Dworschak, 1988

J. Martin

P. S. Z. N. I.: Marine Ecology, 9 (1): 51–77 (1988)
Accepted: October 2, 1987

ISSN 0173-9565

The Biology of *Upogebia pusilla* (PETAGNA) *(Decapoda, Thalassinidea)*

III. Growth and Production

PETER C. DWORSCHAK

Institute of Zoology, University of Vienna, Althanstr. 14, A-1090 Vienna, Austria.

With 10 figures and 2 tables

Key words: *Upogebia pusilla, Decapoda, Thalassinidea,* moulting, growth, breeding, production, Mediterranean.

Table of contents:

52 Problem
52 Material and Methods
53 Results
53 1. Measurements related to growth
55 2. Size frequencies
56 3. Sex ratios
58 4. Growth
58 a. Moulting
58 b. Exuviae
58 c. Duration of intermoult period
59 d. Moult increment
61 e. Growth rates
62 5. Reproduction
62 a. Breeding period
62 b. Size at maturity
63 c. Eggs
63 1. Attachment of eggs
63 2. Egg numbers
64 3. Egg size
65 4. Egg weight
65 5. Egg masses
65 6. Incubation time
65 d. The ovaries
67 e. Breeding sequence
68 f. Larvae
68 6. Parasites and diseases
69 7. Energetic aspects of production
70 Discussion
73 Summary
74 Acknowledgements
75 References

Abstract. Populations of the thalassinidean shrimp *Upogebia pusilla* were studied on tidal flats in the Northern Adriatic Sea. Biometric analysis showed a sexual dimorphism, especially in propodus size. Size frequency distributions revealed the presence of large animals during all seasons; recruitment by juveniles occurred in autumn. Moult intervals and moult increments were determined in the laboratory and used to generate growth curves which were compared with those calculated from size frequency distributions. The life span of *U. pusilla* is over 5 years. Ovigerous females occurred between March and September. Egg numbers were high in spring, lower in summer and increased with body size. The incubation time of embryos was 35 days; a female produces an estimated number of three egg batches during the breeding season. A total annual production of 994 kJ was estimated for a theoretical population of 100 animals; 13.5 % is spent for somatic growth, 31 % for egg production of females, and 55.2 % is lost as exuviae. The population structures, growth and breeding patterns, as well as embryonic and larval development within the *Upogebiidae* and *Callianassidae* are discussed.

U.S. Copyright Clearance Center Code Statement: 0173-9565/88/0901-005135$02.50/0

Problem

The *Thalassinidea (Decapoda)* are among the most common burrowing organisms in littoral and sublittoral sediments; they are found – sometimes in very high densities – from the intertidal zone down to at least the shelf break, and occur in all types of environments from brackish to euryhaline.

In the Mediterranean Sea, *Upogebia pusilla* is the most common member of the family *Upogebiidae.* This study, which is the third of a series dealing with the biology of *Upogebia pusilla,* describes the biometry, population structure, growth, and production of this species.

U. pusilla occurs on the East Atlantic from Mauretania in the south to Brittany in the north (DE SAINT LAURENT & LELOEUFF, 1979); occasionally it is found as far north as Norway (PESTA, 1918; BOUVIER, 1940; ZARIQUIEY ALVAREZ, 1968). The shrimp is common all around the Mediterranean including the Black Sea and has been reported from the Red Sea (MONOD, 1930). It lives from the intertidal zone down to a depth of 45 m (POPOVICI, 1940) in sediments ranging from a mixture of gravel, sand, silt, and clay to mud (Md 23–888 µm) with a subsieve fraction (< 63 µm) between 1 and 93 %. Its salinity range is from marine (36 ‰) down to 9 ‰ (DWORSCHAK, 1987).

The present study was undertaken at three tidal flats in the Northern Adriatic Sea: (1) the lagoon of Grado, (2) Lido di Staranzano, and (3) Val Saline, Rovinj (see DWORSCHAK, 1987).

Material and Methods

Animals were captured with different methods according to the sediment type at the sampling location. In the lagoon of Grado where the sediment is soft, a big hole was dug out and the sediment brought to the surface was sieved. At Lido di Staranzano a shovel was pushed into the firm sediment near the water's edge and moved back and forth. This creates an alternating water flow in the burrows; the animals are swept out of their burrows and can be collected by hand or a net. In Rovinj, with its very soft sediment, walking through the mud brings animals to the surface. Additionally, at all three sampling locations samples were taken with a box corer (HERTWECK, 1974) and sieved.

Collected animals were either transported alive to the laboratory in Vienna or fixed immediately in 4 % buffered formaldehyde-seawater.

The following parameters were determined in all animals:
- sex, based on the presence (female) or absence (male) of the first pair of pleopods;
- total length (TL in mm) from the tip of the rostrum to the end of the telson in a petri dish on graded paper;
- carapace length (CL in mm) from the tip of the rostrum to the end of the carapace using sliding calipers or (in small animals) under a dissecting microscope using a calibrated eye-piece.

Additional measurements include:
- propodus length (PL in mm) of the first pereiopod in the middle line from the carpus to the insertion of the dactylus and
- propodus width (PB in mm) in the middle of the propodus just behind the dilatation of the fixed finger in all animals from Grado and Rovinj;
- wet weight (ww in g) to a precision of 0.01 g in 116 specimens from Grado;
- dry weight (dw in g) in 57 specimens from Grado. Living animals were anaesthetized, dried for 24 h in an oven at 80 °C, brought to room temperature in a desiccator, and weighed on a semi-analytical balance to 0.0001 g.

Animals sampled at all three sites between March 1977 and June 1979 were dissected and the presence of endoparasites and state of reproductive organs noted. The ovaries were removed from all females; ovaries and remaining body were dried and weighed separately.

Eggs of ovigerous females were removed from the pleopods, a subsample counted, and the egg number recalculated from the dry weight of the subsample and the total egg mass. This also enabled calculation of the dry weight of a single egg. Egg diameter was determined under a dissecting microscope using a calibrated eye-piece. Stages of the embryonic development were classified according to Rodrigues (1976); stages 1 to 4 ("uneyed eggs") and stages 5 to 9 ("eyed eggs") were pooled when giving egg numbers, egg weight, and egg diameter.

Two indices, EI and GI, were used to compare the egg and ovary masses between seasons and sites independent of the size of the female. EI represents the egg mass (dw), GI the ovary mass (dw) as percentage of the net dry weight (ndw), which is the dw of the female without eggs and ovary.

In the laboratory, animals were kept singly in narrow aquaria filled with sediment from the sampling site. Aquaria were maintained in an air-conditioned room at 17.5 °C under a cycle of 12 h artificial daylight (6:00–18:00) and 12 h darkness (18:00–6:00). Artificial seawater with a salinity of 36 ‰ was used.

Date and location of moulting was recorded; exuviae were removed, measured, and weighed. Only the first two moults in the laboratory were used for determination of moult interval and moult increment.

Growth curves for animals from Grado were generated by using data on moult increments and moult intervals. Additionally, von Bertalanffy growth curves were calculated from size frequency distributions using the programme ELEFAN (Pauly & David, 1981; Brey & Pauly, 1986).

Time required until hatching of larvae was recorded for ovigerous females carrying freshly extruded eggs.

The organic content of animals, eggs, ovaries, and exuviae was determined as weight loss on ignition in a muffle furnace at 500 °C for 3 h.

Results

1. Measurements related to growth

All measurements show a marked sexual dimorphism in *U. pusilla*. Generally, males reach a larger size than females, with maximum size differing between the three sampling sites.

The carapace length is linearly related to total length. There is only a small difference between males and females up to a total length of 50 mm; males > 50 mm have a longer carapace than females of the same total length. The relation of carapace length to total length was the same at all sampling sites. The formulae for the relation between TL and CL are:

males: $CL = 0.3505\ L + 0.52$; $r = 0.99$; $n = 43$

females: $CL = 0.319\ L + 1.17$; $r = 0.99$; $n = 35$

The propodus length is also linearly related to total length (Fig. 1). No significant difference between the PL of males and females up to a total length of 35 mm ($P > 0.05$, t-test) was detected. From this size on, PL of males continue to increase further with TL, whereas the increase in PL of females is negligible. The mean PL of a 60 mm male is 13.7 mm, that of an equally sized female 8.7 mm. This difference is less marked in animals from Rovinj due to the smaller size of the specimens from this location.

Sexual dimorphism is also apparent in propodus width (Fig. 2). At the same PL the propodus of males is wider than that of females. Whereas the width of the female's propodus is limited due to its length, it continues to become wider with increasing length in males.

The result is a different relation between propodus length and propodus width (PL/PW). The PL/PW of females ranges from 2 to 3.6 (mean = 2.77;

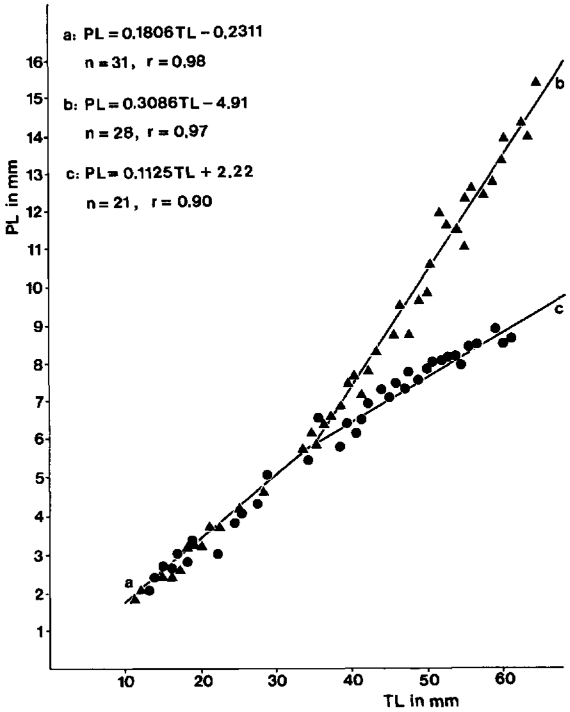

Fig. 1. Propodus length (PL in mm) (mean of 1 mm size classes) in relation to total length (TL in mm) for males (▲) and females (●). Line a: males and females with TL < 35 mm; line b: males > 35 mm; line c: females > 35 mm.

