

## Studies on the Population Ecology of *Upogebia deltaura* (Leach) (Crustacea, Thalassinidea)

Björn Tunberg<sup>a</sup>

Kristineberg Marine Biological Station, S-450 34 Fiskebäckskil, Sweden

Received 23 April 1985 and in revised form 22 August 1985

**Keywords:** crustacea; Decapoda; population studies; Sweden Coast

*Upogebia deltaura* was collected quantitatively and qualitatively between June 1980 and August 1982 from a level, sandy bottom at a 12 m depth in the archipelago of Lysekil (on Gullmarsfjorden) about 70 km north of Göteborg, in western Sweden. A total of 347 individuals were obtained. The deepest burrows reached a depth of more than 65 cm into the substrate. During the cold season, *U. deltaura* was situated much deeper in the substrate than it was during the summer, probably as a result of 'hibernation'. The average density was 5.0 individuals  $0.1 \text{ m}^{-2}$ , and the maximum of 10 specimens was found in one  $0.1 \text{ m}^2$  sample. Out of the 341 individuals identifiable as to sex, 186 (54.6%) were females and 155 (45.4%) were males. Berried females were found between May and August, and the average number of eggs carried was 4757. Ecdysis took place between May and August; most females moulted in the middle of June and most males about one month later, in mid July. The chelipeds of large males were proportionally bigger than were those of large females. Maximum total body length of the females was 65.7 mm, and that of the males was 65.3 mm.

### Introduction

In the sea, a large exchange of energy and dissolved substances takes place between the bottom substrate and the water mass (Riedl, 1971). The extent of this exchange is, among other things, dependent on the sediment surface, water movements over this surface, the thickness of the oxidized layer, and also the degree of bioturbation (Dworschak, 1981). *Upogebia* usually construct deep, extensive burrows in the bottom substrate (MacGinitie, 1930; Pearse, 1945; Dworschak, 1983).

Two species of *Upogebia* occur on the west coast of Sweden: *Upogebia deltaura* (Leach) and *Upogebia stellata* (Montagu), the former of which is the larger and more abundant. In Gullmarsfjorden, *U. deltaura* is found in shallower water than *U. stellata* (Gustafson, 1934). It is noteworthy that the females of both species possess modified copulatory appendages, and may be recognized by them, as they are absent in the males.

<sup>a</sup> Present address: Florida Institute of Technology, Department of Oceanography and Ocean Engineering, Melbourne, Florida 32901, U.S.A.

The two species are described by e.g. de Morgan (1910), de Man (1927), and Poulsen (1941), and the larval stages are described by Webb (1919).

The macrofauna communities in sandy bottoms between approximately 10 and 20 m depth in Gullmarsfjorden and the archipelago of Lysekil are often dominated in terms of volume and biomass by *U. deltaura*. The aim of this study was, on one hand, to obtain quantitative data on the macrofauna for a comparative analysis to a shallow, sandy bottom in western Norway (as described by Tunberg, 1981; 1982), and on the other hand to study the biology of *U. deltaura*, with emphasis on population structure, distribution, reproduction, moulting, and biometry (as presented in this paper).

The reason that *U. deltaura* has been more or less overlooked as an abundantly occurring and probably important species in shallow, sandy bottoms on the western coast of Sweden is probably due to its sheltered position deep in the coarse, hard substrate, out of the reach of conventional sampling equipment.

### Material and methods

The study was carried out at Bredholmen (58°14.7'N, 11°22.2'E), a skerry in the archipelago of Lysekil (at the mouth of Gullmarsfjorden), approximately 70 km north of Göteborg on the west coast of Sweden. The study site had a level bottom at a 12 m depth. It was exposed to occasional heavy wave action and currents of varying direction. The sediment consisted mainly of medium shell sand mixed only with a little mud.

To sample the substrate quantitatively, an 80 m<sup>2</sup> area was divided into four equal sectors, each with 20 numbered squares 1 m<sup>2</sup> in size. To avoid disturbance effects, a new sampling area of the same size was established 20.5 m north of the first one in April 1981. The centre point was marked with a heavy weight attached to a buoy at the surface. Before each sampling date, one square was randomly selected in each sector. The middle points of the sampling squares were located in the field by measuring the length and direction from the centre point to each square with a measuring line and a compass (SCUBA-diving). Two replicate, round samples, each 0.1 m<sup>2</sup> and 20 cm deep, were taken in the middle of each square by a diver-operated suction sampler, as described by Tunberg (1983).

During the whole study period between 26 June 1980, and 5 August 1982, a total of 108 quantitative samples were collected in these areas (collections 1-5, 7-10, 12, 13, 15, 16, and 18 in Table 1). No replicate samples were collected on 14 October 1981 (no. 18). In addition, 40 quantitative (nos 6, 11, 17, 21-26, and 28) and 4 large qualitative (nos 14, 19, 20 and 27) samples were collected randomly in a 8 × 2 m area between the actual sampling area and the rocky bottom of Bredholmen. On 3 November 1980, 2 April 1981, and 24 August 1981 (nos 6, 11, and 17), the quantitative (3 × 0.1 m<sup>2</sup>) samples were collected in consecutive sections (5 cm intervals) down to a substrate depth of 20 cm, and at 10 cm intervals between depths of 20 and 40 cm for an analysis of the vertical distribution of the macrofauna. On 7 September 1982, sections of substrate were removed at 5 cm intervals (3 × 0.1 m<sup>2</sup>) down to a substrate depth of 65 cm for a visual analysis of the vertical distribution of *U. deltaura* burrows.

