

Substratum Preferences, Burrowing and Righting in *Ebalia tuberosa* (Pennant) (Crustacea: Decapoda: Leucosiidae)

PATRICK J. SCHEMBRI†

University Marine Biological Station, Millport, Isle of Cumbrae, Scotland KA28 0EG

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When given a choice, *Ebalia tuberosa* prefers sediment to a smooth plastic surface. Gravel is preferred to either sand or mud but no preference is shown between coarse and fine gravel. When overturned, the crabs may take from 2 to 900 s to right again, but males right in a shorter time than females, probably because they are less massive. *E. tuberosa* burrows by digging backwards into the sediment till half-covered. A variety of different mechanisms are then used to cover the remainder of the body. The crabs take from 130 to 1000 s to burrow completely and larger crabs of both sexes take longer to burrow than do smaller individuals.

INTRODUCTION

Almost nothing is known of the behaviour of any species of leucosiid crab. *Ebalia tuberosa* (Pennant) is a typical member of the family and is found in subtidal coarse sediments (Allen, 1967; Schembri, 1980). *E. tuberosa* buries itself in the substratum but does not construct a permanent burrow (Gosse, 1856) and shows numerous morphological and physiological adaptations for this mode of life (Balss, 1940; Glaessner, 1969; Schembri, 1979a,b, 1980, and papers in preparation). Apart from the semi-anecdotal descriptions of burrowing in *E. tuberosa* by Gosse (1856) and in *Philyra laevis* by Hale (1926), no other information on the burrowing and related behaviour of leucosiids is available and no experimental work on their substratum preferences has been carried out.

In the present study, the substratum preferences of *E. tuberosa* were investigated in the laboratory and a detailed analysis of burrowing and righting behaviour was made.

† Present address: Portobello Marine Laboratory, P.O. Box 8, Portobello, New Zealand.

MATERIAL AND METHODS

Crabs were collected from off Farland Point, Isle of Cumbrae, Scotland by dredging and were kept in the laboratory on their natural substratum in aquaria supplied from an open seawater circulation system. The crabs were fed every 3–4 days on pieces of scallop meat or on polychaete worms. The animals were used within seven days of collection.

Substratum preference experiments

Substratum preferences were tested by offering the crabs a choice of substrata. The five substrata tested were: mud (M), sand (S), fine gravel (FG), coarse gravel (CG) and a smooth "Perspex" surface (P). The sediments consisted of: (i) that fraction of mud which passed through a $63\ \mu\text{m}$ sieve; (ii) that fraction of beach sand which passed through a $500\ \mu\text{m}$ sieve but was retained by a $250\ \mu\text{m}$ sieve; (iii) that fraction of *Lithothamnion* gravel which passed through a 4 mm sieve but was retained by a 2 mm sieve; and (iv) that fraction of gravel which was retained by a 4 mm sieve. All these sediment types were washed several times in distilled water and air-dried before use.

Experiments were of two types, multi-choice and two-choice. The multi-choice chambers consisted of circular opaque plastic aquaria (diameter 24 cm \times depth 12 cm) which were divided into five equal segments by "Perspex" partitions to a depth of 2 cm. Each segment was filled with test substratum to the top of the partition. Each replicate aquarium contained all five test substrata which were not arranged in any particular order relative to each other. Five adult crabs were placed in each aquarium (either 3 ♂♂, 2 ♀♀ or 2 ♂♂, 3 ♀♀) one each on the five substrata. The aquaria were then covered with a light-proof black polythene sheet and left undisturbed for 50 h after which the number of male and female crabs on each substratum was counted. During the experiments a gentle flow of running seawater ($10 \pm 1^\circ\text{C}$) was maintained through each aquarium.

