ACTIVITY AND MOBILITY OF *COROPHIUM VOLUTATOR*: A FIELD STUDY

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The distribution of the intertidal amphipod *Corophium volutator* is heterogeneous at scales of cm to km. Whilst habitat preferences, interspecific and intraspecific interactions are factors affecting patterns of heterogeneity, these are moderated by mobility. A field investigation of small-scale (cm to m) mobility was carried out on the Ythan estuary, Aberdeenshire, during immersion and after the ebb of the tide. Observations on immigration to, emigration from and activity within small areas of sediment indicated that mobility is low, but animals that do move are adult males which crawl over the sediment rather than swim. These individuals moved only short distances and they frequently re-used existing burrows. This movement is probably related to reproductive behaviour. The low mobility and the short distances moved indicated that mobility has little impact on at least large and intermediate scale heterogeneity, but shows that small-scale patterns are constantly dynamic in time and space.

Keywords: Amphipod; *Corophium*; mobility; distribution

INTRODUCTION

Patchiness in the distribution of the intertidal amphipod *Corophium volutator* has been described from scales of km to cm (Flach, 1996 Lawrie, 1996). Patchiness at scales of km to m shows no consistent size or form and seems to be related to a complex of abiotic and biotic features (e.g. sediment grade, salinity, and cover by macroalgal mats), whereas at the cm-scale consistent high density patches 0–6 cm occur which are distributed randomly over the sediment, probably related to intraspecific interactions (Lawrie, 1996).

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In the absence of external forcing factors, such as habitat heterogeneity, an important factor affecting patch characteristics is the mobility of individuals in relation to patch size (Den Boer, 1981; Hansson, 1991; Caswell and Cohen, 1991). If patch size is larger relative to distances moved by individuals, then demographic processes internal to the patch, for example, birth and death of individuals, will be a major determinant of patch character. However, if mobility is great relative to patch size then processes external to the patch (e.g. emigration and immigration) will have a major effect.

For many species, different kinds of individuals show different scales of mobility, for example, those which have highly mobile planktonic juvenile stages and relatively sessile adult stages, such as bivalves, barnacles and many polychaetes. For such organisms large scale heterogeneity will largely be determined by the recruitment and subsequent survival of juveniles. In contrast, Gammarid amphipods like *Corophium* are quite mobile as adults and juveniles, but brood their young. Even limited adult mobility becomes important in such species for the maintenance of small scale patterns which are potentially much more dynamic in space and time than for sessile species, often reflecting aspects of individual behaviour and/or intraspecific interactions.

Corophium volutator can move by either swimming (and passive transport in flowing water) or crawling, the former potentially allowing movement over much greater distances than the latter. Several workers have investigated either one or both of these behaviours. A low frequency of adult swimming activity, with occasional periods of intense juvenile swimming activity, and crawling activity dominated by adult males seems to be the rule (Meadows and Reid, 1966; Fish and Mills, 1979; Hughes, 1988; Essink et al., 1989; Hughes and Horsfall, 1990; Lawrie, 1996; Lawrie and Raffaelli, 1997).

Here we describe the *in situ* activity of *Corophium* on the surface of small areas of sediment, specifically emigration into and immigration out of these areas during tidal immersion and after the ebb of the tide. The observations were made at three locations with differing *Corophium* densities. The results are considered in relation to the maintenance of spatial heterogeneity both at small and at larger scales.

MATERIALS AND METHODS

Observations were made on the Ythan estuary, Aberdeenshire, at three sites (1–3), identical to those described elsewhere (Lawrie, 1996; Lawrie and Raffaelli, 1997) and having intermediate, high and low densities of

Corophium respectively (Lawrie, 1996; see also Results). Observations on activity and movement were made at each site over the entire period of immersion, and for up to 135 minutes after the tide had receded from each site, on five separate occasions in June and July 1995. All observations were made during the day (sunrise, 0500h BST, dusk 2200h BST), from a raised platform through a viewing tube which could be fixed in a stationary position at differing heights from the sediment surface according to water depth. The number of animals active on the sediment surface within a 10 cm diameter circle and their size and sex (on the basis of visible morphology) were recorded every five minutes and grouped into the following categories: juveniles < 2 mm, juveniles 2–4 mm, males 4–6 mm, females 4–6 mm, males 6–8 mm, females 6–8 mm, males > 8 mm and females > 8 mm. Although smaller individuals were more difficult to sex, even the smallest juveniles could be clearly observed within the small area visible. The size and sex and times of arrival and departure (crawling and swimming), of immigrants (animals entering the area) and emigrants (animals leaving the area) and the number of tourists (individuals swimming over the site without stopping) were also recorded. Water depth, period of immersion and the number of burrow openings visible were noted. Once the water had fully ebbed from the site a core was immediately taken from the 10 cm diameter area observed, but observations continued in an adjacent 50 cm × 50 cm area. However, for these observations only the number of animals active (crawling) on the sediment surface during each five minute interval was recorded. The cores were sieved on a 500 μm mesh and the abundance, size and sex of *Corophium* determined.