The salinity and temperature of the water at the surface and 10 cm above the bottom were measured before most collections during the period July 1980 to November 1981.

All samples were transported to the surface and into a sieve with 2 mm round holes. The samples were kept in running sea water in the laboratory. Sorting was completed within 5-7 days after sampling. The macrofauna was preserved in 4% formalin. All

TABLE 1. Samples collected at Bredholmen between 26 June 1980 and 5 August 1982. The sex of one specimen could not be determined (collected on 14 May 1982) (see the text)

No.	Date	Samples	Total number of individuals	Females	Males	Juveniles	Berried females
1	26 Jun 1980	8 quant.	19	6	13	0	0
2	22 Jul 1980	8 quant.	7	2	4	1	2
3	18 Aug 1980	8 quant.	13	4	9	0	0
4	16 Sep 1980	8 quant.	0	0	0	0	0
5	16 Oct 1980	8 quant.	0	0	0	0	0
6	3 Nov 1980	3 quant. (vert.)	11	4	7	0	0
7	13 Nov 1980	8 quant.	1	0	0	1	0
8	11 Dec 1980	8 quant.	3	1	2	0	0
9	28 Jan 1981	8 quant.	3	1	2	0	0
10	16 Mar 1981	8 quant.	0	0	0	0	0
11	2 Apr 1981	3 quant. (vert.)	8	5	3	0	0
12	27 Apr 1981	8 quant.	6	2	3	1	0
13	19 May 1981	8 quant.	4	1	1	2	0
14	30 May 1981	1 qual.	16	7	9	0	0
15	3 Jul 1981	8 quant.	3	2	1	0	2
16	11 Aug 1981	8 quant.	3	1	2	0	0
17	24 Aug 1981	3 quant. (vert.)	7	6	1	0	0
18	14 Oct 1981	4 quant.	1	0	1	0	0
19	26 Nov 1981	1 qual.	21	13	8	0	0
20	14 May 1982	1 qual.	48	32	15(+1?)	0	0
21	2 Jun 1982	5 quant.	27	16	11	0	2
22	11 Jun 1982	5 quant.	25	14	11	0	8
23	18 Jun 1982	4 quant.	21	12	9	0	9
24	29 Jun 1982	5 quant.	25	17	8	0	14
25	6 Jul 1982	4 quant.	17	10	7	0	7
26	16 Jul 1982	3 quant.	16	8	8	0	6
27	26 Jul 1982	1 qual.	18	8	10	0	5
28	5 Aug 1982	5 quant.	24	14	10	0	1

quant.—quantitative; qual.—qualitative; vert.—vertically.

collected individuals of *U. deltaura* were determined as to sex, and the numbers of berried females and newly moulted soft specimens were noted. The following biometrical measurements were taken by means of calipers to the nearest 0.1 mm: Length from the posterior edge of the carapace to the tip of the rostrum ( $C_1$ ), length from the posterior edge of the carapace to the cervical groove ( $C_2$ ), length ( $L$ ) and width ( $W$ ) of the proximal portion of the propodus of the left cheliped (Figure 1). The cheliped measurements were taken on a limited, randomly selected number of specimens. Total body length measurements were taken between the tip of the rostrum and the posterior edge of the telson. When only 'carapace length' is mentioned in the text, it refers to  $C_1$  in Figure 1.

Visual inspection of the distribution of *U. deltaura* burrows in the archipelago of Lysekil was carried out during numerous SCUBA dives in the area during the summer of 1983.

Linear, exponential, logarithmic, and power functions were applied to all sets of data points of biometrical relations in order to find the best fit (the highest coefficient of determination). The program used applied the least-square method, either to the