The two-choice chambers consisted of rectangular opaque plastic aquaria (length 34 cm \times width 25.5 cm \times depth 14 cm) which were divided into two equal halves by transverse "Perspex" partitions 2 cm high. Each half was filled with test substratum to the top of the partition. The following substratum pairs were tested: P/M, M/S, S/FG, and FG/CG (one pair per aquarium). Six adult crabs (3 ♂♂, 3 ♀♀) were placed on each half of each aquarium. The aquaria were placed in a natural light-dark cycle of LD 15:9 with a maximum intensity of ~ 300 lux during the light phase. After 24 h the number of male and female crabs on each half of the aquaria was counted. The water was not circulated and the ambient temperature was $15 \pm 1^\circ\text{C}$.

Righting and burrowing behaviour

Righting and burrowing were studied by recording sequences on videotape using a closed-circuit television camera and videorecorder. Crabs were filmed in a "Perspex" aquarium (length 30 cm × width 20 cm × depth 20 cm) supplied with running seawater and containing a 3 cm deep layer of muddy gravel which had been passed through a 2 mm sieve to remove the larger pebbles. To screen the crabs from any disturbances, a black polythene hood with a small aperture in one side to take the TV camera lens was arranged round the aquarium. The only source of light was a 60 W red tungsten lamp fitted with a diffusion reflector to give an even illumination of ~40 lux over the field of view of the camera lens. Each crab was sexed and measured before filming and was used once only.

For recording sequences, the following procedures were adopted: For righting behaviour, the videorecorder was switched on and a crab was placed dorsal surface down on the substratum. Filming was continued till the crab had righted itself. If the crab had still not righted after 10 min, filming was stopped. For burrowing behaviour, crabs were placed in the aquarium and filmed for a period of 15 min. Filming was only continued if the crab had started excavating. Only those sequences in which the crabs completely buried themselves and then remained quiescent for at least 10 min were used for analysis. Times were measured from the videotape records using a stopwatch.

RESULTS

Substratum preference experiments

Multi-choice experiments Forty-two replicate experiments were carried out. Of the total of 210 individuals used, 102 were male and 108 female. The χ^2 test showed that there was no significant differences in substratum preference between replicates ($P > 0.10$ in all cases) and the data from all 42 replicates were therefore pooled (Table I). Further χ^2 testing of these pooled data showed no significant difference in substratum preferences between sexes ($\chi^2 = 7.68$, d.f. = 4, $0.1 < P < 0.25$), thus, the results for the two sexes were pooled. Substratum preferences were analysed by taking the substrata in pairs and using goodness-of-fit χ^2 to test for deviations from a 1 : 1 ratio (Table II). There is no significant preference between the two gravels, but a strong preference is shown for the gravels over all other substrata. Sand is preferred to "Perspex" but not to mud. Mud is not preferred to "Perspex".

Two-choice experiments Ten replicate experiments were performed for each substratum pair using a total of 120 crabs (60 ♂♂, 60 ♀♀). As in the multi-choice

experiments, χ^2 testing showed no significant differences in substratum preferences amongst replicates or between sexes ($P > 0.25$ in all cases), so the data for sexes and replicates were pooled (Table III). The results of each substratum pair were tested for deviations from a 1:1 ratio with the χ^2 test (Table IV). There is again no preference between the two gravels. Fine gravel is

TABLE I

The substratum preferences of male and female *E. tuberosa* when offered a simultaneous choice of five different substrata; P—"Perspex", M—mud, S—sand, FG—fine gravel, CG—coarse gravel. Figures are the number of crabs found on each substratum after 50 h

	Substratum				
	P	M	S	FG	CG
Males	4	6	8	52	32
Females	5	13	17	39	34
Totals	9	19	25	91	66

TABLE II

The combined male and female results of the multi-choice substratum preference experiments (Table I) tested in pairs for deviation from a 1:1 ratio. Figures are goodness-of-fit χ^2 values

	P	M	S	FG	CG
P	—				
M	2.89 NS	—			
S	6.62 †	0.57 NS	—		
FG	165.65 ‡	48.83 ‡	36.42 ‡	—	
CG	41.81 ‡	24.89 ‡	17.58 ‡	3.67 NS	—

† Significant at $P < 0.05$.

‡ Significant at $P < 0.001$.

NS Not significant at $P = 0.05$.