For the purposes of data analysis each tidal observation period was divided into three equal sections: flood, slack and ebb and comparisons made between sites and between flood, slack and ebb periods using Kruskall–Wallis and ANOVA followed by *post-hoc* tests as appropriate. The size frequency distributions and sex ratios of mobile individuals were compared between sites and with those in the ambient sediment using the X^2 and G statistic. The relationships between abundance of immigrants, emigrants and active individuals with *Corophium* and burrow opening abundance were explored graphically and by Spearman's rank correlation.

RESULTS

As anticipated, the density of *Corophium* within the sediment was similarly highest at site 2 followed by site 1, with site 2 having a significantly greater
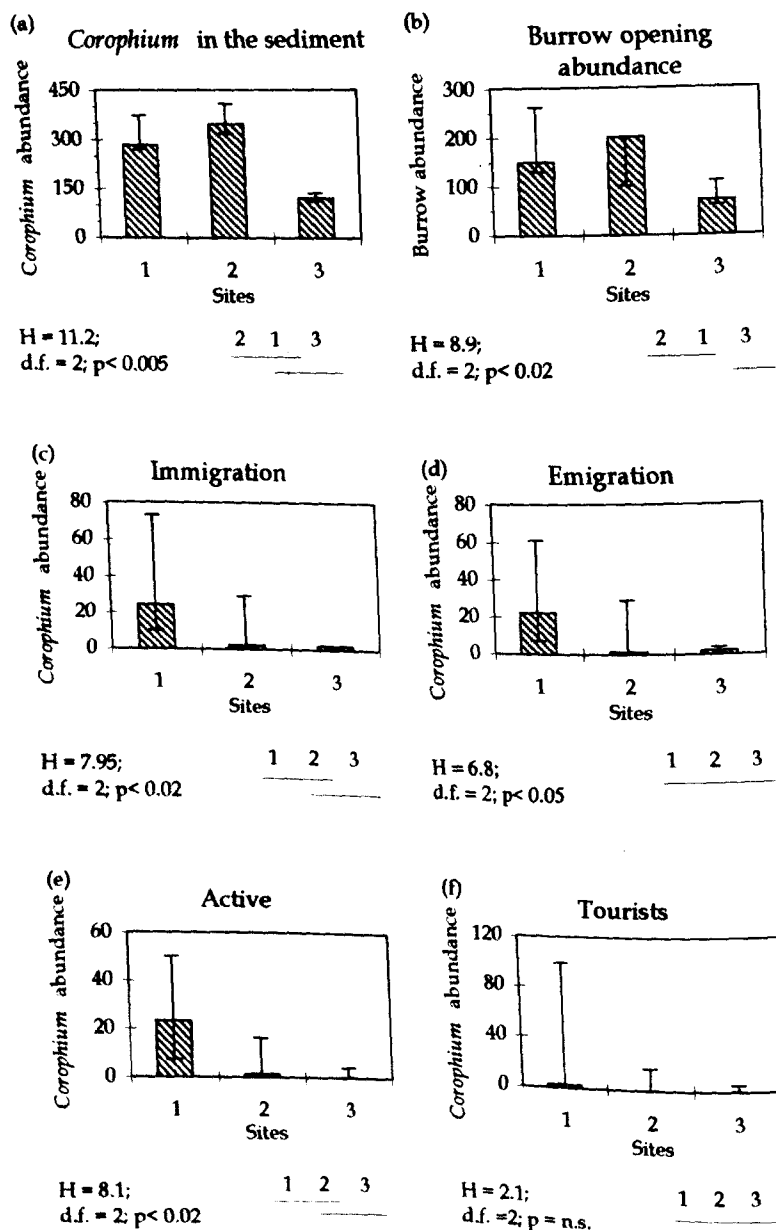
FIGURE 1   Comparisons between sites with respect to (a) *Corophium* abundance (b) number of burrow openings in the sediment, (c) number of immigrants, (d) number of emigrants, (e) individuals active on the sediment surface and (f) tourists passing over the 10 cm diameter areas within each site. Values are medians with 95% confidence intervals; the results of Kruskall–Wallis 'H' and non-parametric *post-hoc* tests are shown below, where sites jointly underlined indicate no significant difference at the 5% level.