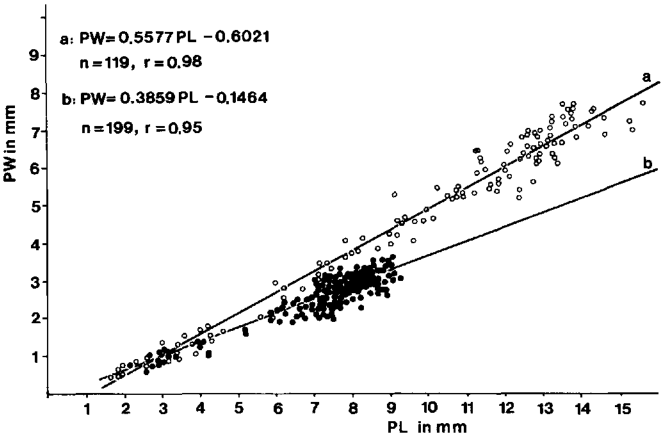

Fig. 2. Propodus width (PB in mm) in relation to propodus length (PL in mm) for males (○, line a) and females (●, line b).

$n = 199$), that of males from 1.7 to 3.6 (mean $= 2.16$; $n = 119$). The difference between the means is significant ($P < 0.001$, t-test).

Wet weight is correlated to total length by approximately the third power:
males: $\log ww = 3.128 \log TL - 4.835$; $r = 0.99$; $n = 58$
females: $\log ww = 2.837 \log TL - 4.458$; $r = 0.98$; $n = 48$

There is a strong overlap in ww of males and females up to TL of 50 mm, which is due to different stages in ovary development of females. From the equation, a 60 mm male weighs 5.3 g; a female of corresponding length weighs 4.3 g (ww).

The dry weight also shows a correlation to TL by the third power:
males: $\log dw = 3.417 \log TL - 6.137$; $r = 0.98$; $n = 33$
females: $\log dw = 3.338 \log TL - 6.054$; $r = 0.97$; $n = 24$

A male with $TL = 60$ mm has a dw of 0.8674 g and is 14 % heavier than a female of the same size ($dw = 0.7600$ g). 26 % of the dw of a male of this size is made of the two propodi; in females they account for only 10 %. Without the propodi, however, the female is heavier than an equally sized male because of ovary weight (see below).

A linear relationship between dw and ww was calculated:
males: $dw = 0.1608 ww + 0.0146$; $r = 0.94$; $n = 33$
females: $dw = 0.1931 ww - 0.0277$; $r = 0.95$; $n = 24$

As the intercept is very small in both equations, dw may be expressed as percentage of ww. It is approximately 16 % in males and 19 % in females.

The ndw of adult females varied with the degree of calcification, parasitation (see below), and stage of the hepatopancreas, *e. g.*, for $TL = 50$ mm, ndw ranged from 0.1914 to 0.5074 g (mean $= 0.2759$). There was no significant difference between the mean ndw of same-sized females from different seasons ($p < 0.05$, t-test). The relationship between ndw and TL was nearly the same for all seasons.

The mean organic content of entire animals is 53 % ($SD = 15.1$) of dw in males and 57 % ($SD = 10$) in females. The organic content as percentage of dw is 45 % ($SD = 0.6$) in females without ovaries and eggs and 86 % ($SD = 3.5$) in ovaries and freshly extruded eggs (stages 1–4).

2. Size frequencies

Size frequency distributions of the samples from Grado show the presence of large animals during all seasons (Fig. 3). Most males captured had CL between 20 and 22 mm ($TL = 55$–61 mm) and were larger than the most abundant size class of females (CL between 16 and 18 mm; $TL = 46$–52 mm). A sexual difference was also observed in the maximum size (TL_{max}), which was 66 mm in males and 60 mm in females. A difference exists in the seasonal occurrence of middle-sized animals: males are found in several distinct size classes whereas in females distinct modes cannot be distinguished due to the smaller size of larger individuals. Juveniles were found only in late fall; the smallest animal ($CL = 4$ mm) was captured in September 1977.

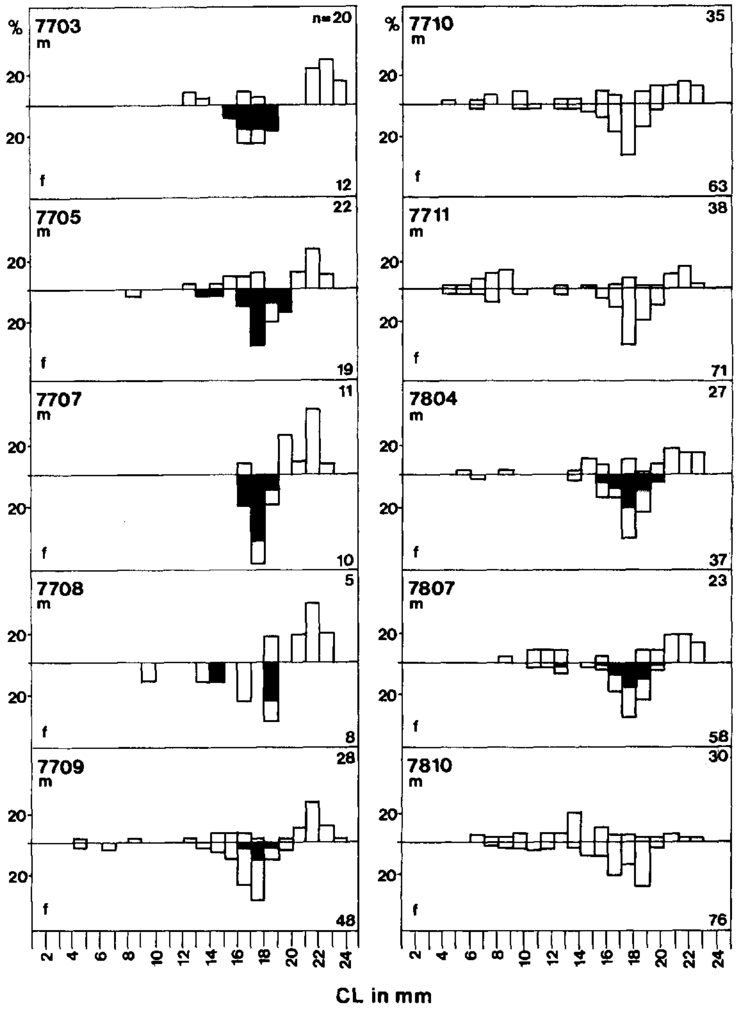

Fig. 3. Size frequency histograms (carapace length CL in mm) for the Grado samples. m: males; f: females; shaded: ovigerous females.

Size frequency distributions of animals caught in Val Saline (Fig. 4) show that both sexes were represented year-round with individuals having CL between 5 and 15 mm. The largest shrimp found here measured 47 mm (TL) and the smallest (CL = 2 mm) were caught in fall.

At Lido di Staranzano, small and large animals were present in all seasons, the smallest occurring again in fall. There was a notable absence of middle-sized (CL around 11 mm) animals in April (1979) and September (1984). TL_{max} and size difference between sexes are similar to Grado.

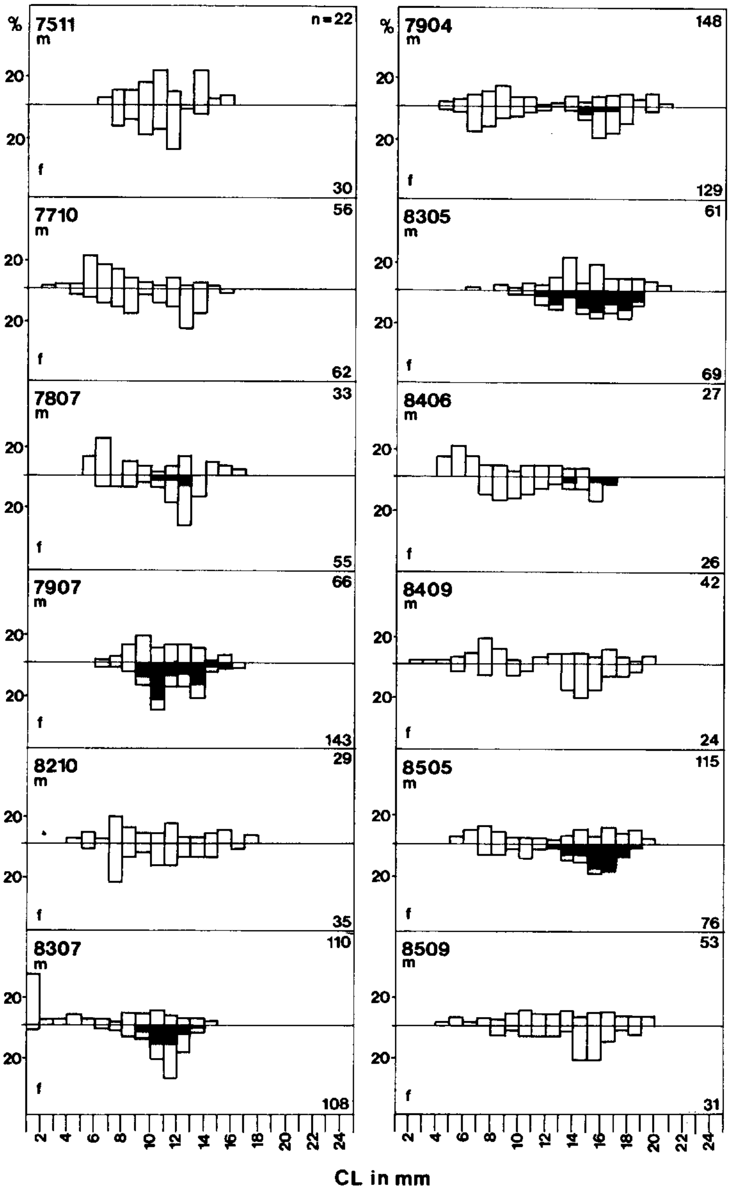

Fig. 4. Size frequency histograms (carapace length CL in mm) for the samples from Rovinj (left) and Lido di Staranzano (right). m: males; f: females; shaded: ovigerous females.

3. Sex ratios

Males predominated at Grado from March to July 1977, whereas females prevailed from August on, most pronounced in October 1978 with a male to female ratio of 1 : 2.6. In adult animals (CL > 12 mm) the predominance of females was even more marked in November 1977 and July 1978; they represent 76 % of all animals. A sex ratio of 1 : 1 was observed for juveniles.

Females always outnumbered males in the samples from Rovinj, the greatest difference was observed in July 1979 with a sex ratio of 1:2.1. The predominance of females was most pronounced in adults, whereas juveniles showed again a sex ratio of nearly 1:1.

With the exception of May 1983 and June 1984 when the sex ratios were 1 : 1.1 and 1 : 1, more males than females were captured always in Staranzano. The sex ratios ranged from 1.1:1 (April 1979) to 1.8:1 (September 1984).

4. Growth

a. Moulting

In aquaria *U. pusilla* always moulted at night. Ecdysis takes place within the burrow, and moulting animals could never be observed on the sediment surface. In one case, a moulting animal was entombed *in situ* during resin casting. In some cases, the animal stored its exuvia in a part of its burrow. Such exuviae are brought to the surface after several days, often in a desintegrated state. Usually, however, the exuvia is brought to the surface in the night of moulting.