TABLE III

The substratum preferences of male and female *E. tuberosa* when offered a choice of two different substrata. Figures are the number of crabs found on each substratum after 24 h. Symbols as in Table I

	Substratum choice			
	P/M	M/S	S/FG	FG/CG
Males	5/55	31/39	8/52	27/33
Females	7/53	32/28	6/54	27/33
Totals	12/108	63/57	14/106	54/66

TABLE IV

The combined male and female results of the two-choice substratum preference experiments (Table III) tested for deviation from a 1:1 ratio. Figures are goodness-of-fit χ^2 values

Substratum choice			
P/M	M/S	S/FG	FG/CG
75.21	0.21	69.01	1.01
†	NS	†	NS

† Significant at $P < 0.001$.

NS Not significant at $P = 0.05$.

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clearly preferred to sand. There is no preference between sand and mud but mud is preferred to "Perspex". These results confirm those of the multi-choice experiments.

Righting behaviour

Sequences of righting behaviour were recorded for 26 male and 30 female *E. tuberosa*. Each sequence was considered to be made up of discrete behavioural acts which in the description below are identified by code letters and numbers.

When handled, the crabs retract their appendages. The chelae are held folded close to the body, either with the mani parallel to the sediment surface (Ch), or at an angle of $\sim 60^\circ$ to it (Cv). When placed dorsal surface down, the crabs remain in this rigid position (Fz, Figure 1a). After a variable length of time the antennules start flicking (AF) and the pereopods are then unfolded (U, Figure 1b).

Righting proper starts when the dactyls of the last pair of pereopods are dug into the substratum (Ry4). The crabs lever themselves up, either using the 5th pereopods alone (Ry5a), or all four pairs of walking legs (Ry5b), or both walking legs and chelipeds (Ry5c), till upright (Ry6, Figure 1c), and then fall gently forward (Ry7, Figure 1d). Immediately after righting crabs perform high (H), medium (M) or low (L) intensity lateral merus displays (Wright, 1968) or else hold the chelipeds stretched out in front of the body (CS).

For each sequence, act frequency distribution and elapsed time from start to U and from U to Ry7 were determined. A sequence was considered complete if no further acts occurred within 100 s from the last act following Ry7.

A total of 266 acts by males and 292 acts by females were recorded. No significant sexual difference in act distribution (Figure 2) was found ($\chi^2 = 4.85$, d.f. = 14, $P > 0.97$). The mean number of acts per sequence was 9.92 ± 0.98 s.d. for males ($n = 26$) and 10.00 ± 0.83 s.d. for females ($n = 30$). There was no

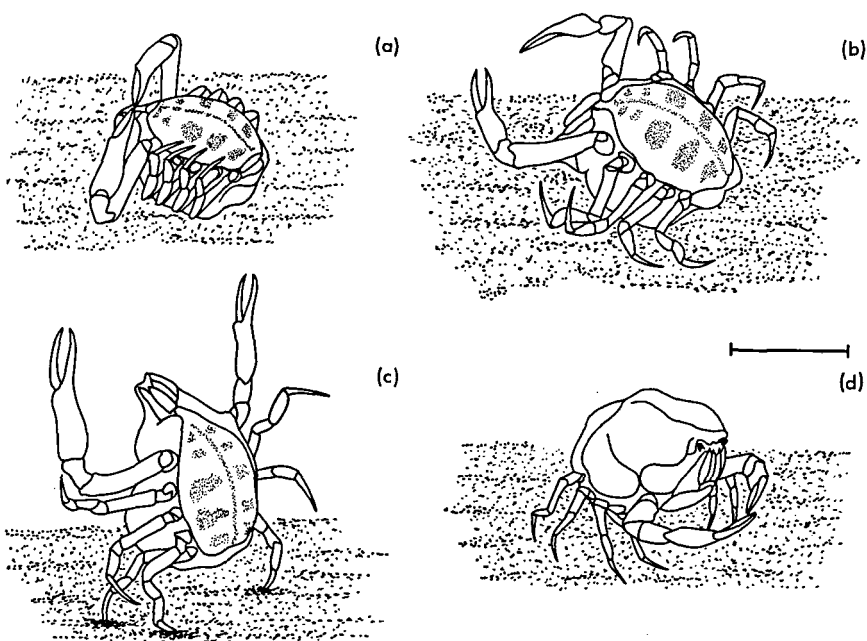


FIGURE 1 Righting sequence in female *E. tuberosa*; drawn from videotape recordings; scale bar, 1 cm; see text for full description.