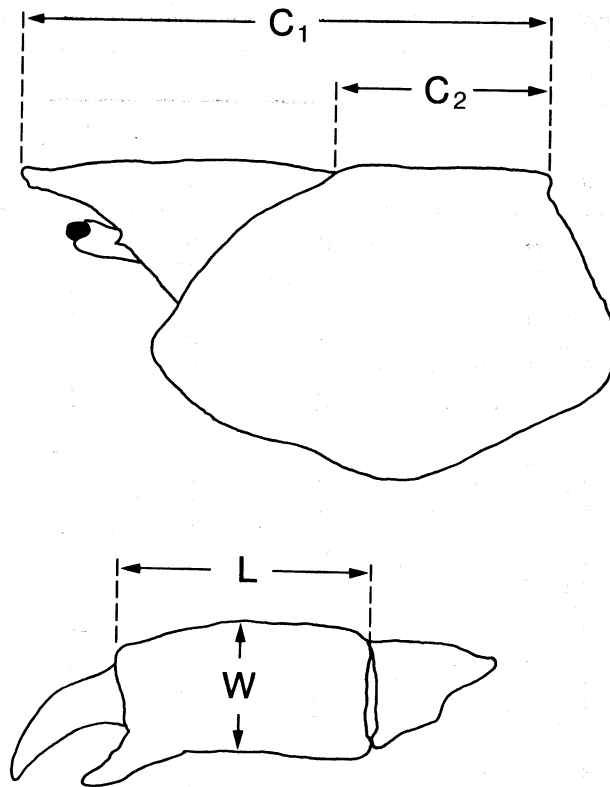


Figure 1. Measurements on *Upogebia deltaura*.  $C_1$ —length from the posterior edge of the carapace to the tip of the rostrum ('carapace length').  $C_2$ —length from the posterior edge of the carapace to the cervical groove.  $L$  and  $W$ —length and width of the proximal portion of the propodus of the left cheliped.

original data (straight line, logarithmic curve) or to the transformed data (exponential curve, power curve). Confidence intervals of the means were calculated at the 95% level.

## Results

### *Salinity and temperature*

There were large, irregular variations in the salinity (Figure 2). The lowest salinities of the bottom water were measured during late winter (min. value 20.4‰, on 13 March 1981) and the highest during fall (31.8‰, on 16 October 1980, and 26 November 1981). The mean salinity of the bottom water from 23 measurements made between July 1980 and November 1981 was 27.2‰ (CI  $\pm$  1.5‰), and that of the surface water was 32.1‰ (CI  $\pm$  1.5‰).

The lowest temperatures of the bottom water were noted between January and March 1981 (0.8–1.0 °C). In the summers of 1980 and 1981 the highest temperatures were measured in August at 18.8 °C and 19.1 °C, respectively.

### *Distribution*

The burrows of *U. deltaura* were very abundant throughout the archipelago in gravel and shell sand bottoms (both clean and mixed with mud). No burrows were found

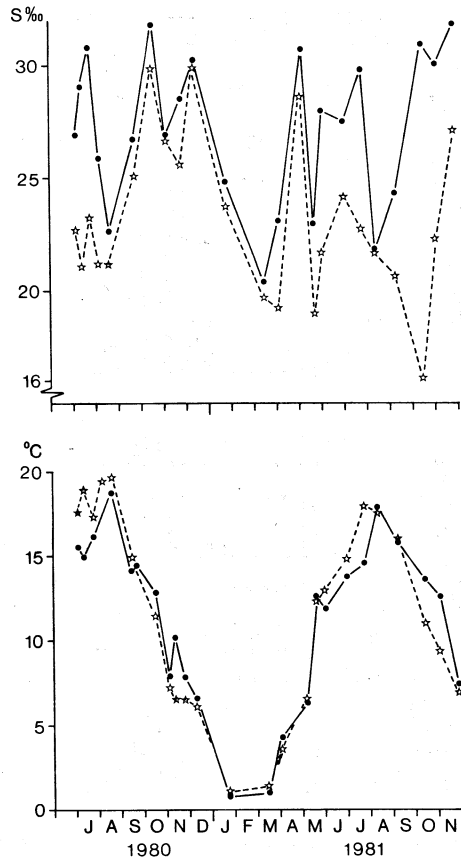


Figure 2. Salinity and temperature readings in the sampling area at Bredholmen, on the bottom at a 12 m depth (continuous line), and at the surface (broken line) between July 1980 and November 1981.

shallower than 6 m nor deeper than 27 m. The number of burrow openings at the sediment surface was counted from a photograph taken at a randomly chosen spot at a 12 m depth at Bredholmen on 6 July 1982. The number of openings in the  $46 \times 39$  cm area was 45, which corresponds to 250 openings  $m^{-2}$ . The mean diameter of these 45 openings was  $13.5$  mm ( $CI \pm 0.9$  mm). The burrow openings were often covered by sand grains, and it was necessary to remove a layer of about 1 cm to uncover all of them.

Many specimens of *U. deltaura* were obtained in the beginning of the sampling period, i.e. in the summer of 1980. During the fall, winter, and spring, however, very few specimens were obtained from the samples (taken to a substrate depth of 20 cm).

Only two specimens of *U. deltaura* were obtained from sediment depths shallower than 20 cm (15–20 cm) from the vertical distribution samples taken on 3 November 1980. The additional nine specimens were all found between 30 and 40 cm in depth. On 2 April 1981, all specimens (eight) were found between 30 and 40 cm in depth. On 24 August 1981, however, all specimens (seven) were found shallower than a depth of 20 cm in the substrate.