Intact exuviae could be observed floating in the water in all sampling sites, especially in spring. Deposited exuviae can be found in box cores. It can be assumed that behaviour in the aquaria is similar to that in nature.

b. Exuviae

The relation between the dw of the exuvia and the total length of the animal before its moult (recalculated from CL of the exuvia) can be expressed by the following equations:

males: $\log dw = 2.8137 \log TL - 5.325$; $r = 0.97$; $n = 35$
females: $\log dw = 2.4701 \log TL - 4.969$; $r = 0.95$; $n = 34$

A sexual difference in the dw of the exuviae is also present. The proportion of the propodi in the dw of the exuvia is 26 % for a male with TL = 60 mm and 12 % for a female of the same size.

The proportion of exuvia-dw to the dw of an entire animal differs with size. It is high in small animals (when calculating from the regressions TL – dw [animal] and TL–dw [exuvia], the exuvia may even weigh more than the entire animal for animals up to TL = 20 mm due to the great variation in dw and the fact that both parameters were not determined for the same specimens). The proportion of the exoskeleton in total weight decreases with increasing size. A female with TL = 60 mm sheds an exuvia whose dw is 34 % of the total dw; this proportion is 54 % in a male of the same size due to the thick exoskeleton of its propodi.

The organic content of large exuviae (TL = 45–56 mm) is 21 % (SD = 3.1) in males and 26 % (SD = 5.9) in females. As the organic content of the exuviae did not differ between sexes ($P < 0.05$, MANN-WHITNEY test), a mean percentage of 25 % is used in further calculations.

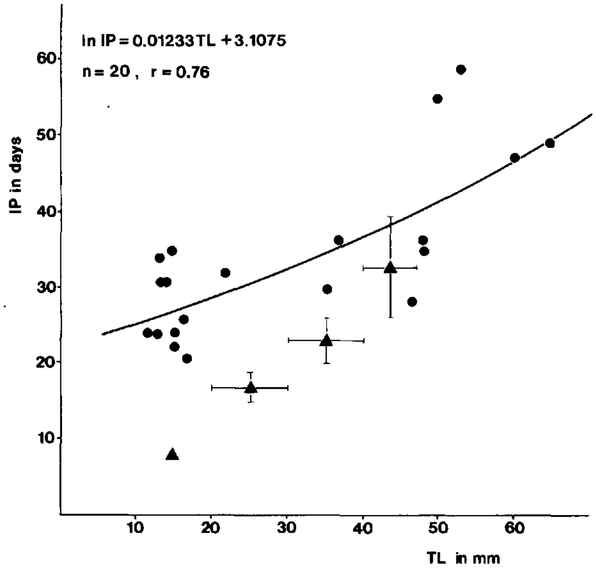

Fig. 5. Intermoult periods (IP in days) in relation to size (TL in mm) at 17.5 °C (●). Means (▲) and ranges (bars) of intermoult periods at 22 to 28 °C after DAGUERRE DE HUREAUX (1970).

c. Duration of the intermoult period

The whole moulting cycle and the duration of the intermoult period (= intervals between successive moults) is chiefly affected by intrinsic factors such as body size and breeding activity, but also by extrinsic factors, especially temperature, salinity, and food supply (PASSANO, 1960; FARMER, 1973; HARTNOLL, 1982, 1983).

Intermoult periods of *U. pusilla* showed great variations in the laboratory (Fig. 5). No difference could be observed in the intermoult periods of males and females. The relation of intermoult period (IP in days) and body size (TL) expressed by the equation $\ln IP = 0.01233\ TL + 3.1075$ best fits the data ($r = 0.766$; $n = 20$). The time span from capture to first moult in the laboratory was always shorter than IP as calculated using the above equation. An extension of the intermoult period in ovigerous females was not observed; in two cases females moulted before all larvae had hatched. Expected intermoult periods for ovigerous females from Grado are always longer than the incubation period of embryos at the same temperature (see chapter 5. c. 6.). Only the expected intermoult period of the small ovigerous females from Rovinj is shorter than the incubation period; an extension of the intermoult period due to breeding activity may occur in this population.

Based on the intermoult periods determined at 17.5 °C and the ranges of intermoult period given by DAGUERRE DE HUREAUX (1970) – assuming a temperature of 22 °C for the longer periods and a temperature of 28 °C for the shorter periods – the multiple regression of intermoult period (IP) in relation to temperature (T) and body size (TL) can be expressed as:

$$\log IP = 1.8513 - 1.0883\ \log T + 0.70857\ \log TL.$$

d. Moult increment

Growth in crustaceans is a discontinuous process occurring in steps in successive moults. The greatest size increase occurs in the hours after exuviation (HIATT, 1948). This increase is usually determined by measuring animals before and

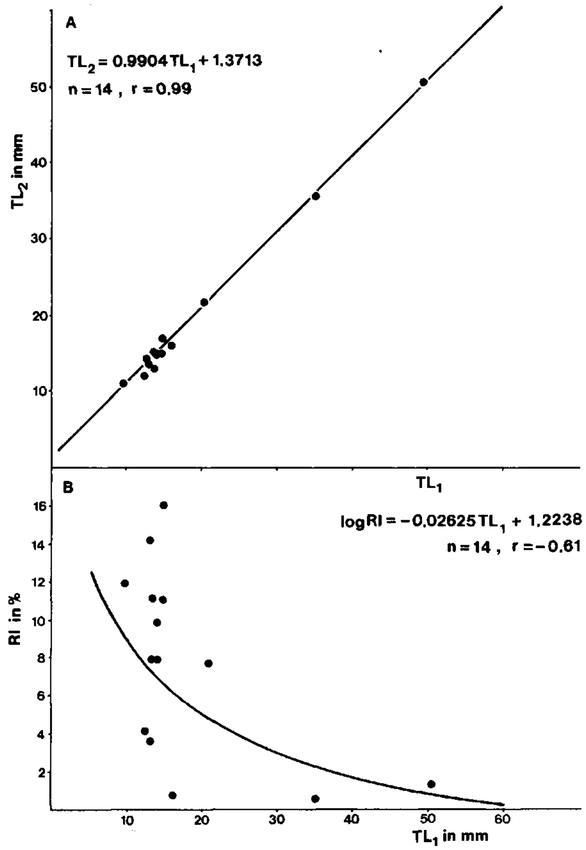

Fig. 6. A. HIATT-diagram of *U. pusilla*. TL_1: size of exuvia of the first moult; TL_2: size of the exuvia of the next moult. B. relative moult increment (RI in % of TL_1) in relation to size (TL_1 in mm).

several days after moults (HIATT, 1948; KURATA, 1962; FARMER, 1973; MAUCHLINE, 1976). As this is not possible in burrowing animals without severe disturbance, the moult increment was determined by measuring the exuviae of two successive moults.

Beside food supply moult increment is mainly affected by the intrinsic factor of body size (FARMER, 1973). The absolute increase in total length between moults was very variable in *U. pusilla* and ranged from 0.2 to 2.5 mm. Fig. 6 A shows the plot of TL of the exuvia at the first moult (TL_1) and TL of the exuvia at the second moult (TL_2) – the HIATT-diagramm – for *U. pusilla*. The linear regression between the two parameters enables prediction of the mean moult increment of a *U. pusilla* with a given size.

The relative increment in size per moult – as percentage of premoult total length – ranged from 0.7 to 16.4 % and decreased with increasing size (Fig. 6 B).

e. Growth rates

Growth curves for males from Grado were generated using both moult increment in relation to size (see Fig. 6 A) and intermoult periods in relation to size and temperature (see chapter 4. c.). The temperature course of the lagoonal water published by Del Piero *et al.* (1978) was used. Two starting points were chosen: the smallest male (CL = 5 mm) caught in April and the smallest male (CL = 4 mm) found in September 1977. The resulting growth curves (Fig. 7 a and b) demonstrate that the long breeding period (see chapter 5. a.) – which results in a long recruitment period – and longevity leads to a crowding of older animals in the larger size classes.

The growth curve for males derived from size frequencies using ELEFAN, however, indicates a higher *in situ* growth rate for males in Grado (Fig. 7 c), whereas the curve for females from Grado (Fig. 7 d) is similar to that calculated for males based on laboratory observations.

From the growth curves a life span of *U. pusilla* of over 5 years can be estimated. Under laboratory conditions, animals with TL 40 to 50 mm lived over 3 years.

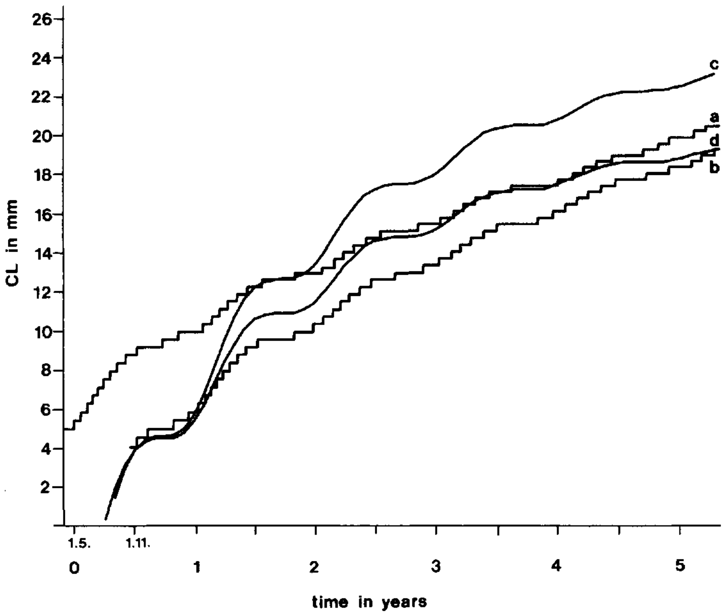

Fig. 7. Growth curves for *U. pusilla* from Grado. a and b: constructed by integrating data on moult increment and intermoult duration; a: starting point April 15th, CL = 5 mm; b: starting point November 1st, CL = 4 mm. c and d: von Bertalanffy growth curve calculated from size frequency histograms using ELEFAN; c: males, k = 0.5, $L\infty = 25.2$; d: females, k = 0.5, $\infty = 21$.

Due to long sampling intervals, it was not possible to calculate growth curves from size frequency distributions of animals from Staranzano or Rovinj. Growth in the Staranzano population, however, seems to be very similar to that in Grado. Assuming a similar life span for animals in Rovinj, as is indicated by the presence of large animals in all seasons, growth rates can be estimated to be 25 % lower than that of males in Grado based on the difference in TL_{max}.

5. Reproduction

a. Breeding period

Ovigerous females were found in Grado between March and September. The early stage of development of all eggs in the March-sample indicate that the 1977 breeding period began in the first day of March. This period ended between September 19th and September 26th: all embryos were ready to hatch. No ovigerous females occurred in October. Thus, the duration of the breeding period was ≈ 190 days. In 1978, early egg stages were first observed in April, indicating a later beginning of the season and an overall shorter duration.