significant sexual difference in number of acts per sequence (Mann-Whitney U -test, $U = 365$, $0.70 < P < 0.50$). The correlation between number of acts per sequence and carapace length was not significant for either sex (Spearman rank correlation; males: $r_s = -0.025$, d.f. = 24, $P > 0.50$; females: $r_s = 0.235$, d.f. = 28, $P > 0.20$).

The mean duration of the pre-righting phase (start to U) and righting proper (U to $Ry7$) and other statistics are given in Table V. No significant difference in duration of the pre-righting phase was found between the sexes (Mann-Whitney U -test, $U = 263.5$, $0.10 < P < 0.05$), however, the duration of righting proper was significantly shorter for males than for females ($U = 262.5$, $0.05 < P < 0.02$). No significant correlation was found between duration of the pre-righting phase and carapace length for either sex (Pearson product-moment correlation; males: $r = -0.185$, d.f. = 24, $0.20 < P < 0.50$; females: $r = 0.306$, d.f. = 27, $0.10 < P < 0.20$). The correlation between duration of righting proper and carapace length was not significant for males, but was significant for females (males: $r = -0.135$, d.f. = 24, $P > 0.50$; females: $r = 0.401$, d.f. = 28, $0.02 < P < 0.05$). Therefore the larger the female, the longer it takes to right.

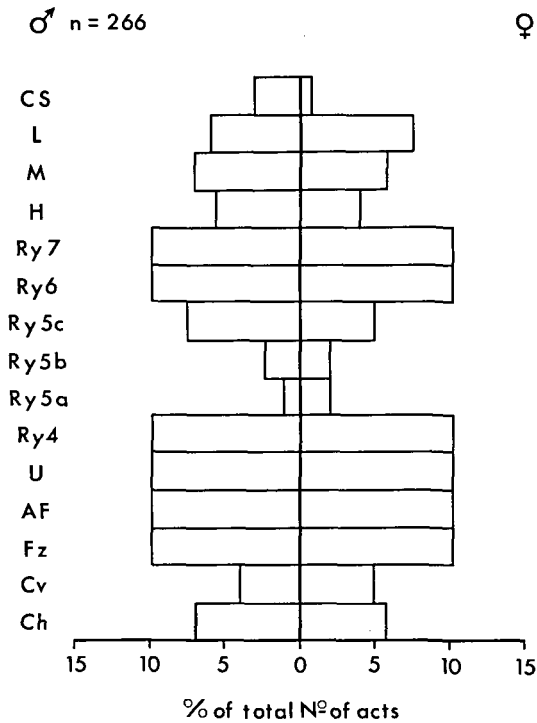


FIGURE 2 Frequency distribution of the 15 behavioural acts observed in righting sequences for male and female *E. tuberosa*; symbols are explained in the text; n, total number of acts observed.

TABLE V

The mean duration of the "pre-righting" and "righting" phases in righting behaviour sequences for male and female *E. tuberosa*

	Sex	Range (s)	Mean duration (s)	s.d. (s)	n
Pre-righting	Male	3-294	55.4	58.3	26
	Female	1-423	95.7	92.5	29
Righting	Male	5-229	44.5	46.9	26
	Female	1-512	90.1	106.2	30

Burrowing behaviour

As with righting, burrowing sequences were split up into discrete acts. Initially, crabs explore the substratum and occasionally probe it with the dactyls of the

periopods (Bur 1, Figure 3a). Digging starts when the crabs tilt their body upwards and push the 4th and 5th pereopods their full length into the sediment (Bur 2); these are then contracted, pulling the crab backwards into the sediment (Bur 3, Figure 3b). This process is repeated till the animals are approximately half buried (Bur 4).