Vertical subsections of the substrate (5 cm intervals) on 7 September 1982, showed that the number of burrows decreased with increasing depth, but even in the deepest

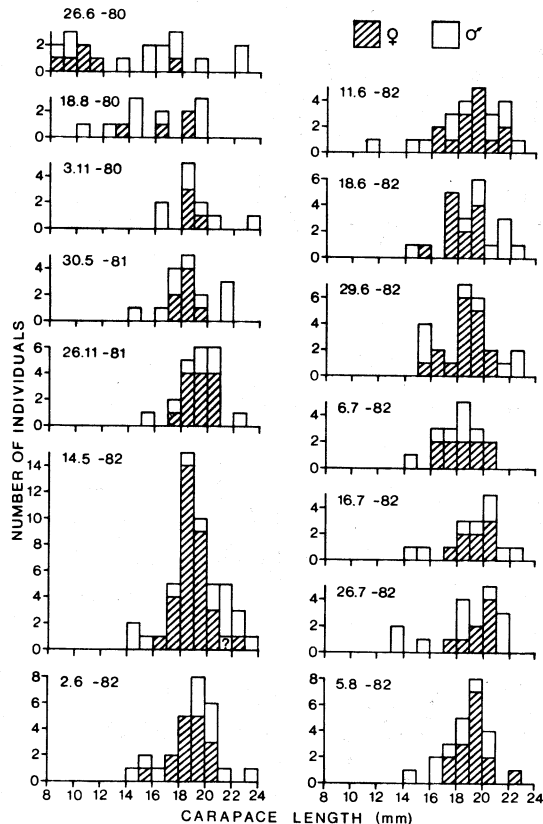


Figure 3. Size (carapace length,  $C_1$ ) frequency histograms for all collections that gave more than ten specimens.

section (65 cm) there were several burrows. As described above, the other samples collected during the study also confirm that *U. deltaura* is situated deeper in the sediment during the winter than during the summer. The specimens collected in the winter all seemed to have been in a state similar to hibernation, since their movements were very slow. Sometimes they were completely motionless. Because of their deep position in the substrate during the cold season the quantitative samples from this period did not give accurate information on the abundance of *U. deltaura* in the sampling area. The 31 quantitative samples collected between 2 June and 5 August 1982, in the  $8 \times 2$  m area between the actual sampling area and Bredholmen, where a total of 155 specimens (91 females and 64 males) were obtained, probably give accurate information on the density of *U. deltaura* in this area. The average density was calculated to  $5.0$  ( $CI \pm 2.2$ ) individuals  $0.1 \text{ m}^{-2}$ . A maximum of 10 specimens were found in one  $0.1 \text{ m}^2$  sample.

#### Size composition

The size (as measured by carapace length,  $C_1$ , Figure 1) composition of *U. deltaura* of collections with more than ten specimens (see Table 1) is presented in Figure 3, and that of all females and males in Figure 4. Five 'juvenile' specimens are not included in Figure 3 (see below). These were collected on 22 July 1980 ( $C_1 = 4.9$  mm), 13 November 1980 ( $C_1 = 4.7$  mm), 27 April 1981 ( $C_1 = 3.4$  mm) and 19 May 1981 ( $C_1 = 4.5$  mm and

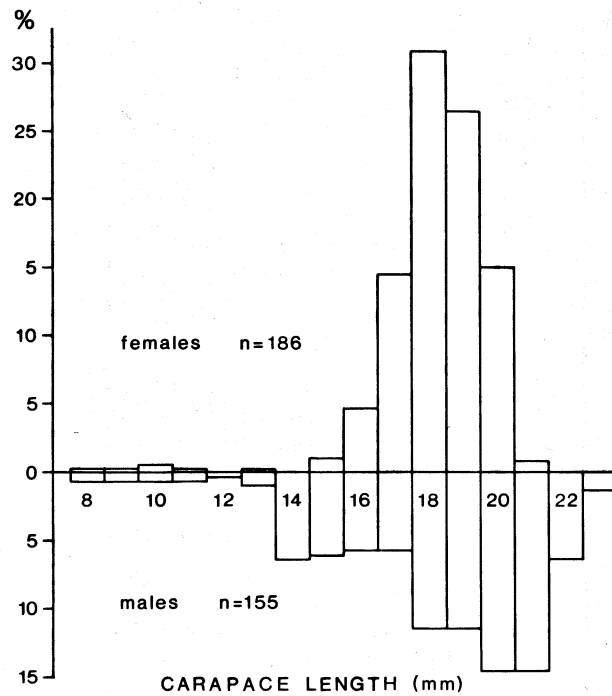


Figure 4. Size (carapace length,  $C_1$ ) frequency histograms for all females and males.

3.7 mm). The number of specimens obtained in the separate samples was too few for an age structure analysis. Because of the difference between males and females in the relationship of carapace length ( $C_1$ ) to total body length (see *Biometry*), it is important to note that even though males reached a greater carapace length ( $C_1$ ) than did the females, the maximum total body length was nearly the same in the two sexes (see below and Figure 5, which also shows the size composition of 513 specimens collected by Gustafson (1934) in three localities in Gullmarsfjorden). Total body length of 55 females and 20 males was not measured, but it was calculated from the relations between carapace length ( $C_1$ ) and total body length for females and males (Table 2).