abundance of *Corophium* than site 3 (Figure 1(a)). Similar variation was seen in the number of burrow openings between the sites (Figure 1(b)), although a higher number of burrow openings was recorded at site 1 than site 2. However, the number of immigrants, emigrants, active individuals and tourists during the period of immersion showed a different pattern of variation between sites (Figures 1(c)–(f)). Much greater variance in the levels of all these types of activities was recorded at site 1. Similarly, the variance in the levels of each type of activity was greater at site 2 than at site 3. The proportion of the population which were immigrants, emigrants and active individuals over one tide was low overall (0–25%) (Figure 2) and varied between sites as before. Separating immigrants and emigrants into those individuals crawling and those swimming, indicated that the majority of immigrants and emigrants crawl rather than swim (Figures 3(a)–(d)). Although, similar variation between sites was found for swimming immigrants and emigrants and crawling immigrants and emigrants, between-site differences were only significant for swimming immigrants and emigrants (Figures 3(b), (d)).

Two-way ANOVA of immigration, emigration, active individuals and tourists in relation to the flood, slack and ebb tidal states at the three sites (Figure 4), revealed significant differences between sites (all $p < 0.001$, except for tourists), but differences between tidal states were only significant for emigrants ($F = 5.7$, df $= 2$; $p < 0.01$). Within-site analysis using Kruskall–Wallis and non-parametric *post-hoc* tests indicated that only emigrants from site 1 varied significantly between tidal state; the slack period having significantly lower emigration than either the flood or the ebb
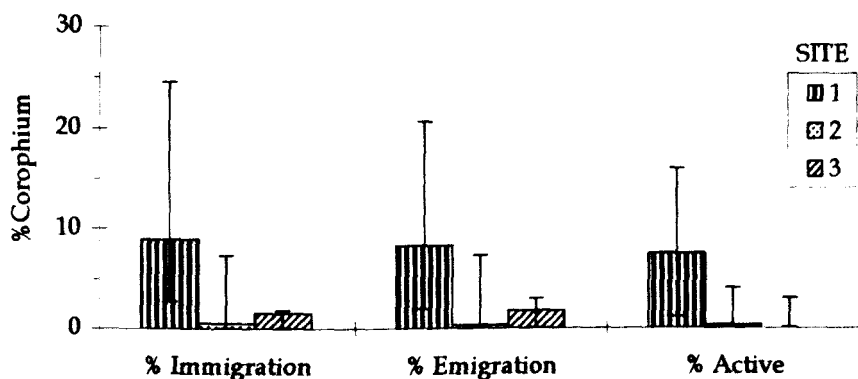

FIGURE 2 Immigration, emigration and activity as a percentage of the population in the sediment for each of the three sites. Values are median percentages and 95% confidence intervals.
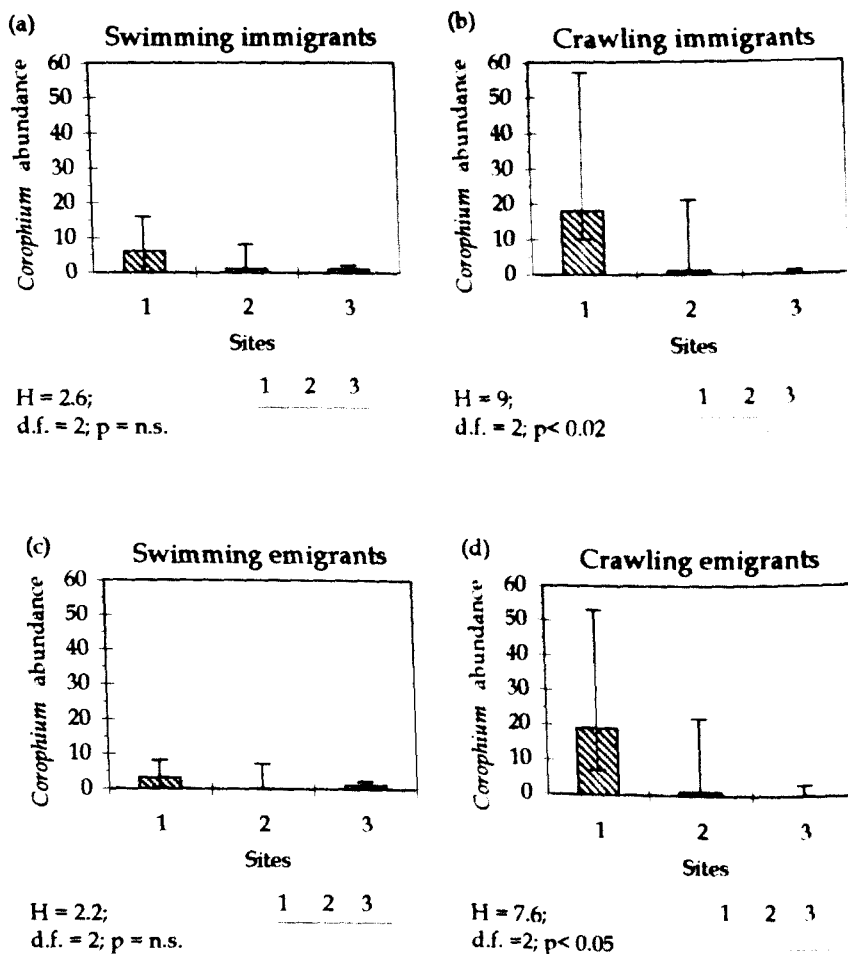
FIGURE 3   Comparisons between sites and in the numbers of swimming and crawling. immigrating and emigrating individuals. Values are medians and 95% confidence intervals: the results of Kruskall–Wallis 'H' and non-parametric *post-hoc* tests are shown above. where sites jointly underlined indicate no significant difference at the 5% level.