Three different techniques are used to cover the remainder of the body; (i) the crabs rise on the extreme tips of the dactyls (Figure 3c) and slam down onto the sediment stirring up the finer particles which then settle on the carapace (Bur 5, Figure 3d); (ii) using the dactyls, propodites, carpopodites and meropodites of the chelipeds as shovels, the crabs gather a small mound of

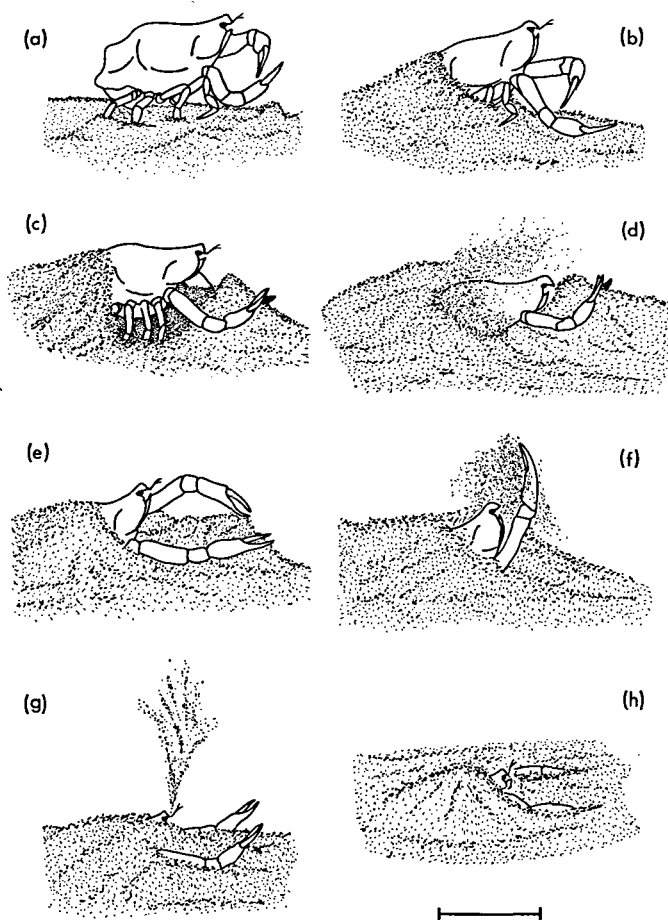


FIGURE 3 Successive stages in digging in a female *E. tuberosa*; drawn from videotape recordings; scale bar, 1 cm; see text for full description.

sediment (Figure 3e) which is then pushed backwards and laterally over the carapace (Bur 6); (iii) sediment is scooped up using the mani of the chelipeds which are held together to form a concave shovel, and thrown over the carapace (Bur 7, Figure 3f). Individuals use various combinations of these acts till the body is completely covered. The respiratory channels are cleared of sediment by blowing out a jet of water through the exhalant canals (Bur 8, Figure 3g). When burrowing is completed, the eyes, antennules and anterior tip of the carapace are cleaned by the 3rd maxillipeds (Bur 9) and the crabs remain quiescent with only the extreme tip of the carapace showing above the sediment (Bur 10, Figure 3h).

Of the 45 individuals filmed, complete sequences of burrowing behaviour were recorded for 10 males and 15 females and only these were used in the analysis. The act frequency distribution is shown in Figure 4. No significant difference in act distribution between the sexes was found ($\chi^2 = 2.608$, d.f. = 9, $P > 0.97$). The number of acts per sequence ranged from 5–23 for males (mean 11.1 ± 5.7 s.d., $n = 10$) and 5–28 for females (mean 12.5 ± 5.7 s.d., $n = 15$); no significant sexual differences in number of acts per sequence were found ($U = 62.5$, $P > 0.20$). Carapace length and number of acts per sequence were positively correlated for males but not for females (males: $r_s = 0.800$, d.f. = 8, $0.02 < P < 0.05$; females: $r_s = -0.120$, d.f. = 13, $P > 0.50$). Thus, in males, larger individuals perform more acts per sequence than do smaller crabs.