Ovigerous females were found in Staranzano in April (1979), May (1983 and 1985) and June (1984); no ovigerous female occurred in September (1984 and 1985). In Rovinj, ovigerous females were caught in July (1978, 1979, and 1983). In the laboratory, animals caught in November carried eggs in April.

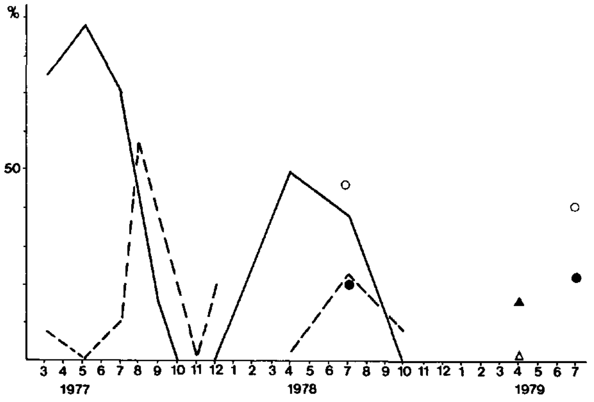

Fig. 8. Proportion of adult females which were ovigerous in Grado (solid line), Rovinj (●), and Staranzano (▲). Proportion of adult females with "plumose setae" in Grado (stipled line), Rovinj (○), and Staranzano (△).

The proportion of ovigerous females in the total number of adult females in the same sample (1977) was very high in March and May (75 and 88 %, respectively), decreased to 70 % in July and 44 % in August, and fell to only 15 % in September. A smaller proportion of ovigerous females was found in 1978 (50 % in April and 38 % in July) (Fig. 8).

This proportion was much lower in Rovinj, being 22, 24, and 31 % in July 1978, 1979, and 1983, respectively. In Staranzano, the proportion of ovigerous females was low in April 1979 (8 %) and June 1984 (11 %) and high in May 1983 and 1985 (70 and 60 %).

b. Size at maturity

The smallest ovigerous female from Grado had a TL of 36 mm (July 1978), the smallest female with well-developed ovaries a TL of 34 mm. Much smaller were ovigerous females from Rovinj (26 mm); filled ovaries occurred at 25 mm. The smallest ovigerous female from Staranzano measured 34 mm (TL).

The mean total length of ovigerous females was nearly equal in all samples from Grado and ranged from 53.3 mm in March 1977 to 50.3 mm in July 1978. It was significantly smaller in Staranzano ($TL_{mean} = 46.6$ mm) and Rovinj ($TL_{mean} = 33.1$ mm).

Size frequency histograms (see Figs. 3 and 4) show that ovigerous females from all three sites are represented by two size-classes, the smaller being 2 years old, the larger females 3 years and older.

Testes and vasa deferentia could be recognized in all males larger than 17 mm (TL). The testes of middle-sized males (TL around 35 mm) were always better developed than those of larger males. In histological investigations, TUCKER (1930) found testes in their definite form in 7 mm (TL) males, spermatogonia and well-developed vasa deferentia in 10 mm (TL) males; males larger than 15 mm were sexually mature.

c. Eggs

1. Attachment of eggs. The eggs are attached to the setae of the first pleopod and to the setae of the endopodites of pleopods 2–5. 80 % of all eggs were carried on the first three pleopods: 30.4 % on the first, 29.3 % on the second, 25.1 % on the third, and 18.5 % on the fourth. Only very few eggs (0.6 %) were attached to the fifth pleopod.

Females showing "plumose setae" (according to TUCKER, 1930) could be found in great numbers during and after the end of the breeding season. The occurrence of plumose setae thus seems to indicate the beginning or the end of one egg batch. In the latter case several empty egg capsules were still present.

2. Egg numbers. Egg number in *U. pusilla* is very variable. Even the general relation between body size and egg number (JENSEN, 1958) showed a great variation (Fig. 9). Because eggs are lost during the incubation period, only uneyed eggs were used for calculating the relation between egg number and female size (TL) in Grado.

A good correlation exists in May (1977) ($r = 0.71$; $n = 11$; $P < 0.05$) and April (1978) ($r = 0.65$; $n = 16$; $P < 0.01$) for Grado and in July (1979) ($r = 0.72$; $n = 28$; $P < 0.001$) for Rovinj. This correlation was less good for females from Grado in July (1978) ($r = 0.44$; $n = 11$; $P > 0.05$) and Staranzano (April 1979) ($r = 0.48$; $n = 10$; $P > 0.05$).

This indicates a seasonal variation in egg number. Numerous eggs are carried in spring; egg number is correlated by nearly the fourth power to TL. Fewer eggs are carried in summer and the variation in egg number within one size class is greater (Fig. 9).

In addition to seasonal variations within the same population, a great variation in egg numbers exists between the three different localities. The egg numbers of ovigerous females from Staranzano are very similar to those of the comparable sample (April) from Grado. Females from Rovinj, however, carry much fewer eggs not only due to their smaller size, but also compared with similar sized females from Grado (see Fig. 9).

In Rovinj (July 1979) the number of eyed eggs was between 5 and 74 % (mean 35.9 %) lower than the number of un-eyed eggs.

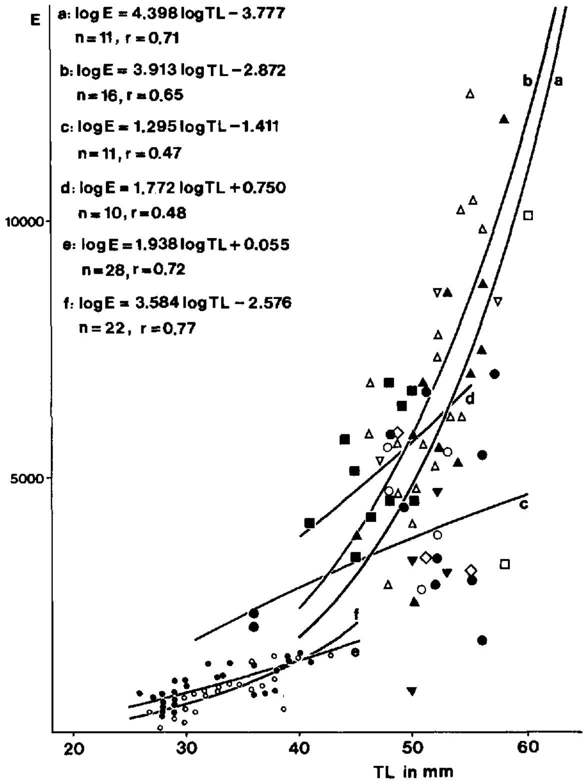

Fig. 9. Egg numbers in relation to female size (TL in mm). Grado: 7703 (□): un-eyed eggs; 7705 (▲, line a): un-eyed eggs; 7707 (◊): eyed eggs; 7708 (▽): eyed eggs; 7709 (▼): eyed eggs; 7804 (△, line b): un-eyed eggs; 7807 (●, line c): un-eyed eggs, (○): eyed eggs. Lido di Staranzano: 7904 (■, line d): un-eyed eggs. Rovinj: 7907 (○, line e): un-eyed eggs, (●, line f), eyed eggs.

3. **Egg size.** Egg size was not correlated with animal size ($r = 0.022$; $n = 60$; $P > 0.05$) but rather with egg number ($r = 0.29$; $n = 58$; $P < 0.05$); it also varied with the stage in embryonic development. In Grado, the mean diameter of eggs in stages 1–4 was 490.7 µm, that of eyed eggs (stages 5–9) 521.3 µm. This difference is significant ($P < 0.01$, t-test) and indicates an increase in volume of 20 % (from 61.8 to 74.2 µl) during embryonic development. In Rovinj, the mean diameter of un-eyed eggs was 473.3 µm, that of eyed eggs 501 µm. The difference between the stages is significant ($P < 0.001$, t-test) and corresponds to an

increase in volume of 19%. The difference in egg size between Rovinj and Grado is significant for both stages ($P < 0.05$, t-test). Eggs from Staranzano had a mean diameter of 500 µm and were not significantly ($P > 0.25$, t-test) larger than those of the same stages from Grado; they were significantly larger ($P < 0.001$, t-test) than eggs of the same stages from Rovinj.

4. Egg weight. The mean dry weight of one un-eyed egg was 21.4 µg in Grado. Eyed eggs had a mean dry weight of 14.4 µg and lost 33.3% weight during embryonic development. This difference is significant ($P < 0.001$, t-test). The mean dry weight of an un-eyed egg from Rovinj was 18.3 µg; a single eyed egg weighed 14.8 µg. This significant difference ($P < 0.001$, t-test) represents a weight loss of 19%. The mean dry weight of one un-eyed egg was 22.4 µg in Staranzano.

The difference in the weight of un-eyed eggs is significant only between Grado and Rovinj ($P < 0.001$, t-test) and between Rovinj and Staranzano ($P < 0.001$, t-test). No significant difference in weight exists between Grado and Staranzano ($P > 0.05$, t-test).

5. Egg masses. The egg mass (dry weight of all eggs from one female) varied with season, stage in embryonic development, and size of the female. It (stages 1–4) varied in Grado between 0.046 ($TL = 55$ mm, $ndw = 0.291$ g; July 1978) and 0.3145 g ($TL = 60$ mm, $ndw = 0.462$ g; March 1977). The egg masses of females from Staranzano had a similar range, while those from Rovinj were much lower, ranging from 0.007 ($TL = 28$ mm, $ndw = 0.048$ g) to 0.034 g ($TL = 39$ mm, $ndw = 0.111$ g).

The EI was size-independent; the smallest female from Grado ($TL = 36$ mm) had an EI of 70, the largest ($TL = 60$ mm) an EI of 68. Minimal, maximal, and mean EI values showed great seasonal variations in Grado (Fig. 10 A). The EI of un-eyed eggs was always higher than that of eyed eggs. The values from Rovinj ranged between 14.4 and 40.5 (mean = 29.5) and were much lower than for females with un-eyed eggs from Grado (EI between 12 and 70, mean = 41). The EI of ovigerous females from Staranzano ranged between 21.7 and 71.8 and was similar to that from Grado (mean = 55 in April).

6. Incubation time. The time required for freshly extruded eggs to hatch in laboratory animals ranged from 27 to 43 days (mean = 35.9 days, $n = 15$). Within one species, incubation time varies with temperature; WEAR (1974) showed that several crustaceans from temperate waters show a similar relationship between incubation time and temperature. Therefore, the slope of the equation given by HILL (1977) for the incubation time (I in days) in relation to temperature (T in °C) in *U. africana* was used for *U. pusilla:* $\log I = -1.881 \log T + 3.826$.

d. The ovaries

The ovaries in *U. pusilla* are situated dorsal to the hepatopancreas in the cephalothorax and reach far into the abdomen. They can already be recognized in very small females and are well developed at $TL > 31$ mm in Grado and at

TL > 21 mm in Rovinj. TUCKER (1930) found oocytes in histological sections at a TL > 15 mm in a population where ovigerous females were larger than 24 mm (TL). Mature ovaries almost completely fill the abdomen and can be recognized from the outside by their green colour.