(Kruskall–Wallis $H = 8.5$; df $= 2$; $p < 0.02$). No obvious relationships were apparent between abundance of immigrants, emigrants or active individuals with period of inundation.

The size frequency distributions of immigrants, emigrants and active individuals during the period of immersion (Figure 5) indicated that individuals between 4 mm and 8 mm in length dominated at all sites, and that site 1 had more individuals between 4 mm and 6 mm than the other
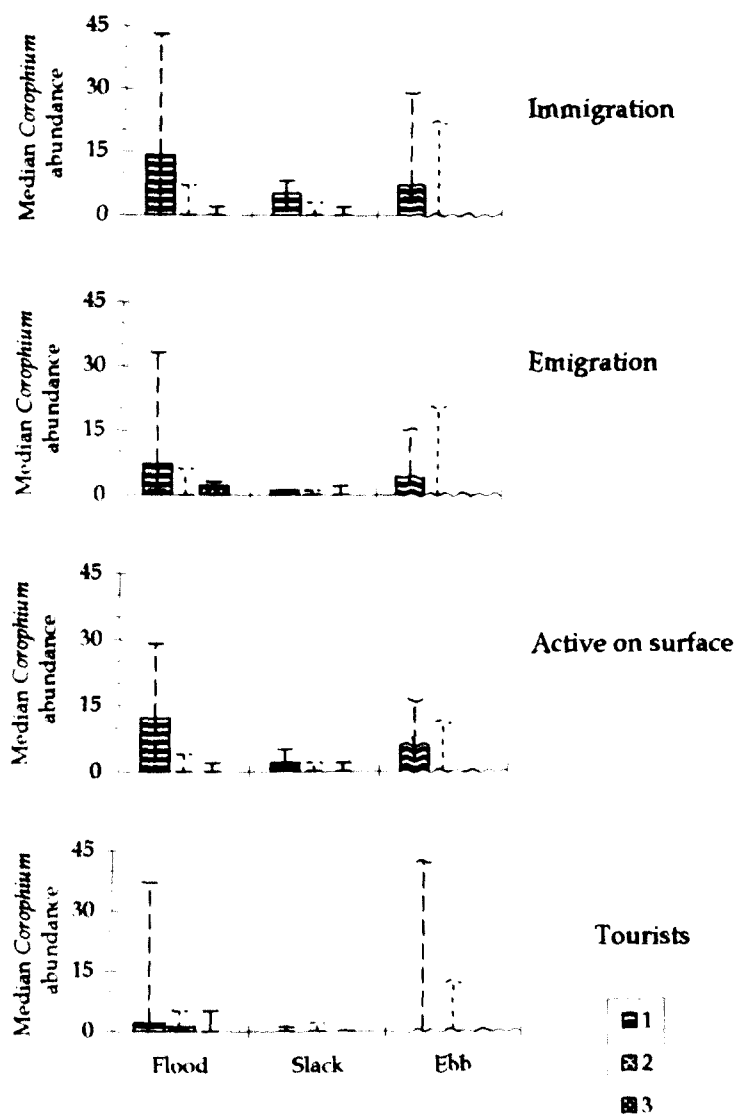
FIGURE 4 Variation in the number of immigrants, emigrants, active individuals and tourists between sites and between the flood, slack and ebb periods of the tide. Values are medians with 95% confidence intervals.

