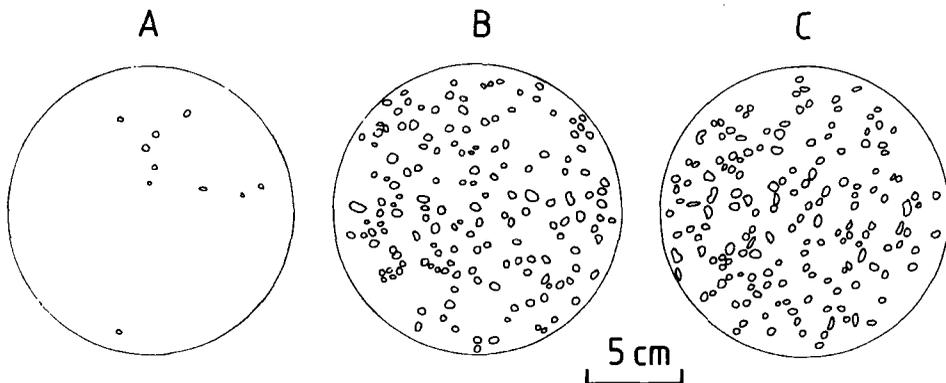


FIG. 6. Drawings of colour transparencies of cores of soil taken at the Missel Edge site, July 1980; (A) just outside and (B) just inside a dense *Bledius* aggregation, and (C) underneath a dense stand of *Halimione* at the edge of the main beetle zone. The cores are 15 cm in diameter and have been sectioned at a depth of 3 cm. All pores larger than 1 mm are shown. Most of these are *Bledius* burrows, but some are old root holes. Note in (C) irregular-shaped holes, which appear to be old beetle burrows invaded by plant roots.

TABLE 2. Mean maximum burrow dimensions and mean beetle density (24 July 1981) at Missel Marsh for each of the life-stages of *Bledius spectabilis*. For further details, see Wyatt (1986).

Stage	Mean burrow depth (mm)	Mean diameter of living chamber (mm)	Mean density (m <sup>-2</sup> )	Mean cross-sectional area (% of total)
First instar	21.2	3.1	255	0.2
Second instar	37.6	4.0	461	0.6
Third instar (+pupae)	51.4	4.9	1539	2.9
Adult male	51.6	5.6	62	0.2
Adult female	59.6	5.9	419	1.1
Total			2736	5.0

the total soil volume. The space was made up of 35% current *Bledius* burrows, 30% old *Bledius* burrows, and 35% old root and other spaces.

The resin-infilling method underestimates the air-space contributed by *B. spectabilis* in the upper layers of the soil, since it measures the volume down to 8 cm, whereas only the top 2 cm is penetrated by all the life-stages of the beetle (Table 2). A better estimate of the *Bledius* air-space in the top 2 cm was made by measuring the mean living-chamber cross-sectional area of each life-stage of the beetle and multiplying this by the mean mid-July density of each stage (Table 2). The cross-sectional area occupied by current *Bledius* burrows during mid-July 1981 was 5% of the total area. The resin infills showed that for every 5% of current *Bledius* burrow there is 4% of old burrows. Therefore, at a depth of 2 cm the total area of *Bledius* burrows was about 9% of the cross-sectional area, which is very similar to the value that can be obtained independently from Fig. 6B. The total volume contributed by the beetles would be slightly less, because of the narrow neck at the top of each burrow (see Wyatt (1986) for full description of burrow structure).

The areas of high burrow density are also areas of rapid drainage (Fig. 5), but the rate of drainage from beetle burrows can vary greatly. In the middle of a large aggregation at the Missel Edge site, the burrows drained rapidly ( $10.1 \pm 3.3 \text{ cm}^3 \text{ h}^{-1}$  ( $n=13$ )), whereas the rate of drainage from isolated beetle burrows below the main aggregation was much slower ( $0.7 \pm 0.1 \text{ cm}^3 \text{ h}^{-1}$  ( $n=15$ )).

## Discussion

The intertidal beetle *Bledius spectabilis* is abundant on Scolt Head NNR, occurring at densities

of up to 4000 m<sup>-2</sup>, and its distribution is clearly defined. The beetle aggregations are restricted to a narrow zone about 1 m wide along the edges of large and small creeks draining the low marsh areas of the island, and the vertical range is restricted to a zone between 0.85 and 1.55 m above Ordnance Datum. The majority of the aggregations and the highest densities are found between 1.2 and 1.37 m O.D., that is about 25–40 cm below MHWN (mean high water at neap tides) (Admiralty Tide Tables). These aggregations are covered by about 600 high tides each year (i.e. by about 85% of the annual high tides). What factors limit the beetles' distribution?