Ovary dry weight varied according to stage and season; in adult females from Grado it varied between 0.001 (in all sizes) and 0.2394 g (TL = 51 mm, ndw = 0.3981, April 1978). In adults from Rovinj ovary dry weight ranged from 0.001 to 0.02 g. Ovary weight did not differ significantly in ovigerous and non-ovigerous females. Females with "plumose setae" had ovaries of all stages.

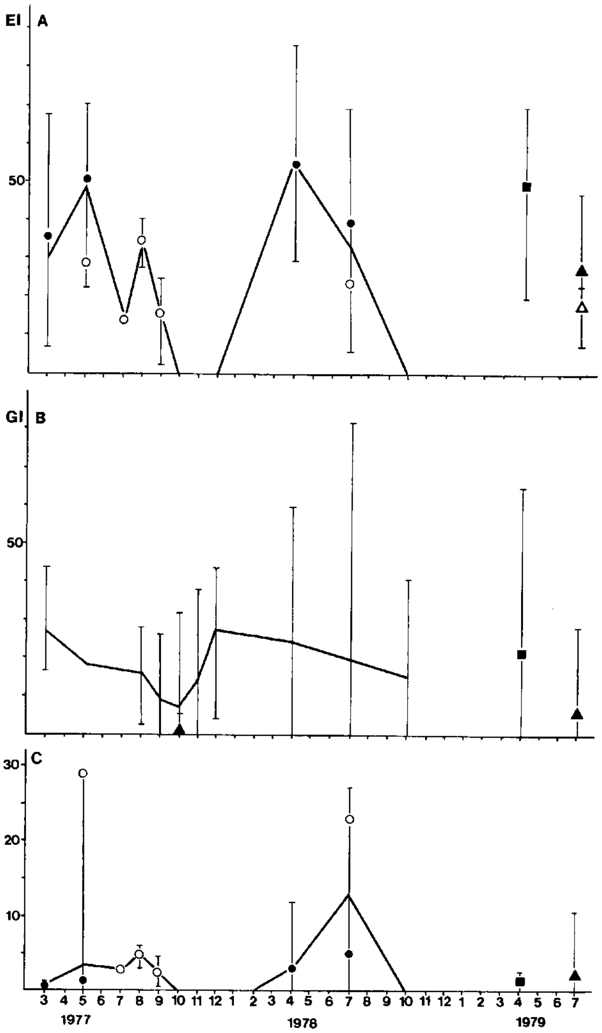

Fig. 10. A. Relative egg masses (EI in % of ndw) of ovigerous females. Grado: mean EI of eggs in all stages (solid line), mean EI of un-eyed (●) and eyed (○) eggs. Rovinj: mean EI of un-eyed (▲) and eyed (△) eggs. Staranzano: mean of un-eyed eggs (■). Relative ovary masses (GI in % of ndw) of non-ovigerous (B) and ovigerous females (C). Grado: mean GI (solid line); mean GI of females with un-eyed (●) and eyed (○) eggs. Mean GI of females from Rovinj (▲) and Staranzano (■). Vertical bars indicate ranges of EI and GI, respectively.

Mean and maximal GI values of non-ovigerous females decreased in Grado from March to October (1977), increased during winter; mean values decreased again from April to October (1978), whereas maximum values increased until July and decreased from October on (Fig. 10 B). The lowest value was below 0.1 in all seasons; the highest value was 82.3 in July 1978.

Mean and maximum GI values were always higher in non-ovigerous females than in ovigerous females. In ovigerous females they increased from spring to summer and decreased in autumn (Fig. 10 C).

Similar to the relationship in the case of egg masses, GI values for females from Rovinj were lower (GI_{mean} = 5.7, GI_{max} = 28 in non-ovigerous; GI_{mean} = 2.3, GI_{max} = 11.4 in ovigerous females) than those of females from the July (1978) sample from Grado (GI_{mean} = 20.3, GI_{max} = 82.3 in non-ovigerous and GI_{mean} = 12.9, GI_{max} = 27.8 in ovigerous females); GI values from Staranzano were in the same range (GI_{mean} = 22.5, GI_{max} = 65.4 in non-ovigerous females) as those from the April sample from Grado (GI_{mean} = 25.1, GI_{max} = 60.4).

Ovaries of females which carried un-eyed eggs were always less filled than those with eyed eggs. This is independent of season as shown by the May 1977 and July 1978 samples from Grado and the July 1979 sample from Rovinj. In May, the only female with eyed eggs had a GI of 29.5; the mean GI of the females with un-eyed eggs was 1.0. In July, this relation was 19.6–27.8 (GI_{mean} = 23.5; eyed) and 0.1–15.2 (GI_{mean} = 5.3; un-eyed). The GI difference is less pronounced in Rovinj: GI_{mean} = 0.4 and GI_{max} = 5.5 in females with un-eyed eggs and GI_{mean} = 3.3 and GI_{max} = 9.5 in females with eyed eggs.

From the time between embryonic stages (calculated using incubation time in relation to temperature), the increase in ovary weight can be estimated. In Grado this increase is 28.2% and 18.2% of ndw within 20 and 18 days, respectively. In Rovinj, the corresponding increase was only 2.9%. This increase is much slower at the end of the breeding season, with a mean of 12.4% within two months (October to December). Together egg mass and ovary mass represent reproductive mass (RI as % of ndw); RI increases from December (RI_{mean} = 27.1) to April (RI_{mean} = 44.4). This is a weight increase of 17.3% of ndw within 4 months. Slower ovary development during the winter, however, results in more numerous eggs and higher egg masses than the rapid development during the breeding season.

e. Breeding sequence

The maximum number of egg batches which could theoretically be incubated per cycle is 6 for the year 1977 in Grado (calculated by dividing the breeding cycle – 190 days – by the length of the incubation time at the mean temperature; Hill, 1977).

As not all females are continuously ovigerous, the number of batches varies individually and lies well below the maximum number. It was not possible to determine which proportion of the females in the population carried 1, 2, or more egg batches. The incubation time, however, indicates that the ovigerous females of the different samples carried separate batches in time; *e. g.*, the eggs in March were to hatch before May, therefore ovigerous females caught in May were to a high proportion carrying their second batch. Summing the percentages of ovigerous adult females in the samples over the breeding period results in an estimated mean number of batches per female of 2.85 in 1977 (Grado). The stages in ovary development from May and July indicate a possible separate batch at that time which was not recognized due to the long sampling interval. Thus, the actual mean number of batches in 1977 might have been higher.

f. Larvae

Hatching during laboratory maintenance occurred over two to three successive nights. The larvae are transported out of the burrow by the current generated by the female's pleopods. Once in the water, the larvae move actively to the surface, sink down passively, and swim upwards again. They show a positive phototactic reaction. Many larvae remained in parts of the burrow; their decay was visible several days later as black dots in the burrow wall. Larvae which were caught in the basket of the female induced a flight reaction of the female. Mean total length of larvae was 1.9 mm.

The complete larval development of *U. pusilla* is known from plankton samples. CANO (1891) described 4 larval stages – with total lengths of 1.3, 2.0, 2.5, and 3.5 mm – and one postlarval stage of TL = 5 mm. After reaching the postlarval stage the animal begins to burrow.

The duration of larval development in *U. pusilla* is not known. The first larvae are to be expected in Grado from the beginning of May to mid-September. Following the growth of juveniles found in September 1977 (TL = 10 mm) back to postlarval size indicates settlement at the end of July. A minimal larval development of 35 days can be assumed.

6. Parasites and diseases

The bopyrid *Gyge branchialis* was the only obvious ectoparasite; it can be recognized by the swelling of one gill chamber, corresponding to the location of the asymmetrical female and the attached dwarf-male. The degree of parasitation by this bopyrid in Grado was 6.2 % in males in March, 2.4 % in May, 2.6 % in September, and 6.6 % in October 1977. Parasitized females (1.3 %) were found only in October 1977. The TL of parasitized animals ranged from 22 to 56 mm.

In July 1979, 4.8 % of the females from Rovinj had this parasite. In Staranzano, 0.8 % of the females and 1.3 % of the males were parasitized in April 1979, 1.6 % of the males in May 1985.

Trematode metacercariae were found as endoparasites in nearly all animals. The cysts are of ellipsoid shape (425 × 300 μm) and had a thick, two-layered cuticle. They occurred in the cephalothorax – attached to the hepatopancreas – as well as in the abdomen. Between 20 and 80 % of all females from Grado were parasitized with low numbers of cysts.

Infestation in Rovinj was much more severe; here, the cysts almost filled the body cavity and the proportion of parasitized animals ranged from 65 to 100 %. In Staranzano only single cysts were found (5 % of the animals).

Up to 20 acanthor- or acanthella-stages, the flattened encysted stage of the acanthocephalan *Arythmorhynchus,* were found between the lobes of the hepatopancreas inside Staranzano females (28.4%); in males single cysts were found in 5.9%. Only two animals from Grado had these cysts; no cysts were found in Rovinj.

The "burned spot disease" (Stewart, 1980) which can be recognized as brown to black spots in the cuticle, especially at articulations, was observed in several animals from all locations.

7. Energetic aspects of production

A mean caloric content of 5.6 kcal · g^{-1} (= 23.5 kJ · g^{-1}), given by Winberg (1971) for the organic matter of several aquatic invertebrates, was used to convert organic matter of different parts of *U. pusilla* into energetic equivalents:

males (entire animals):	12.4 kJ · g $(dw)^{-1}$
females (ndw):	10.3 kJ · g $(dw)^{-1}$
eggs and ovaries:	19.9 kJ · g $(dw)^{-1}$
exuviae:	5.6 kJ · g $(dw)^{-1}$

Over one year, a male with TL = 50 mm (6 moults; growth curve in chapter 4.e.) releases 1.93 g (dw) exuviae (= 10.9 kJ) and increases its weight by 0.1875 g (dw) (= 2.3 kJ). The same growth rate of a female of TL = 50 mm yields a weight increase of 0.1002 g (dw) (= 1.03 kJ) within one year. Due to the lower weight of female exuviae (see 4. b.) only 0.9595 g (dw) (= 5.4 kJ) is released. An egg batch of a female of this size (50% of ndw) is equivalent to 2.9 kJ. Considering the difference in annual exuvia production of 6.7 kJ between males and females and the lower weight increase, more than two batches of eggs are energetically possible for a female of this size. As the growth rate is lower in females, even more egg batches could be produced.