two sites. The size frequency distributions of the individuals in the sediment at all sites were dominated by *Corophium* < 4 mm. The size distributions differed significantly from those in the sediment with more individuals > 4 mm and fewer individuals < 4 mm than expected within the
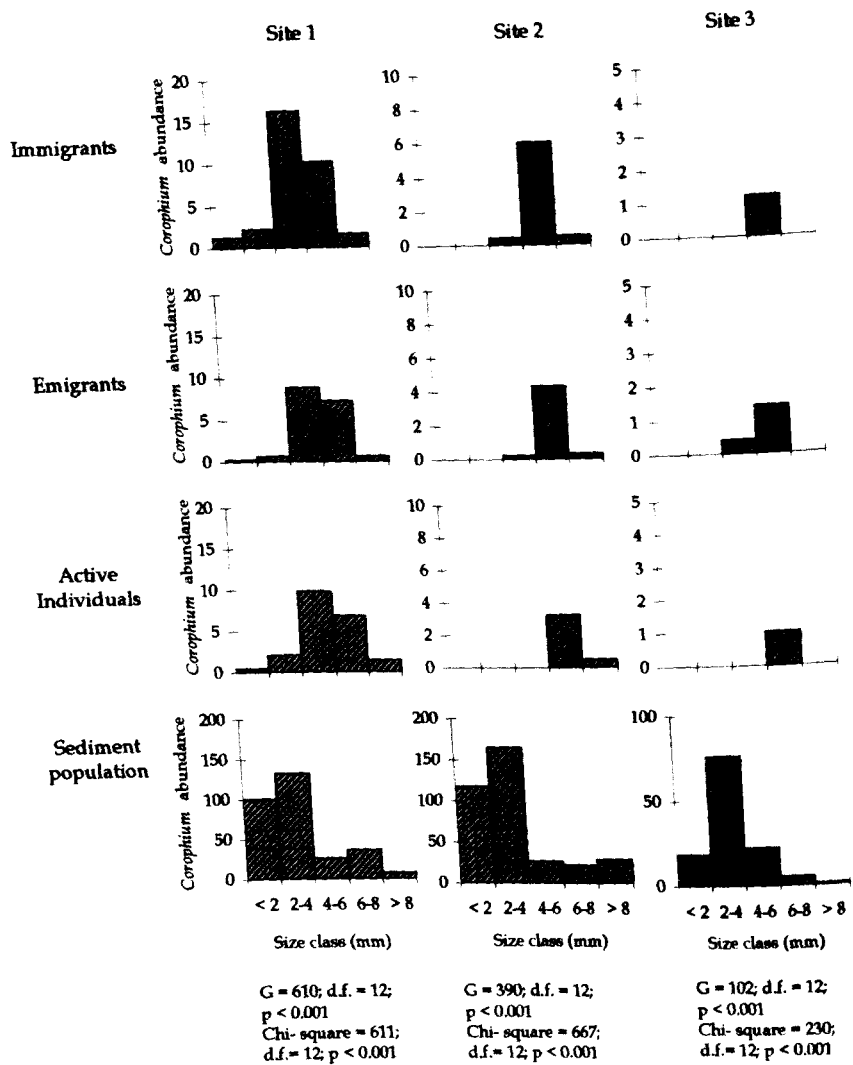
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FIGURE 5 Size frequency distributions of immigrants, emigrants, active individuals and *Corophium* in the sediment at the three sites. Samples for all occasions are represented. Results of comparisons between the mobile individuals and sediment population using G-statistics and Chi-square test are shown above.

immigrant, emigrant and active populations. The abundance of males and females in the immigrant, emigrant and active populations (Table 1) showed a male bias at sites 1 and 2, but at site 3 females were more abundant than males. These ratios differed markedly from those in the sediment at the three sites, which were generally dominated by females except at the

TABLE I Mean sex ratios of males to females of the immigrant, emigrant, active (both during immersion and after the ebb of the tide) and sediment populations at the three sites

Site	Immigrants	Emigrants	Active during immersion	Active after the ebb	Sediment population
1	3 : 2	5 : 4	3 : 2	5 : 2	2 : 3
2	3 : 1	23 : 1	5 : 1	3 : 2	2 : 3
3	1 : 2	1 : 2	3 : 2	5 : 1	1 : 1

low density site (3) where male and female abundances were roughly equivalent (Table I).

Activity after the ebbing of the tide varied both within and between sites but the variation within sites was large and there were no statistical differences between sites (Kruskall–Wallis $H = 0.39$; df = 2; n.s.). On three of the five occasions when observations were made at site 3, no activity occurred after the ebb of the tide. Similarly, at site 1, activity was limited on some occasions after the ebb of the tide, but at site 2 activity was almost always high. Activity could continue on the sediment surface for up to at least 135 min after the ebb and was frequently recorded for over 60 min (since activity had not always stopped when recording ceased the upper time limit could not be accurately determined).