In the present study, maximum carapace length ( $C_1$ ) of the females was 21.8 mm and that of the males 23.6 mm. The maximum measured total body lengths of females and males were 65.7 mm and 65.3 mm, respectively.

#### *Sex distribution and reproduction*

Five specimens out of a total of 347 were categorized as juveniles (carapace length ( $C_1$ ) less than 5 mm). The sex of one individual with a  $C_1$  of 22.0 mm, could not be determined. This specimen, collected on 14 May 1982, possessed all of the male characters: genital openings on the 5th thoracic appendages (none on the 3rd), with the tuft of setae around these arranged as in other males. It had large chelipeds, but also, however, one copulatory appendage (on the left side). The remaining 341 individuals consisted of 186 (54.6%) females and 155 (45.4%) males.

In late spring the abdomen of the females seemed to be almost completely filled with eggs. Berried females were obtained between May and August (Figure 6). The egg-carrying period is probably about 8 weeks.

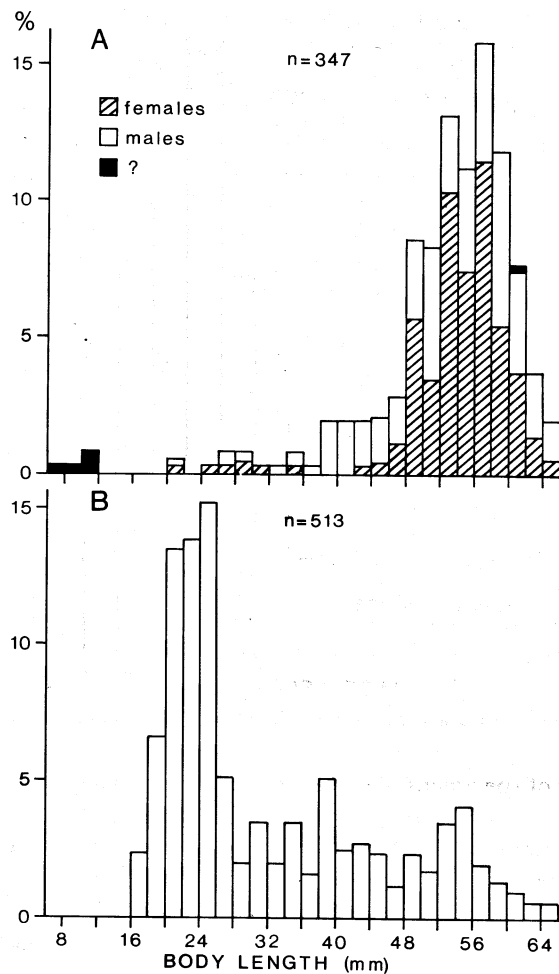


Figure 5. Total body/length frequency histograms for: A—all specimens collected, B—specimens collected in three localities in Gullmarsfjorden by Gustafson (1934).

The size composition (carapace length,  $C_1$ ) of 56 berried females is presented in Figure 7.

The number of eggs were counted on 4 randomly selected females collected on 11 June, 18 June, 29 June and 6 July 1982 (carapace lengths,  $C_1$ : 16.6 mm, 18.9 mm, 18.0 mm, 18.1 mm). The average number was 4757 ( $CI \pm 547$ ). There was no significant difference between carapace length and number of eggs. The size of 20 randomly selected eggs was measured from each of six egg-carrying females collected between 18 June and 26 July (stereomicroscope with micrometer,  $\times 50$  magnification). The mean diameter of these 120 round eggs was 0.558 mm ( $CI \pm 0.003$  mm). There was no significant difference in mean size of the eggs of the different individuals.

#### *Ecdysis*

Soft specimens were found only between May and August, but most specimens moulted in June and July (Figure 8). Figure 9, however, shows that the moulting period differs



TABLE 2. The biometrical relationships expressed by means of power curves ( $Y = aX^b$ ).  $C_1$ —length from the posterior edge of the carapace to the tip of the rostrum (carapace length),  $C_2$ —length from the posterior edge of the carapace to the cervical groove,  $L$  and  $W$ —length and width of the proximal portion of the left cheliped (see Figure 1) ( $N$ —number of individuals,  $R^2$ —coefficient of determination). Significance levels of comparisons between females and males are indicated

	$C_1(X)$ —Total body length ( $Y$ )				$C_2(X)$ —Total body length ( $Y$ )			
	$N$	$a$	$b$	$R^2$	$N$	$a$	$b$	$R^2$
All specimens	270	2.308	1.074	0.952	269	6.705	1.053	0.916
Females	130	2.364	1.072	0.863	130	7.815	0.979	0.758 <sup>NS</sup>
Males	134	2.994	0.978	0.941*	135	10.789	0.802	0.814 <sup>NS</sup>
	$C_1(X)$ — $L(Y)$				$L(X)$ — $W(Y)$			
	$N$	$a$	$b$	$R^2$	$N$	$a$	$b$	$R^2$
Females	75	0.444	1.006	0.873**	50	0.608	0.880	0.861**
Males	91	0.316	1.160	0.915**	76	0.435	1.100	0.924**

Significance levels: NS—not significant, \*\*— $P < 0.001$ , \*— $P < 0.01$ .