The production of a theoretical population of 100 animals with the same size and sex distribution as in November 1977 (Grado) was calculated using the hypothetical growth curve for males and a 10% lower growth rate for females; additional assumptions include the same number of moults in both sexes and 3

Table 1. Annual production of a theoretical population of 100 animals at Grado in g (dw) · $year^{-1}$ and kJ · $year^{-1}$ for males and females, and percentages of somatic growth, exuviae, egg and ovary production of the total population.

	males		females		total	
	g (dw)	kJ	g (dw)	kJ	% (g)	% (kJ)
somatic growth	4.3	52.4	6.9	81.7	8.7	13.5
exuviae	47.3	259.0	52.0	289.0	77.5	55.2
eggs and ovaries			17.6	311.3	13.8	31.3
total					128.1 (100%)	994.3 (100%)

egg batches annually (November to November) for each adult female. The values in g (dw) and kJ as well as the percentages of somatic growth, exuviae, egg and ovary in total annual production are summarized in Table 1. Production of spermatophores could be neglected.

Discussion

The occurrence of a larger cheliped in male decapods is an indicator of sexual maturity and is often used to separate growth phases (HARTNOLL, 1978). HARTNOLL (1982) mentions that different patterns of relative growth are responsible for the development of sexual dimorphism from the more or less undifferentiated early instars. That this differentiation becomes visible at sexual maturity has been shown in thalassinids for *Upogebia pusilla* (TUCKER, 1930); *Callianassa australiensis* (HAILSTONE & STEPHENSON, 1961); *C. filholi* (DEVINE, 1966); and *C. major* (RODRIGUES, 1985). TUCKER (1930) suggested that larger chelae size is due to the fact that males have no drain on their resources for egg-production. He demonstrated this by the influence of the parasitation by the bopyrid *Gyge branchialis:* parasitized males have slender propodi like females and their testes are not influenced; parasitized females also had smaller chelae, but in addition showed reduced ovaries up to the point of castration. A similar effect of parasitic castration has been reported for *C. laticauda (= C. tyrrhena)* by REVERBERI (1942).

Size frequency distributions are generally dependent on the population dynamics and seem to be mainly influenced by individual growth rates. A size frequency distribution similar to that in Rovinj has been described for *U. pusilla* from Naples (TUCKER, 1930), whereby males were found in 3 distinct size classes: 8.5 mm CL (TL = 22.7 mm), 11.5 mm CL (TL = 31.3) and 14.5 mm CL (TL = 39.9 mm) in summer; no distinct size classes were recognized in females. Three modes can always be recognized when size frequencies of males and females are combined; such histograms have been presented for *U. pusilla* by POPOVICI (1940) and for *U. deltaura* by GUSTAFSON (1934).

Sex ratios of *U. pusilla* varied in the three study sites, although no clear pattern emerged. A sex ratio (male : female) of 2 : 3 was observed in a *U. pusilla* population by TUCKER (1930); in juveniles, males predominated. Twice as many females as males were found by DEVINE (1966) in *C. filholi;* in this population the sex ratio of juveniles was balanced. The prevalence of adult females in a population of *C. australiensis* was explained by migration (HAILSTONE & STEPHENSON, 1961). HILL (1977) observed a balanced sex ratio or a prevalence of adult females in *U. africana* populations from different localities.

The relative moult increment as well as the number of moults per year (hypothetical growth rate) of *Upogebia pusilla* are in the same range as described for several crustaceans (*e. g.,* HIATT, 1948; KURATA, 1962; MAUCHLINE, 1976; HARTNOLL, 1982, 1983). The increment in size per year lies in the same order of magnitude as in *C. australiensis* (mean of 9.5 mm CL; HAILSTONE & STEPHENSON, 1961), in *C. filholi* (8 mm CL; DEVINE, 1966), and *C. kraussi* (6 mm CL in the first and 3 mm in the second year in males; FORBES, 1977).

The life span of over 5 years in *U. pusilla* is the longest reported for the *Upogebiidae.* A life span of at least 3 years was suggested from size frequency distributions by Tucker (1930) and Popovici (1940) for *U. pusilla* and by Gustafson (1934) for *U. deltaura*. Chaud (1984), however, mentions that *U. pusilla* in Brittany lives only for a maximum of two years. Additional estimates are 4 years for *C. filholi* (Devine, 1966), at least 2 to 3 years for *C. australiensis* (Hailstone & Stephenson, 1961) and *C. kraussi* (Forbes, 1977), and 10 years for *C. californiensis* (MacGinitie, 1935).

The breeding season generally depends on the temperature cycle of the biotope; in the Mediterranean and Black Sea, ovigerous *U. pusilla* always occurred between March and October (LoBianco, 1909; Tucker, 1930; Popovici, 1940).

Egg numbers of different species depend, in addition to the size of the ovigerous female, mainly on egg size and number of larval stages. High egg numbers with small egg sizes in most burrowing *Upogebia*-species (Table 2) are related to a relatively long planktotrophic larval development with high larval mortality. Sponge-dwelling *Upogebia*-species carry few, large eggs (*e. g.*,

Table 2. Egg numbers (E) of ovigerous females with TL, CL (in mm), diameter of one egg (ED in µm), incubation period (in days) at temperature T (in °C), number of larval stages (l: larval; pl: post-larval), duration of larval development (LD in days), a: life habit of larvae (p: planktonic; b: benthic), b: life habit of adults (b: burrowing; s: in sponges) of *Upogebia*- and *Callianassa*-species. Sources: (1) Andryszak, 1986; (2) Cano, 1891; (3) Devine, 1966; (4) Dolgopolskaya, 1969; (5) Forbes, 1973; (6) Forbes, 1977; (7) Gurney, 1924; (8) Gurney, 1937; (9) Hailstone & Stephenson, 1961; (10) Hart, 1937; (11) Hill, 1977; (12) Kurata, 1965; (13) Lutze, 1938; (14) McCrow, 1972 after Johnson & Gonor, 1982; (15) Ngoc-Ho, 1977; (16) Pearse, 1945; (17) Pohl, 1946; (18) Rodrigues, 1976; (19) Rodrigues, 1984; (20) Sakai, 1975; (21) Samuelsen, 1974; (22) Sandifer, 1973; (23) Sankolli & Shenoy, 1975; (24) Shenoy, 1967; (25) Thompson, 1972; (26) Tunberg, 1986; (27) Vaugelas *et al.*, 1986; (28) Webb, 1919; (29) this study.

Species	E	TL [mm]	CL [mm]	ED [µm]	I [d]	T [°C]	stages	LD [d]	a	b	sources
U. affinis	10,000	47–75		450			4l, 1pl,		p	b	(16), (22), (1)
U. africana	300–2000		12–20	450	52	17.5			p	b	(11)
U. danai							4l, 1pl		p	b	(7)
U. darwini		31		1000			2l, 1pl	5	p	s	(15)
U. deltaura	4700	40	14	500–558			4l, 2pl	30–60	p	b	(27), (21), (26)
U. kempi							4l, 2pl	22	p	b	(24)
U. major							3l		p	b	(12)
U. pugettensis				1000			3l, 1pl	14	p	b	(10), (25)
U. pusilla	400–12,000	36–60	8–19	400–490	35.5	17.5	4l, 1pl	35	p	b	(2), (29)
U. savignyi		35		1000			1l	–	b	s	(8)
U. stellata		53	18	500			4l, 2pl		p	b	(28), (21)
C. armata		100		850–1050	19.5	26			p	b	(27)
C. australiensis			9–12		45		6l, 1pl	120	p	b	(9)
C. californiensis							5l, 1pl	42–56	p	b	(14)
C. filholi	660–1500	34–54			38.5	14	5l, 1pl	150	p	b	(3)
C. kewalramanii				700–900			2l, 2pl	7–9	p	b	(23)
C. kraussi	12–193		6–11	900–1800	32.5	20	2l	3–5	b	b	(5), (6)
C. major	8200	136		875–1020	33	23	3l	14	p	b	(17), (18)
C. mirim							2l, 1pl	14	p	b	(19)
C. subterranea	7000	47		500–600	30	18	4l, 1pl	35	p	b	(13)

U. digitana with ED of 900 µm in a female with TL = 16 mm; SAKAI, 1975). NGOC-HO (1977) described an abbreviated larval development in *U. darwini* (see Table 2). In *U. savignyi* only one larval stage exists; immediately after hatching it moults into the juvenile (GURNEY, 1937). This indicates that burrowing shrimps show an adaptation for larval dispersion whereas species inhabiting sponges or corals show a trend towards abbreviated larval development. Such a trend is apparent in several crustaceans having restricted and specialized habitats (RABALAIS & GORE, 1985). In burrowing *Callianassa*-species, eggs are also larger when larval development is short (Table 2).

WEAR (1974) demonstrated the influence of temperature on the incubation period of crustacean eggs; in animals from similar temperate regions no differences due to egg size exist. STEELE & STEELE (1975), however, reported that the duration of embryonic development is inversely correlated with egg size in *Crustacea*.

A decrease in egg weight and increase in egg volume during embryonic development is a common phenomenon in crustaceans; the first is due to the metabolization of yolk, whereas the second is due to water uptake (WEAR, 1974). The general volume increase of the egg batch together with the female's ventilation activity leads to an egg loss ranging from 5 to 74 % in *U. pusilla*. The mean egg loss of 36 %, however, lies in the range of average brood mortalities (27 to 55 %) reported for several *Natantia* and *Brachyura* (summarized in BALASUNDARAM & PANDIAN, 1982).

The number of larval stages and duration of larval development within the burrowing *Upogebiidae* are relatively uniform. Abbreviation of larval development occurs in some sponge-inhabiting species (Table 2). A much longer larval life and more stages have been reported for most of the *Callianassidae* (Table 2). But in this family, abbreviation of larval development also occurs; a completely suppressed planktonic phase was reported for *C. kraussi* (FORBES, 1973).

Larvae of *U. pusilla* have been found in the Mediterranean always immediately after the respective breeding period (CANO, 1891; LOBIANCO, 1909; BOURDILLON-CASANOVA, 1960). MAKAROV (1976) described their diurnal vertical migration and concentration at night in the upper 0.5 m water layer near the shore. EMMERSON (1983) reports that 97.1 to 99.9 % of the first larval stage of *U. africana* are swept out of the adult's estuarine habitat during nocturnal ebb tide and dispersed by longshore currents. After completion of larval development near the shore, recruitment of the estuarine population occurs through postlarvae entering with the flood tide. A similar net flux of larvae out of an estuary has been reported for *C. californiensis* by JOHNSON & GONOR (1982).