The size frequency distributions of individuals active on the sediment surface during the first 55 min after the ebb of the tide (the shortest time period over which recordings were made), indicated that *Corophium* in the range 2–8 mm predominate (Figure 6), although some differences between the sites were apparent. These size distributions differed markedly from those found in the ambient sediment, which were dominated by *Corophium* < 4 mm, mainly due to more individuals than expected between 4 mm and 8 mm at both sites 1 and 2, and between 2 mm and 6 mm at site 3. In the active population males were dominant at all sites, in contrast to the ambient sediment population (Table I).

There was a suggestion that density-dependent relationships may exist with respect to number of burrow openings (Figures 7(a)–(c)). The proportion of the sediment population immigrating, emigrating and active increases with increasing number of burrow openings (immigration $r_s = 0.43$, $p < 0.05$; emigration $r_s = 0.51$, $p < 0.05$; active $r_s = 0.48$, $p < 0.05$) but this was not the case with *Corophium* density. Since the burrows created by adults are the most visible, and adults dominated in all of the activities recorded, the relationship between adult *Corophium* in the sediment and the proportion of immigrants, emigrants and active individuals was investigated (Figures 7(d)–(f)), but there was little evidence of
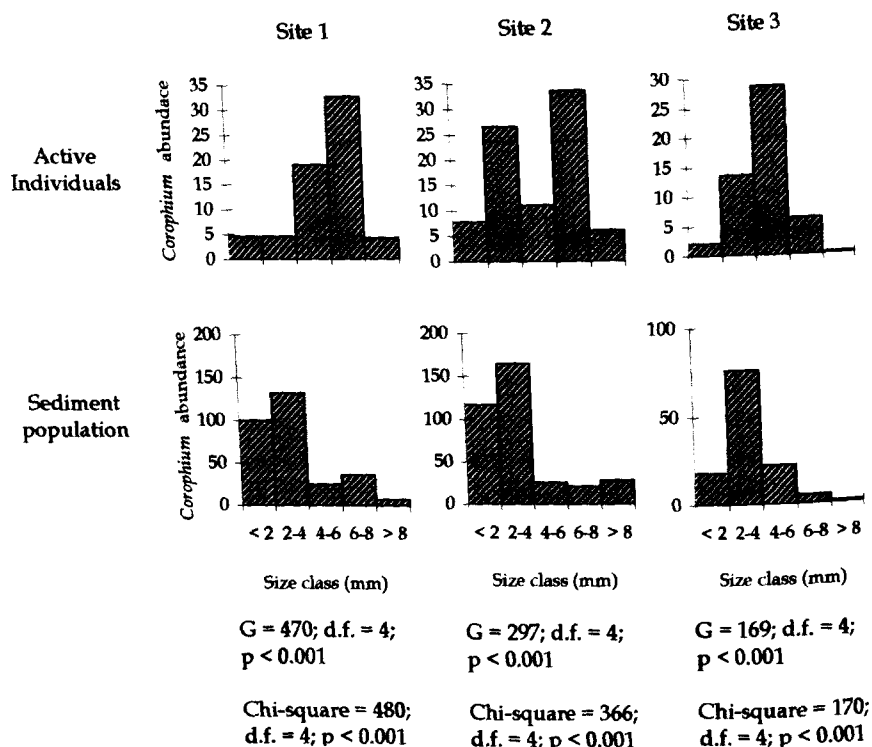
FIGURE 6   Size frequency distributions of individuals active on the sediment surface, within a 55 min period after the ebb of the tide and individuals in the sediment at the three sites.

any density dependence (immigration $r_s = 0.25$, n.s.; emigration $r_s = 0.22$, n.s.; active $r_s = 0.24$, n.s.).