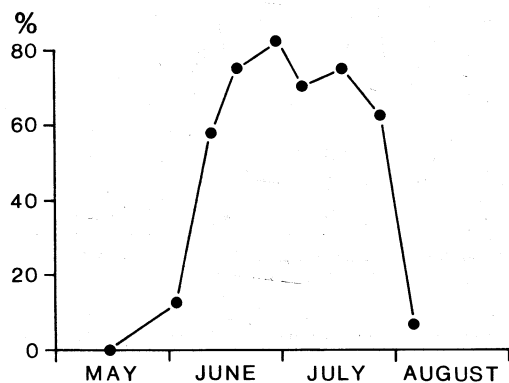


Figure 6. Percentage of egg-carrying females between May and August 1982.

between the sexes. Most females moult in the middle of June and most males about one month later, in mid July. There is a strong correlation between ecdysis and berrying, which indicates that the eggs are extruded shortly after ecdysis.

#### Parasites

No large ectoparasites were observed on the 347 examined specimens. The left first antennae of a female (with a 18.2 mm carapace length ( $C_1$ ), collected on 14 May 1982) was, however, densely covered by specimens of the bryozoan *Triticella koreni* G. O. Sars.

#### Biometry

The biometrical relationships are presented in Table 2. The relationship between carapace length ( $C_1$ ) and total body length had a better fit than that between the length

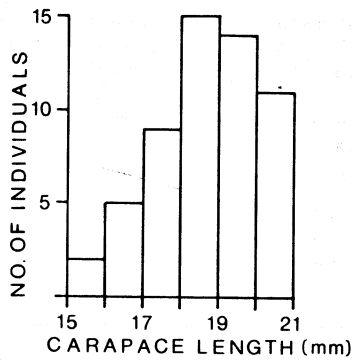


Figure 7. Size (carapace length,  $C_1$ ) frequency histograms for the 56 berried females found in this study.

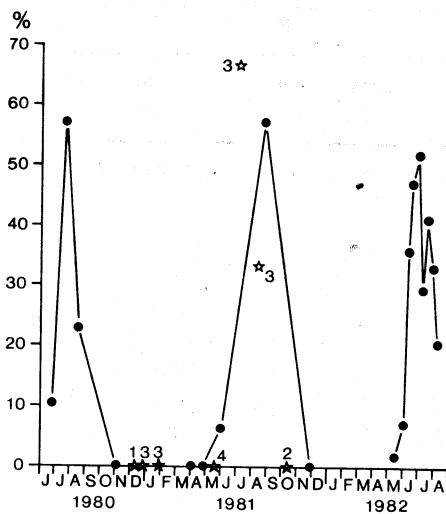


Figure 8. Moulting period. Percentage of soft specimens during the period 1980-1982. Stars—fewer than a total of six individuals.

from the posterior edge of the carapace to the cervical groove ( $C_2$ ) and total body length ( $R^2=0.952$  and  $0.916$ , respectively). Carapace length ( $C_1$ ) was therefore used as the basic measure of the size of *U. deltaura*.

The analyses of covariance indicated significant differences between males and females in all relationships except between the length from the posterior edge of the carapace to the cervical groove ( $C_2$ ) and total body length (not significant at the 0.05 level) (see Table 2). Only the power functions are presented in Table 2, because they gave the best fit. The small divergence from straight lines, however, indicates only minor allometry concerning these variables.

Large females had proportionally shorter carapace length ( $C_1$ ) than did large males, while the opposite applied to small individuals. The corresponding power curves intersect at carapace lengths ( $C_1$ ) of about 12 mm. The propodus of the left chelipeds of large males were proportionally bigger (longer and wider) than were those of large females.

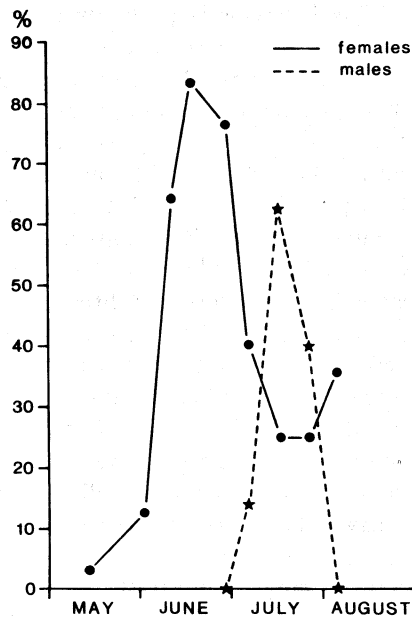


Figure 9. Moulting period. Percentage of soft females and males between May and August 1982.