Time taken to burrow was measured from the videotape records. Burrowing was taken to start when the last two pairs of pereopods were pushed their full

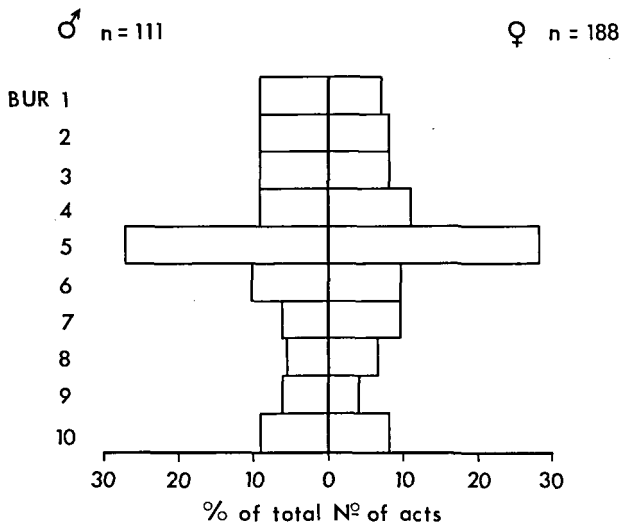


FIGURE 4 Frequency distribution of the 10 behavioural acts observed in digging sequences for male and female *E. tuberosa*; symbols are explained in the text; n , total number of acts observed.

TABLE VI

The mean duration of digging behaviour sequences for male and female *E. tuberosa*

Sex	Range (s)	Mean duration (s)	s.d. (s)	<i>n</i>
Male	133-591	373.8	150.1	10
Female	206-990	515.2	216.9	15

length into the sediment (Bur 2) and to end when the crab had completely covered itself, except for the antennules, and ceased moving (Bur 10). The mean duration of burrowing and other statistics are given in Table VI. No significant sexual difference was found in time taken to burrow in the same "standard" sediment ($U = 43$, $0.05 < P < 0.10$). As might be expected, a significant positive correlation was found for both sexes between time taken to burrow and length of the burrowing sequence in terms of number of acts (males: $r_s = 0.966$, d.f. = 8, $P < 0.002$; females: $r_s = 0.610$, d.f. = 13, $0.02 < P < 0.05$). More interestingly, a significant positive correlation was found for both sexes between carapace length and duration of burrowing (males: $r = 0.691$, d.f. = 8, $0.02 < P < 0.05$; females: $r = 0.675$, d.f. = 13, $0.001 < P < 0.01$). Larger crabs of both sexes take longer to burrow than do smaller individuals.

DISCUSSION

Substratum preferences

The results of the substratum preference experiments clearly show that *E. tuberosa* prefers coarse substrata. As might be expected, no difference in substratum preferences was found between the sexes. Combining the results of both types of choice experiments, the five substrata tested may be placed in order of decreasing preference as follows:

$$FG = CG \gg S = M > P$$

Individuals of *E. tuberosa* are normally active during darkness (Gosse, 1856; Schembri, 1980). In the two-choice experiments the crabs were placed in the choice chambers in the light phase of the LD cycle used. The majority of crabs burrowed into the substratum they happened to be on within minutes, while those on the "Perspex" surface usually moved over to the other half of the chamber and buried themselves in the mud. During the dark phase, the crabs must have dug themselves out and explored the aquarium before digging themselves in again during the next light phase. The crabs are therefore able to

burrow in all four sediment types provided and during stressful situations, as for example during daytime when they would presumably be exposed to predators, they will conceal themselves in the nearest available sediment irrespective of its nature. During the night, the crabs then seek out a more suitable sediment type.