DISCUSSION

Comparison with Other Studies

The numbers of mobile individuals during immersion and after the ebb of the tide were low, compared to those in the sediment, and were dominated by crawling adult males, whilst juveniles dominated overall in the sediment. Fish and Mills (1979) also noted that adult males predominated in the population crawling on the sediment surface after the ebb in the Dovey estuary, Wales. They related this behaviour to breeding, males searching for receptive females in their burrows. Meadows and Reid (1966) noted that both swimming and crawling in the laboratory was dominated by the
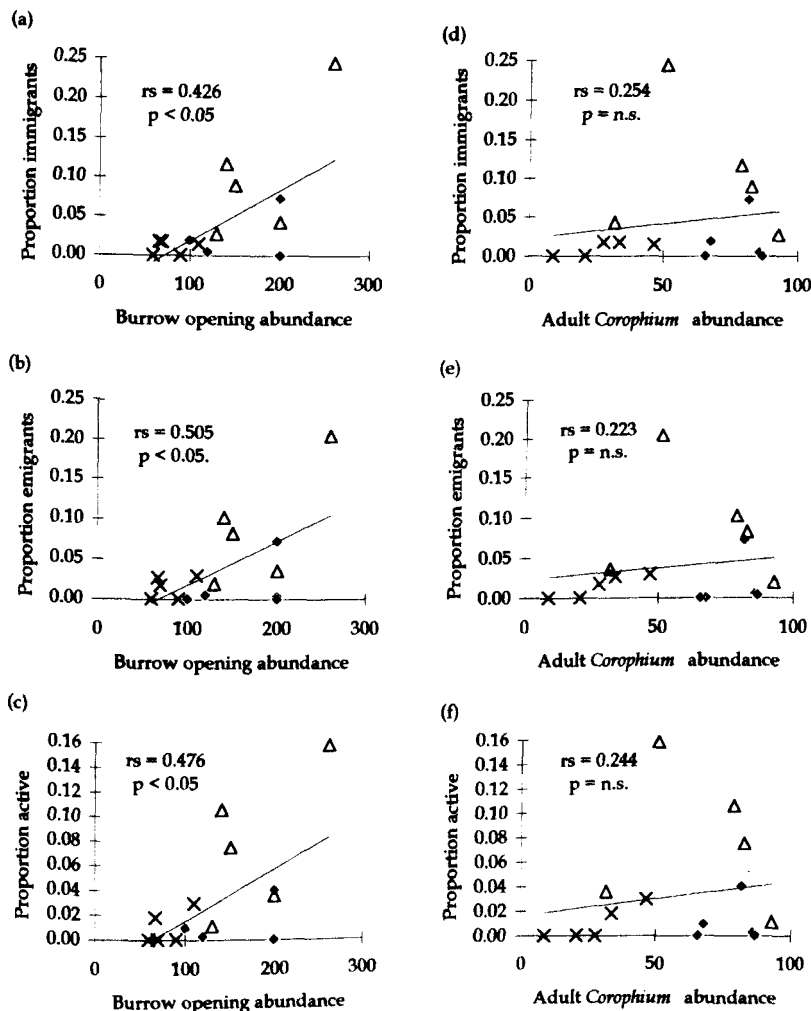
FIGURE 7 Relationships between the proportions of immigrants, emigrants and active individuals with respect to the sediment population density for each area with (a–c) number of burrow openings and (d–f) adult *Corophium* abundance. Different sites are represented by different symbols: Site 1 = triangles; Site 2 = diamonds; Site 3 = crosses. Values of Spearman's rank correlation 'r_s' and their significance 'p' are given.

largest adults, with crawling being the most frequent form of locomotory activity. Although Hughes (1988) found that *in situ* swimming behaviour on the Stour estuary, East Anglia, was generally dominated by juveniles, he also noted that large numbers of swimming animals only occurred periodically (on spring tides at night), with a high proportion of large adults compared to the sediment population. Studies on the Ythan (Lawrie, 1996;

Lawrie and Raffaelli, 1997) have also indicated high numbers of juveniles swimming periodically on one or two nights of the period of rising spring tides, but have shown that for the majority of the time swimming activity is extremely low and dominated by large adults especially males.

Although there was no overall significant difference in the occurrence of activity, immigration, emigration and numbers of tourists between the periods of the tide, examination of the raw data suggests that this was largely due to zero or low counts, for all periods of the tide on several occasions. However, when these activities did occur it was during the flood and ebb with little activity during the slack period. Other studies have noted peaks in swimming activity on the ebb tide (Morgan, 1965; Hughes and Horsfall, 1990) or on the flood tide (Essink et al., 1989), and Hughes (1988) found swimming activity to start on the flood and continue through slack water and the ebb. However, no previous studies seem to have noted a pattern of activity like that observed on the Ythan. Immigration, emigration and activity on the sediment surface were dominated by crawling rather than swimming individuals, but tourists were always swimming. It seems unlikely therefore that these between-study differences are due to differences in periods of activity of swimming and crawling animals. Hughes and Horsfall (1990) related geographic variation in the timing of activity to adaptations of individuals to habitat differences. They suggested that the ebb swimming of Corophium on the Afon Dwyrwd estuary, Wales, compared to the flood, slack and ebb swimming of Corophium on the Stour estuary, East Anglia, might occur because the population on the Stour estuary was 15 km up a narrow estuary, whereas the population on the Welsh estuary was close to the sea. Thus, if individuals only swam on the ebb on the Stour, this would result in a net movement of the population down the estuary. However, it is not clear what advantage is gained from swimming only on the ebb tide in a population close to the sea since this may well result in individuals washing out to sea.