### Discussion

*Upogebia deltaura* is found in sandy bottoms (with or without mud). The type of substrate is noteworthy, since other representatives of this genus (mud-shrimps) have been found mostly in muddy bottoms, while *Callianassa*, on the other hand, usually prefers sand (Pearse, 1945; Weimer & Hoyt, 1964; Ott *et al.*, 1976).

The influence of *Upogebia* on the associated fauna is probably highly significant. The presence of irrigated tubes and burrows made by the infauna (including *Upogebia*) may cause dramatic changes in the processes controlling chemical, biological, and physical characteristics of a deposit (Aller, 1980; Aller & Dodge, 1974; Aller *et al.*, 1983). The burrows of *Upogebia* radically increase the contact surface between the substrate and the overlying water mass. The volume of the oxidized layer increases dramatically (Ott *et al.*, 1976).

According to Peterson (1977), ghost-shrimps (*Callianassa* spp.) may on certain occasions be of vital importance to the structure of the benthic infauna. MacGinitie (1934) states that the continual turning over of the soil and the aeration of the subsoil by *Callianassa californiensis* Dana are important to the entire community of muddwellers; however, the bioturbation activity of *Callianassa* is probably greater than that of *Upogebia*, since the burrows of the latter are more permanent structures than are those of the former. The burrows of *U. deltaura* are stable and do not collapse easily. Probably the oxygenation of the substrate by *U. deltaura* is high during the summer, but decreases during the inactive period in the cold season. Whether this has any significant effect on the associated macrofauna is not known.

Specimens of *U. deltaura* kept in an aquarium without sediment were very aggressive towards each other, regardless of sex. They used their chelipeds to mutilate, and

sometimes even to kill each other. This behavior is probably a density-controlling mechanism. According to Buchanan (1963), *Calocaris macandreae* Bell is territorial, and the reason for the stability of the populations may be due to dead individuals being replaced very quickly by new ones from surrounding areas (neighbourhood stability). Whether or not this applies to *Upogebia* was not investigated. Young specimens are found in shallower waters than are adults (Gustafson, 1934), and may possibly occupy vacant space quickly in the adult population. Sporadic and irregular recruitment may also be a cause for this depth segregation (see below). This zonation of age may explain why only a few small specimens were obtained at Bredholmen, in contrast to Gustafson's samples. He measured 513 specimens collected at three localities between 8 and 15 m depth in Gullmarsfjorden (see Figure 5). He separated three size-classes with total body lengths of 17–32 mm, 32–47 mm, 47–65 mm (which corresponds to carapace lengths,  $C_1$ , of 6.6–11.6 mm, 11.6–16.4 mm, 16.4–22.0 mm). The specimens collected at Bredholmen in the present study were thus dominated by size group three. The individuals collected by Gustafson (1934) were strongly dominated by size group one.

It is noteworthy that, in contrast to the other collections, small specimens were found in June 1980 (see Figure 3), which may indicate an irregular recruitment during the study period.

The egg-carrying period of about 8 weeks corresponds well to notes on other thalassinids. Aquarium observations by Devine (1966) showed that *Callianassa filholi* Milne-Edwards carried eggs for a period of 5.5 weeks, and according to Hailstone and Stephenson (1961), *Callianassa australiensis* Dana carries eggs for at least 6 weeks. In Oslofjorden, in southern Norway, the larvae of *U. deltaura* have been found in the plankton in August, September, and October (Smedsrud, 1982). As shown, breeding and moulting of *U. deltaura* take place once a year, during the warm season. It is important to note, however, that moulting was studied in large specimens only. Small specimens probably moult more often. *Calocaris macandreae* moult annually from four years of age, but several moults apparently take place throughout the year for young specimens (Buchanan, 1963). Hailstone and Stephenson (1961) found that males of *Callianassa australiensis* moult somewhat earlier than do females, and that this might be expected if hardened males are copulating with soft females. As shown in Figure 9, there is a distinct difference in the moulting period between males and females of *U. deltaura* in that females moult about one month earlier than do males.

Because of their sheltered position in the substrate, thalassinids should have good protection from predation. This was assumed about *Calocaris macandreae* by Buchanan (1963). According to Mattson (1981), however, this species constitutes a considerable portion of the food for certain bottom-foraging fishes in Raunefjorden, in western Norway. I have never seen *U. deltaura* leave its burrow, but it has been found in large numbers in stomachs of cod (*Gadus morhua* L.) on the west coast of Sweden (Alf Josefson, pers. comm.). Selbie (1914) found a few specimens in the stomach of a ray, *Raja clavata* L., and according to Poulsen (1941), it is found fairly often in the stomachs of haddock (*Melanogrammus aeglefinus* (L.)) in the North Sea.

#### Acknowledgements

I gratefully acknowledge the use of the facilities of the Kristineberg Marine Biological Station. Special thanks are due to Jarl-Ove Strömberg for valuable support, and to Stefan Mattson for valuable comments on the manuscript. I thank Mary Ann Nelson for

correction of the English. This study was partly financed by a grant from the Nordic Council for Marine Biology.