In decapods which construct permanent burrows, burrow shape and stability are related to the physical properties of the sediment (Hughes, 1966; Fielder, 1970; Hartnoll, 1973; Atkinson, 1974; Berrill, 1975; Jones, 1976; Vannini, 1976). Likewise, in detritus-feeding decapods, the efficiency of food extraction is also related to the nature of the sediment (Miller, 1961; Ono, 1965; Griffin, 1971; Hartnoll, 1973; Crane, 1975; Vannini, 1976). *E. tuberosa* does not construct permanent burrows and feeds principally on small invertebrates (Schembri, 1980), hence these factors are probably less important. The properties of the substratum may, however, influence the distribution of food organisms and hence, indirectly, those of the crabs.

When buried in gravel, *Ebalia* are much less conspicuous than when buried in either sand or mud. On their natural substratum of muddy gravel with pebbles, *Ebalia* are virtually indistinguishable from the surrounding pebbles, particularly when carrying epizoid organisms on their carapaces (Schembri, 1980). The cryptic habits of *E. tuberosa* may be a significant factor in determining its substratum preferences.

Initial choice of substratum is made by the larvae but the adult crabs retain the ability to search for and recognize the preferred substratum if displaced from it by a short distance.

Righting

The survival of a cryptic animal depends on its ability to remain undetected. In *E. tuberosa* the abdomen, which is normally hidden from view, is marked with asymmetrical red blotches which make the crabs very conspicuous if overturned. The crabs may be accidentally overturned either during intraspecific agonistic encounters (Schembri, 1980) or due to turbulence in the topmost layers of sediment, perhaps caused by strong currents, or during the passage of some larger animal. The ability to right quickly following overturning is clearly of adaptive value to *Ebalia*.

Ebalia are sexually dimorphic, adult females being more massive than adult males of the same age-class because of the large dome-like abdomen of the females. This dimorphism is reflected in the behaviour of the crabs in that females take significantly longer to right than do males, presumably because of their greater bulk. Moreover, the duration of the righting sequences proper is positively correlated with size in females. No sexual differences were found in

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pre-righting behaviour probably because no morphologically different structures are involved in this.

Burrowing

In *Ebalia* burrowing is clearly a strategy for remaining inconspicuous and supplements the cryptic shape and coloration of the crabs. Using the terminology of Warner (1977), *Ebalia* is a back-burrowing crab, the animals effectively walking backwards and downwards into the sediment till half-buried. The relatively hard nature of the substratum probably makes further penetration difficult and a variety of techniques are used to cover the carapace. The use of the different "covering" techniques may depend on the nature of the sediment; for example, the body-slam method (Bur 5) will be more efficient on a fine, semi-fluid surface sediment than on a hard compact one.

E. tuberosa takes between 5–10 min to burrow which is longer than in the leucosiid *Philyra laevis* which takes "a few seconds only" (Hale, 1926). Because of their dome-shaped abdomens, female *E. tuberosa* are less streamlined than males and might be expected to take longer to burrow; no sexual differences in duration of burrowing were found, however. For both sexes the smaller crabs burrow in less time than do larger individuals. This may be due to the larger crabs having a greater area of carapace to cover or may be correlated with differences in activity in different sized individuals.

The only other leucosiid whose burrowing behaviour has been described, *Philyra laevis*, burrows in mud in very shallow water (Hale, 1926). *Philyra* excavates by tilting its anterior end upwards till the crab is in an upright position and then pulls itself backwards into the mud, assisting this process by clasping mud with the chelipeds and pulling it towards the body (compare with Bur 6 in *E. tuberosa*) and then thrusting it outwards (Hale, 1926). During the present study, digging was also observed in single individuals of *E. cranchi* and *E. tumefacta* and in these, this process was almost identical to that in *E. tuberosa*. Burrowing behaviour thus appears to be substantially the same in all leucosiids, but may differ in details perhaps depending on the nature of the substratum.