### Upper limits

(1) *Drainage*. The edge regions to which the beetles are confined are better drained than most other sites and do not retain standing water after the tide has ebbed, as observed by Foster & Treherne (1975, 1976a) at Scolt Head. Elsewhere on the low marsh, the surface remained waterlogged and effectively submerged for long periods. The present observations show that beetle density is positively correlated with drainage rate (Fig. 5). However, several reasons suggest that it is the layer of standing water, rather than the anaerobic nature of waterlogged soil, that limits the beetles' distribution away from the marsh edges. Firstly, the beetles' behaviour (blocking and unblocking their burrows as the tide covers and uncovers them) allows them to colonize anaerobic soil but not sites covered by standing water (Wyatt, 1986). The saltmarsh plants (e.g. *Spartina*, *Salicornia*) that can colonize these water-covered depressions have air-filled conduits that connect the shoots and roots (e.g. Anderson, 1974): beetle burrows do not have the benefit of

a snorkel. Secondly, laboratory experiments show that adults cannot survive more than 96 h continuous submergence in anaerobic seawater (Wyatt, 1986). First instar larvae survive even less well: all were dead within 36 h of submergence in anaerobic seawater. Thirdly, adult beetles did not colonize shallow depressions in the saltmarsh surface that retained a pool of water after covering tides. Fourthly, the larvae that did invade these depressions during periods of neap tides suffered massive mortality (43%) when the tides returned.

Unlike adult *Bledius*, these larvae did not have the response to prolonged submergence observed by Larsen (1953) and van Wingerden *et al.* (1981) in marshes in Denmark and the Netherlands. There, adult *B.spectabilis* abandoned burrows that had been covered for several days and floated passively to new habitats. This behaviour was not observed at Scolt Head, because the edge sites were never submerged in this way.

In Danish and Dutch saltmarshes, those beetles (including *B.spectabilis*) whose summer breeding areas became permanently flooded in winter migrated to overwinter in dry sand-dune areas (Larsen, 1953; van Wingerden *et al.*, 1981). The Scolt Head *B.spectabilis* sites were not permanently flooded in winter and the beetles did not migrate to spend the winter in the dunes (Wyatt, 1984). These differences, and the differences between the sites on Scolt Head, are probably caused by very local differences in topography, in particular whether the beetles remain covered by water impounded after high tide.

(2) *Vegetation.* Although poor drainage might explain why *B.spectabilis* is limited to edge regions, it does not explain why the beetles are absent from higher vegetated regions of the marsh, many of which are well-drained (see Foster & Treherne, 1975). The present observations suggest that the upper limit of the distribution of *B.spectabilis* may be set by plants. The transplant experiment showed that *Halimione*, without the confounding variables of surface height or distance from an edge, could displace *Bledius spectabilis*, probably by shading the algae on which the beetles feed. A rocky shore analogy may be provided by the distribution of *Tessieropora* barnacles in New South Wales. Their lower limit (equivalent to the upper limit for *Bledius*) is partly set by biotic interactions: in

this case hard substrate for settling, rather than light, is taken by plants (macroalgae) (Denley & Underwood, 1979). In effect, *B.spectabilis* is confined to the *Salicornietum*, the pioneer saltmarsh community, which includes few macrophytes apart from *Salicornia* (Beetink, 1977). The thin upright form of *Salicornia* casts little shade and even at the highest densities covers little of the soil, for example, only about 10% at 1400 plants m<sup>-2</sup> (Wyatt, 1984). Thus, indirectly, the distribution of *B.spectabilis* is controlled by the factors affecting the pattern of vegetation on saltmarshes (for reviews, see Chapman, 1974, 1976, 1977; Beetink, 1977).

#### *Lower limits*

At very low levels, the substrate becomes too waterlogged, for example in the bottom of creeks, or too mobile to sustain the beetles. However, the algae on which the beetles feed clearly extend below the main aggregations, and it is perhaps surprising that the beetles do not colonize this unexploited resource. The beetle transplant experiments establish that the adults can successfully rear their young below the level of the main aggregations, and suggest that the adults are not at their physiological lower limit in the marsh. In contrast, the larvae may extend closer to their physical limits in the marsh: the marginal areas (e.g. salt pans, depressions, low regions of the transects) are colonized almost exclusively by larvae (Fig. 2), which often suffer heavy mortality in these areas (Table 1).

#### *Influence of Bledius on saltmarsh development*

Saltmarsh organisms, in contrast to those from rocky shores, can have a crucial effect on the development and growth of their habitat. It has long been accepted that saltmarsh plants play a major role in the accretion of saltmarsh sediments, but the role of animals, apart from vertebrate grazers, has been almost completely neglected. It is well known that invertebrates can have a profound effect on soil structure and drainage: earthworm burrows, for example, can constitute over 5% of the total soil volume and can improve drainage by 4–10 times (see Edwards & Lofty, 1972). Woodell (1974) showed that ant-hills produced by *Lasius flavus* on a Scolt Head marsh had different vegetation from that of the surrounding marsh, probably

because of improved drainage. It has been suggested that the burrowing activity of fiddler crabs may have an important effect on saltmarsh drainage. For example, *Uca pugnax* may reach densities of up to 196 m<sup>-2</sup> (Wolf *et al.*, 1975): assuming a burrow diameter of 2 cm, this gives a burrow volume of about 6% of total soil volume.

The present observations suggest that *Bledius spectabilis* has an important effect on soil drainage and hence perhaps on plant growth and saltmarsh development: the beetles can produce abundant burrows (about 9% of soil volume) in the soil at a very early stage of saltmarsh development; most of the burrows are large (>4 mm diameter) and persistent. High burrow density is associated with rapid soil drainage (Fig. 5): this is probably not simply because the beetles choose only well-drained soil, since they are able to colonize poorly draining soil in marginal areas (Figs 2 and 3).

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