The decrease in egg numbers and egg masses of succeeding batches has also been observed in *Macropipus depurator* by WEAR (1974). Protein and lipid synthesis for ovary formation together with mobilization of lipid from the hepatopancreas and protein from muscles is limiting during the peak of breeding activity whereas during the long breeding pause in winter these processes increase (PILLAY & NAIR, 1973). The number of egg batches depends on incubation time and thus on temperature during the breeding season. HILL (1977) calculated between 3 and 7 theoretically possible egg batches for *U. africana* populations from biotopes with different temperature regimes.

Information on population dynamics of *Upogebiidae* and *Callianassidae* are sparse. Hailstone & Stephenson (1961) demonstrated the influence of bait digging on *C. australiensis;* recruitment balances removal by bait digging. Forbes (1978) showed that recruitment into areas where females are not reproductive due to low salinity takes place by movement of *C. kraussi* postlarvae.

Exuviae of *U. pusilla* have a relatively high caloric value: 5.6 kJ · g^{-1} (dw); the result is the loss of a high proportion of total production through exuviae. Koop (1979) determined a value of 10.2 kJ · g^{-1} (ash free dry weight) for exuviae of the isopod *Ligia dilatata* but did not incorporate this value in the energy budget. Willows (1987) determined an energy content of 7.38 J · mg^{-1} (dw) for *Ligia oceanica* exuviae, resulting in 13.3 kJ · m^{-2} · y^{-1} loss – equivalent to 21 % of total production. Berry & Smale (1980) found that in the rock-lobster *Panulirus homarus,* which has a more strongly calcified exoskeleton than *Upogebia* and an energy content of 18.35 kJ · g^{-1} (acid treated dry weight) and moults as an adult only once a year, the energy loss by exuvia-production is 28.14 kJ · m^{-2} · y^{-1} or 59 % of total production. In the krill *Nyctiphanes australis,* this value was 42.01 mg (dry weight) · m^{-3} · y^{-1} or 33.6 % of the total annual production (Hosie & Ritz, 1983). The authors mention that these exuviae are an important source for the detrital food web. Hartnoll (1983) summarized patterns and advantages of the two growth strategies – indeterminate and determinate growth – represented in crustaceans and lists the high energy loss through exuvia-production as one of the important disadvantages of indeterminate growth.

The generally smaller size of individuals in Rovinj is most probably due to a lower growth rate. This lower growth rate may be due to the following reasons:

(1) a higher salinity (36 ‰) than at Grado (mean 27.7 ‰) or Staranzano (14–26 ‰); Popovici (1940) found *U. pusilla* up to TL = 65 mm at 17 ‰, whereas Tucker (1930) and Daguerre de Hureaux (1970) caught animals with maximum sizes of 50 mm and 47 mm at 36 ‰, respectively. Kinne (1971) gave several examples of the influence of supra- and subnormal salinities on the final size of invertrebrates. Optimal salinity for *U. pusilla* seems to lie around 26 ‰. This is supported by the fact that respiration rates in small animals (< 2.5 g ww) at temperatures between 15.0 and 17.5 °C, and in large animals (> 2.5 g) at temperatures between 20.0 and 22.5 °C are lowest at 26 ‰ (Dworschak, in prep.);

(2) the extremely high population density in the isolated Rovinj population. This may be due to the low water exchange in this sheltered enclosed bay, which leads to a long retention time of larvae and a high proportion of resettlement within the Val Saline. This dense population is probably food limited;

(3) finally, the high degree of parasitation may be a consequence of the bad nutritional status and may further reduce growth and fecundity.

Summary

U. pusilla shows a marked sexual dimorphism. Males from Grado and Staranzano become larger (66 and 60 mm total length) than females (60 and 58 mm TL). From a total length of 35 mm, males have stronger chelipeds than females, this results in a sexual difference in all other measurements such as wet weight,

dry weight, and proportion of exoskeleton to total weight. Animals from Rovinj are generally smaller (TL_{max} = 47 mm) and sexual dimorphism less marked. Size frequency distributions show the presence of large animals in all seasons; variations exist in middle-sized animals. Juveniles are found in all three populations in early autumn. In the laboratory, *U. pusilla* moults at night in its burrow, buries the exuviae, and later transports it onto the surface. Size-dependent moult intervals at 17.5 °C range from 20 to 60 days. The moult increment is between 0.7 and 16.4 % of the premoult size and decreases with increasing size. Growth rates generated using data on moult intervals and moult increments are somewhat lower than growth rates of males from Grado and similar to those of females as calculated from size frequency histograms. The life span of *U. pusilla* is over 5 years. Growth of animals from Staranzano is similar to that of the Grado population. Animals in Rovinj have a markedly lower growth rate. Ovigerous females occur in Grado between March and September, in Staranzano in May and June, and in Rovinj only in July. The proportion of ovigerous females in Grado is high (in spring 1977) – between 75 and 80 % of adult females – and decreases towards summer and autumn. 60 to 70 % of the females are ovigerous in Staranzano in spring, while in Rovinj this proportion is much lower (12 to 31 %). Ovigerous females from Rovinj are generally smaller (TL_{mean} = 33 mm) than those from Grado (TL_{mean} = 50 mm) and Staranzano (TL_{mean} = 46 mm), and carry absolutely and relatively less eggs (1,200). Size-dependent egg numbers show seasonal variation in Grado; they are high in spring (up to 12,000), lower in summer. The mean incubation time of embryos is 36 days at 17.5 °C; egg weight decreases by 33 %, egg number by 35 %, whereas egg size increases. Stages of ovary development, incubation time, and the proportion of ovigerous females during the breeding period indicates that each adult female produces at least 3 egg batches per year. The duration of planktonic larval development – 4 larval and one postlarval stage – is estimated to last 35 days. The ectoparasitic bopyrid *Gyge branchialis* occurs on some animals. 20 to 80 % of the shrimp from Grado are infested by trematode metacercarians; the infestation is nearly 100 % in Rovinj and very low in Staranzano. Here, *U. pusilla* is regularly infested by an acanthocephalan. Production of a theoretical population of 100 animals was calculated using growth, breeding sequences, and caloric content of animals, eggs and exuviae. This total annual production amounts 128 g dry weight or 994 kJ. The proportion of somatic growth is 8.7 % by dw (13.5 by kJ), that of exuviae-production 77.5 % by dw (55.2 by kJ), and that of egg production 13.8 % by dw (31.5 % by kJ).

Acknowledgements

This study was supported by the Hochschuljubiläumsstiftung der Stadt Wien and the projects P 5059 and P 5915 of the Fonds zur Förderung der wissenschaftlichen Forschung in Österreich. The author is grateful to the entire staff of the "Laboratorio di Biologia Marina, Sorgenti di Aurisina" (Italy) for their hospitality and for providing essential facilities. My thanks are due to Drs. J. OTT and M. STACHOWITSCH for critical reading of the manuscript.

References

ANDRYSZAK, B.L., 1986: *Upogebia affinis* (SAY) – its postlarval stage described from Louisiana plankton, with a comparison to postlarvae of other species within the genus and notes on its distribution. J. Crust. Biol., **6** (2): 214–226.

BALASUNDARAM, C. & T.J. PANDIAN, 1982: Egg loss during incubation in *Macrobrachium nobilii* (HENDERSON & MATHAI). J. Exp. Mar. Biol. Ecol., **59:** 289–299.

BERRY, P.F. & M.J. SMALE, 1980: An estimate of production and consumption rates in the spiny lobster *Panulirus homarus* on a shallow littoral reef off the Natal Coast, South Africa. Mar. Ecol. Prog. Ser., **2** (4): 337–343.

BOURDILLON-CASANOVA, L., 1960: Le méroplancton du Golfe de Marseille. Les larves des Crustacés Décapodes. Recl. Trav. Stn Mar. Endoume, **30** (18): 1–286.

BOUVIER, E.L., 1940: Décapodes Marcheurs. In: Faune de France, 37. Lechevalier, Paris; 404 pp.

BREY, T. & D. PAULY, 1986: Electronic length frequency analysis. A revised and expanded user's guide to ELEFAN 0, 1, and 2. Berichte aus dem Institut für Meereskunde an der Christian-Albrechts-Universität Kiel, Nr. 149; 76 pp.

CANO, G., 1891: Svillupo postembrionale della *Gebia, Axius, Callianassa* e *Calliaxis.* – Morfologia dei Thalassinidi. Boll. Soc. Nat. Napoli, Ser. 1, Vol. **5:** 5–30.

CHAUD, A., 1984: Biologie et étude d'une population d'*Upogebia pusilla* de la Baie de Chingoudy (Pay Basque). Ann. Soc. R. Zool. Belg., **114** (Suppl. 1): 195.

DAGUERRE DE HUREAUX, N., 1970: Recherches sur *Upogebia littoralis* RISSO (Decapode, Anomoure) I- Etude du cycle d'intermue. Soc. Sci. Nat. Phys. Maroc., **50** (1/2): 66–81.

DEL PIERO, D., G. OREL & M. SPECCHI, 1978: Osservazioni du alcuni parametri ambientali rilevati su una stazione fissa della laguna di Grado (Golfo di Trieste). Atti del primo convegno regionale sulle risorse marine costiere e lagunari, Trieste–Grignano, 23. 4. 1977. Annu. Parco Mar. Miramare (Suppl.), **6** (18): 76–79. WWF-Trieste.

DEVINE, C.E., 1966: Ecology of *Callianassa filholi* MILNE EDWARDS 1878 *(Crustacea, Thalassinidea).* Trans. R. Soc. N.Z. Zool., **8** (8): 93–110.

DOLGOPOLSKAYA, M.A., 1969: Larvae of Decapods. *Macrura* and *Anomura.* In: F.D. MORDUKHAI-BOLTOVSKOI (Ed.), Identification key to the fauna of the Black and Azov seas. 2. Free living invertrebrates. Crustaceans. Akademiya Nauk Ukrainskoi SSR, Institut Biologii Yuzhnykh Morei, Kiew; 536 pp. [In Russian.]

DWORSCHAK, P.C., 1987: The biology of *Upogebia pusilla* (PETAGNA) *(Decapoda, Thalassinidea)* II. Environments and zonation. P.S.Z.N.I.: Marine Ecology, **8** (4): 337–358.

EMMERSON, W.D., 1983: Tidal exchange of two decapod larvae *Palaemon pacificus (Caridea)* and *Upogebia africana (Thalassinidea)* between the Swartskops River estuary and adjacent coastal waters. S. Afr. J. Zool., **18:** 326–330.

FARMER, A.S., 1973: Age and growth in *Nephrops norvegicus (Decapoda: Nephropidae).* Mar. Biol., **23:** 315–325.

FORBES, A.T., 1973: An unusual abbreviated larval life in the estuarine burrowing prawn *Callianassa kraussi (Crustacea: Decapoda: Thalassinidea).* Mar. Biol., **22:** 361–365.