The period of crawling after the ebb observed on the Ythan is longer than at other sites. Fish and Mills (1979) noted that the majority of individuals crawling on the surface had entered burrows after approximately 30 min. In the present study crawling could continue for at least 135 min and was regularly observed for over 60 min before any decline in activity was noted. These differences may be related to habitat differences between study areas, as suggested by Hughes and Horsfall (1990) for the timing of swimming within tidal periods and between tides (see above). One factor which might affect the duration of activity after the ebb is the relative 'wetness' of the sediment. As Hart (1930) noted, Corophium are most plentiful in

habitats where small puddles cover the sediment surface at low tide. Similarly, Beukema and Flach (1995) suggested that *Corophium* was limited in its distribution up-shore by a requirement of a minimum period of immersion. If 'drying out' is a serious problem for *Corophium*, the rate at which sediment dries will limit the duration of crawling activity after the ebb. Fish and Mills (1979) did not quantify this and in the present study observations were rarely made to the point where activity had completely stopped. However, incidental observations show that when the sediment surface was wet throughout the whole low tide period, animals were still active on the sediment surface in the hour previous to re-immersion, whereas when the sediment dried out completely during the low tide period no such activity was observed.

Comparisons between Sites

Activity, immigration and emigration all varied significantly between the three sites, although activity after the ebb did not. In all cases this was due to much greater activity, immigration and emigration at site 1. This could be due to the muddier, wetter and more sheltered environment at this site (Hart, 1930; Beukema and Flach, 1995). There was some evidence of a density-dependent relationship with number of burrow openings, although this was only true when pooling data from all three sites. The lack of a significant relationship when sites were examined individually is probably due to the low sample size ($n = 5$) at each site. Nevertheless, it should be noted that immigrants and active individuals rarely created new burrows, but searched the burrows already present and entered these. Similar behaviour was noted by Fish and Mills (1979). Thus, where more burrows are available more immigration may be possible and since the activity measured is partly a function of immigration, activity would also be greater. Similarly, if on entering a burrow and finding it occupied, an immigrant either emigrates or displaces the original occupant which emigrates, emigration behaviour would be expected to be related to burrow availability.

Implications for Spatial Heterogeneity

The generally low number of active individuals compared to those in the sediment and the predominance of adult males suggests that the activity observed is most likely to be related to reproduction and not to dispersal *per se*. Furthermore, the lack of any density-dependent effects and the fact

that the majority of individuals crawl rather than swim implies that this behaviour plays little part in the generation or maintenance of large-scale (10s to 1000s of m) heterogeneity. Crawling individuals rarely moved further than 50 cm and the mean distance moved was calculated at 16.9 cm (s.d. = 13.05 cm; $n = 28$). Also, movements did not occur in any particular direction, and individuals mainly searched down burrows. Gunther (pers. comm.) has observed *Corophium* individuals crawling over distances greater than 10 m on the extensive mudflats of the Wadden Sea, but this did not occur on the smaller Ythan. Thus, crawling seems unlikely to play a major role in the maintenance of large-scale heterogeneity.

Swimming can potentially take place over much larger distances (10s to 1000s of m) and hence may have greater effects on heterogeneity. McLusky (1968) noted that sites on the Ythan with very low winter salinity, and hence low overwintering populations of *Corophium*, showed a marked increase in population density with the rise in salinity during the summer, partly due to reproduction, but also due to immigration of adults. On the Ythan, swimming adults are unlikely to alter large-scale heterogeneity because of their low abundance. On the other hand, juveniles disperse in large numbers periodically (Hughes, 1988; Lawrie, 1996; Lawrie and Raffaelli, 1997), and the formation and maintenance of large scale heterogeneity may be largely dependent on the dispersal and survival of this age class.

Whilst small-scale (cm) heterogeneity could be affected by limited movement, the tendency of individuals to enter burrows already present, many of which are unoccupied (Fish and Mills, 1979; see above), will reduce its impact. Nevertheless, it seems likely that small-scale heterogeneity will be continually changing in space, though not necessarily in form, through time. Males are most likely to enter female burrows only for mating (Fish and Mills, 1979) but small scale heterogeneity was demonstrated most convincingly for the overwintering population (Lawrie *et al.*, 1997) when searching for females is unlikely. It seems more likely that the formation and maintenance of small-scale heterogeneity is related to some aspect of behaviour common to all *Corophium* individuals, such as feeding behaviour or a negative adult–juvenile interaction or to female behaviour since females appear generally more sedentary. Few studies deal with these factors either at such small scales or in detail, but Meadows (1964) noted that *Corophium* females showed gregariousness in their burrowing and negative adult–juvenile interactions have been suggested by Raffaelli and Milne (1987), Wilson (1989), Jensen and Kristensen (1990) and Limia and Raffaelli (1997).

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