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References

- Allen, J. A. (1967). Crustacea: Euphausiacea and Decapoda. *Fauna of the Clyde Sea Area*, 1–116.
- Atkinson, R. J. A. (1974). The activity rhythm of *Goneplax rhomboides* (L.). *Mar. Behav. Physiol.* **2**, 325–335.
- Balss, H. (1940). Kennzeichen der Ordnung; Erforschungsgeschichte; Morphologischer Teil. In: Bronn, H. G. (Ed.) *Klassen und Ordnungen des Tierreichs*. Vol. 5, part 1: Crustacea (2nd ed.) Book 7 Decapoda pp. 1–160. Akademische Verlagsgesellschaft, Leipzig.
- Berrill, M. (1975). The burrowing, aggressive and early larval behaviour of *Neaxius vivies* (Bouvier) (Decapoda, Thalassinidae). *Crustaceana* **29**, 92–98.
- Crane, J. (1975). *Fiddler crabs of the world (Ocypodidae: genus Uca)*. Princeton University Press, New Jersey, 736 + xxiii pp.
- Fielder, D. R. (1970). The feeding behaviour of the sand crab *Scopimera inflata* (Decapoda, Ocypodidae). *J. Zool., Lond.* **160**, 35–49.
- Glaessner, M. F. (1969). Decapoda. In: Moore, R. C. (Ed.) *Treatise on invertebrate palaeontology*. Part R: Arthropoda 4, Vol. 2, pp. 400–532. The Geological Society of America, Colorado.
- Gosse, P. H. (1856). *The aquarium: An unveiling of the wonders of the deep sea*. (2nd ed.) John Van Voorst, London, 304 + xvi pp.
- Griffin, D. J. G. (1971). The ecological distribution of grapsid and ocypodid shore crabs (Crustacea: Brachyura) in Tasmania. *J. anim. Ecol.* **40**, 597–621.
- Hale, H. M. (1926). Habits of the smooth pebble crab (*Philyra laevis* Bell). *S. Aust. Nat. Adelaide* **7**, 67–69.
- Hartnoll, R. G. (1973). Factors affecting the distribution and behaviour of the crab *Dotilla fenestrata* on East African shores. *Estuar. coast. mar. Sci.* **1**, 137–152.
- Hughes, D. A. (1966). Behavioural and ecological investigations of the crab *Ocypode ceratophthalmus* (Crustacea: Ocypodidae). *J. Zool., Lond.* **150**, 129–143.
- Jones, M. B. (1976). Limiting factors in the distribution of intertidal crabs (Crustacea: Decapoda) in the Avon-Heathcote estuary, Christchurch. *N.Z. J. mar. freshw. Res.* **10**, 577–587.
- Miller, D. C. (1961). The feeding mechanisms of fiddler crabs, with ecological considerations of feeding adaptations. *Zoologica N.Y.* **46**, 89–100.
- Ono, Y. (1965). On the ecological distribution of ocypodid crabs in the estuary. *Mem. Fac. Sci. Kyushu Univ. ser. E (Biol.)* **4**, 1–60.
- Schembri, P. J. (1979a). An unusual respiratory rhythm in the crab *Ebalia tuberosa* (Pennant) (Crustacea: Decapoda: Leucosiidae). In: Naylor, E. and Hartnoll, R. G. (Eds.) *Cyclic phenomena in marine plants and animals*, pp. 327–335. Pergamon Press, Oxford.
- Schembri, P. J. (1979b). Oxygen consumption and the respiratory responses to declining oxygen tension in the crab *Ebalia tuberosa* (Pennant) (Crustacea: Decapoda: Leucosiidae). *J. exp. mar. Biol. Ecol.* **41**, 133–142.
- Schembri, P. J. (1980). Aspects of the biology, behaviour and functional morphology of the crab *Ebalia tuberosa* (Pennant). Ph.D. Thesis, University of Glasgow, 194 + ix pp.
- Vannini, M. (1976). Researches on the coast of Somalia. The shore and the dune of Sar Uanle. X. Sandy beach decapods. *Monitore zool. Ital. n.s. suppl.* **8**(10), 255–286.
- Warner, G. F. (1977). *The biology of crabs*. Elek Science, London, 202 + xv pp.
- Wright, H. O. (1968). Visual displays in brachyuran crabs: field and laboratory studies. *Am. Zool.* **8**, 655–665.