– –, 1977: Breeding and growth of the burrowing prawn *Callianassa kraussi* STEBBING *(Crustacea: Decapoda: Thalassinidea).* Zool. Afr., **12** (1): 149–161.

– –, 1978: Maintenance of non-breeding populations of the estuarine prawn *Callianassa kraussi (Crustacea, Anomura, Thalassinidea).* Zool. Afr., **13** (1): 33–40.

GURNEY, R., 1924: Decapod larvae. Br. Antarct. Terra Nova Exped. Zoology, **8** (2): 37–202.

– –, 1937: Notes on some decapod *Crustacea* from the Red Sea. II. The larvae of *Upogebia savignyi* STRAHL. Proc. Zool. Soc. London, Ser. B., **1937:** 98–101.

GUSTAFSON, G., 1934: On the *Thalassinidea* of the Swedish West Coast. Ark. Zool., **28 A** (1): 1–19.

HAILSTONE, T.S. & W. STEPHENSON, 1961: The biology of *Callianassa (Trypaea) australiensis* DANA 1852 *(Crustacea, Thalassinidea).* Univ. Queensl. Pap. Dep. Zool., **1:** 259–285.

HART, J.F.L., 1937: Larval and adult stages of British Columbia *Anomura.* Can. J. Res., **D15:** 179–220.

HARTNOLL, R.G., 1978: The determination of relative growth in *Crustacea.* Crustaceana, **34** (3): 281–293.

– –, 1982: Growth. In: L.E. ABELE (Ed.), The Biology of *Crustacea,* Vol. 2. Embryology, Morphology, and Genetics. Academic Press, New York: 111–196.

– –, 1983: Strategies of crustacean growth. Austr. Mus. Sydney Mem., **18:** 121–131.

Hertweck, G., 1974: Handstechkasten zur Gewinnung von ungestörten Sedimentproben im Taucheinsatz. Senckenbergiana marit., **6:** 119–127.

Hiatt, R. W., 1948: The biology of the lined shore crab *Pachygrapsus crassipes* Randall. Pac. Sci., **2:** 135–213.

Hill, B. J., 1977: The effect of heated effluent on egg production in the estuarine prawn *Upogebia africana* (Ortmann). J. Exp. Mar. Biol. Ecol., **29:** 291–302.

Hosie, G. W. & D. A. Ritz, 1983: Contribution of moulting and eggs to secondary production in *Nyctiphanes australis (Crustacea, Euphausiacea).* Mar. Biol., **77** (3): 215–220.

Jensen, J. P., 1958: The relation between body size and number of eggs in marine *Malacostraca.* Medd. Dan. Fisk Havunders., **2:** 1–25.

Johnson, G. E. & J. J. Gonor, 1982: The tidal exchange of *Callianassa californiensis (Crustacea, Decapoda)* larvae between the ocean and the Salmon River estuary, Oregon. Estuarine Coastal Shelf Sci., **14:** 501–516.

Kinne, O., 1971: Salinity, Animals, Invertebrates. In: O. Kinne (Ed.), Marine Ecology, **1** (2). Wiley-Interscience, London: 821–995.

Koop, K., 1979: Biology and ecological energetics of the supralittoral isopod *Ligia dilatata.* MSc-thesis, Univ. Cape Town; 103 pp.

Kurata, H., 1962: Studies on the age and growth of *Crustacea.* Bull. Hokkaido reg. Fish Res. Lab., **24:** 1–115.

– –, 1965: Larvae of decapod *Crustacea* of Hokkaido. 9. *Axiidae, Callianassidae* and *Upogebiidae (Anomura).* Bull. Hokkaido reg. Fish. Res. Lab., **30:** 1–10.

LoBianco, S., 1909: Notizie biologiche riguardanti specialmente il periodo di maturita sessuale degli animali del golfo di Napoli. Mitth. Zool. Stat. Neapel, **19** (4): 513–761.

Lutze, J., 1938: Ueber Systematik, Entwicklung und Oekologie von *Callianassa.* Helgol. Wiss. Meeresunters., **1:** 162–199.

MacGinitie, G. E., 1935: Ecological aspects of a California marine estuary. Am. Midl. Nat., **16:** 629–765.

Makarov, Y. N., 1977: Some aspects of the ecology of decapod larvae in the Black Sea and in the Sea of Azov. Okeanologiya, **16** (6): 1076–1081. [Russian with English summary.]

Mauchline, J., 1976: The Hiatt growth diagram for *Crustacea.* Mar. Biol., **35:** 79–84.

McCrow, L. T., 1972: The ghost shrimp *Callianassa californiensis,* in Yaquina Bay, Oregon. M. Sc. Thesis, Oregon State University; 56 pp.

Monod, T., 1930: Crustacés. In: Missions A. Gruvel dans le Canal de Suez. I. Mém. Inst. Egypte, **34:** 1–19.

Ngoc-Ho, N., 1977: The larval development of *Upogebia darwini (Crustacea, Thalassinidea)* reared in the laboratory, with a rediscription of the adult. J. Zool., London, **181:** 439–464.

Passano, L. M., 1960: Molting and its control. In: T. E. Waterman (Ed.), Physiology of *Crustacea,* Vol. 1. Academic Press, New York: 473–536.

Pauly, D. & N. David, 1981: ELEFAN I, a BASIC program for the objective extraction of growth parameters from length-frequency data. Meeresforsch., **28** (4): 205–211.

Pearse, A. S., 1945: Ecology of *Upogebia affinis.* Ecology, **26** (3): 303–305.

Pesta, O., 1918: Die Decapodenfauna der Adria. Versuch einer Monographie. Leipzig und Wien; 500 pp.

Pillay, K. K. & N. B. Nair, 1973: Observations on the biochemical changes in gonads and other organs of *Uca annulipes, Portunus pelagicus,* and *Metapenaeus affinis (Decapoda, Crustacea)* during the reproductive cycle. Mar. Biol., **18:** 167–198.

Pohl, M. E., 1946: Ecological observations on *Callianassa major* Say at Beaufort, North Carolina. Ecology, **27:** 71–80.

Popovici, Z., 1940: Längenmessungen an *Upogebia littoralis* R. aus dem Schwarzen Meere. Bull. Sect. Sci. Acad. Roumaine, **22:** 484–488.

Rabalais, N. N. & R. H. Gore, 1985: Abbreviated development in decapods. In: A. M. Wenner (Ed.), Crustacean growth: larval growth. Crustacean issues, Vol. 2. Balkema, Rotterdam, Boston: 67–125.

Reverberi, G., 1942: Sul significato della «castrazione parassitaria». La transformazione del sesso nei crostacei parassitati da Bopiridi e da Rizocefali. Pubbl. Stn Zool. Napoli, **19:** 225–316.

Rodrigues, S. de A., 1976: Sobre a reproducao, embriologia e desenvolvimento larval de *Callichirus major* Say, 1818 *(Crustacea, Decapoda, Thalassinidea).* Bol. Zool. Univ. S. Paulo, **1:** 85–104.

– –, 1984: Desenvolvimento post-embrionaria de *Callichirus mirim* (Rodrigues, 1971) obtido em condicoes artificiais *(Crustacea, Decapoda, Thalassinidea)*. Bol. Zool. Univ. S. Paulo, **8:** 239–256.

– –, 1985: Sobre o crescimento relativo de *Callichirus major* (Say, 1818) *(Crustacea, Decapoda, Thalassinidea)*. Bol. Zool. Univ. S. Paulo, **9:** 195–211.

Saint Laurent, M. de & P. LeLoeuff, 1979: Crustacés décapodes *Thalassinidea*. I. *Upogebiidae* et *Callianassidae*. Ann. Inst. Océanogr., Paris (Nouv. Ser.), **55** (Suppl.): 29–101.

Sakai, K., 1975: *Thalassinidea* of Kenia collected by Dr. A. J. Bruce *(Crustacea, Decapoda)*. Veröff. Zool. Staatssamml. München, **18:** 1–44.

Samuelsen, T. J., 1974: New records of *Upogebia deltaura* and *U. stellata (Crustacea, Decapoda)* from western Norway. Sarsia, **56:** 131–134.

Sandifer, P. A., 1973: Larvae of the burrowing shrimp, *Upogebia affinis, (Crustacea, Decapoda, Upogebiidae)* from Virginia plankton. Chesapeake Sci., **14** (2): 98–104.

Sankolli, K. N. & S. Shenoy, 1975: Larval development of mud shrimp *Callianassa kewalramanii* Sankolli, in the laboratory *(Crustacea, Decapoda)*. Bull. Dep. Mar. Sci. Univ. Cochin., **7** (4): 705–720.

Shenoy, S., 1967: Studies on larval development in *Anomura (Crustacea, Decapoda)* – II. Mar. Biol. Assoc. India, Symp. Ser., **2:** 777–804.

Steele, D. H. & V. J. Steele, 1975: Egg size and duration of embryonic development in *Crustacea*. Int. Rev. ges. Hydrobiol., **60** (5): 711–715.

Stewart, J. E., 1980: Diseases. In: J. S. Cobb & B. F. Phillips (Eds.), The biology and management of lobsters, Vol. 1. Physiology and behavior. Academic Press, New York: 171–195.

Thompson, R. K., 1972: Functional morphology of the hind-gut gland of *Upogebia pugettensis (Crustacea, Thalassinidea)* and its role in burrow construction. Ph. D. thesis, University of California Berkeley; 202 pp.

Tucker, B. W., 1930: On the effects of an epicaridan parasite, *Gyge branchialis,* on *Upogebia littoralis*. Q. J. Microsc. Sci., **74:** 1–118.

Tunberg, B., 1986: Studies on the population ecology of *Upogebia deltaura* (Leach) *(Crustacea, Thalassinidea)*. Estuarine Coastal Shelf Sci., **22:** 753–765.

Vaugelas, J. de, B. Delesalle & C. Monier, 1986: Aspects of the biology of *Callichirus armatus* (A. Milne Edwards, 1870) *(Decapoda, Thalassinidea)* from French Polynesia. Crustaceana, **50** (2): 204–216.

Wear, R. G., 1974: Incubation in British decapod *Crustacea,* and the effect of temperature on the rate and success of embryonic development. J. Mar. Biol. Assoc. U. K., **54:** 754–762.

Webb, G. E., 1919: The development of the species of *Upogebia* from Plymouth Sound. J. Mar. Biol. Assoc. U. K., **12** (1): 81–111.

Willows, R. I., 1987: Population and individual energetics of *Ligia oceanica* (L.) *(Crustacea: Isopoda)* in the rocky supralittoral. J. Exp. Mar. Biol. Ecol., **105:** 253–274.

Winberg, G. G., 1971: Methods for the estimation of aquatic animals. Academic Press, London; 175 pp.

Zariquiey Alvarez, R., 1968: Crustáceos Decápodos Ibéricos. Invest. Pesq., Barcelona, **32:** 1–510.