### References

- Aller, R. C. 1980 Relationships of tube-dwelling benthos with sediment and overlying water chemistry. In (Tenore, K. & Coull, B. C., eds) *Marine benthic dynamics*, University of South Carolina Press. pp. 285-308.
- Aller, R. C. & Dodge, R. E. 1974 Animal-sediment relations in a tropical lagoon Discovery Bay Jamaica. *Journal of Marine Research* 32, 209-232.
- Aller, R. C., Yingst, J. Y. & Ullman, W. J. 1983 Comparative biogeochemistry of water in intertidal *Onuphis* (polychaeta) and *Upogebia* (crustacea) burrows: temporal patterns and causes. *Journal of Marine Research* 41, 571-604.
- Buchanan, J. B. 1963 The biology of *Calocaris macandreae* (Crustacea: Thalassinidea). *Journal of the Marine Biological Association of the United Kingdom* 43, 729-747.
- Devine, C. E. 1966 Ecology of *Callianassa filholi* Milne-Edwards 1878 (Crustacea, Thalassinidea). *Transactions of the Royal Society of New Zealand, Zoology* 8(8), 93-110.
- Dworschak, P. C. 1981 The pumping rates of the burrowing shrimp *Upogebia pusilla* (Petagna) (Decapoda: Thalassinidea). *Journal of Experimental Marine Biology and Ecology* 52, 25-35.
- Dworschak, P. C. 1983 The biology of *Upogebia pusilla* (PETAGNA) (Decapoda, Thalassinidea) I. The burrows. *Marine Ecology* 4(1), 19-43.
- Gustafson, G. 1934 On the Thalassinidea of the Swedish west coast. *Arkiv för zoologi* 28A(1), 1-19.
- Hailstone, T. S. & Stephenson, W. 1961 The biology of *Callianassa (Trypaea) australiensis* Dana 1852 (Crustacea, Thalassinidea). *University of Queensland Papers, Department of Zoology* 1, 259-285.
- MacGinitie, G. E. 1930 The natural history of the mud shrimp *Upogebia pugettensis* (Dana). *Annual Magazine of Natural History* 6, 36-44.
- MacGinitie, G. E. 1934 The natural history of *Callianassa californiensis* Dana. *American Midland Naturalist* 15, 166-177.
- Man, J. G. de 1927 A contribution to the knowledge of twenty-one species of the genus *Upogebia* Leach. *Capita Zoologica* 11(5).
- Mattson, S. 1981 The food of *Galeus melastomus*, *Gadiculus argenteus thori*, *Trisopterus esmarkii*, *Rhinonemus cimbrius*, *Glyptocephalus cynoglossus* (Pisces) caught during the day with shrimp trawl in a West-Norwegian fjord. *Sarsia* 66, 109-127.
- Morgan, W. de 1910 On the species *Upogebia stellata* and *Upogebia deltura*. *Journal of the Marine Biological Association of the United Kingdom* 8, 475-478.
- Ott, J. A., Fuchs, B., Fuchs, R. & Malasek, A. 1976 Observations on the biology of *Callianassa stebbingi* BORRODAILLE and *Upogebia litoralis* RISSO and their effect upon the sediment. *Senckenbergiana maritima* 8(1/3), 61-79.
- Pearse, A. S. 1945 Ecology of *Upogebia affinis* (Say). *Ecology* 26(3), 303-305.
- Peterson, C. H. 1977 Competitive organization of the soft-bottom macrobenthic communities of southern California lagoons. *Marine Biology* 43, 343-359.
- Poulsen, E. M. 1941 On the occurrence of the Thalassinidea in Danish Waters. *Videnskabelige Meddelelser fra Dansk naturhistorisk forening i København* 104, 207-239.
- Riedl, R. J. 1971 Energy exchange at the bottom/water interface. *Thalassia Jugoslavica* 7, 329-339.
- Selbie, C. M. 1914 The Decapoda Reptantia of the coasts of Ireland. *Scientific Investigations, Fisheries Branch, Ireland* 1, 1-116.
- Smedsrud, K. 1982 En undersøkelse over forekomsten av decapodlarver (Crustacea, Decapoda) i indre og midtre Oslofjord. *Unpublished cand. real. thesis, University of Oslo, Norway*.
- Tunberg, B. 1981 Two bivalve communities in a shallow and sandy bottom in Raunefjorden, western Norway. *Sarsia* 66, 257-266.
- Tunberg, B. 1982 Quantitative distribution of the macrofauna in a shallow, sandy bottom in Raunefjorden, western Norway. *Sarsia* 67, 201-210.
- Tunberg, B. 1983 A simple, diver-operated suction sampler for quantitative sampling in shallow, sandy bottoms. *Ophelia* 22, 185-188.
- Webb, G. E. 1919 The development of the species of *Upogebia* from Plymouth Sound. *Journal of the Marine Biological Association of the United Kingdom* 12, 81-135.
- Weimer, R. J. & Hoyt, J. H. 1964 Burrows of *Callianassa major* Say, geologic indicators of littoral and shallow neritic environments. *Journal of Paleontology* 38(4), 761-767.