Invertebrate Reproduction and Development, 43:1 (2003) 83–90
Balaban, Philadelphia/Rehovot
0168-8170/03/$05.00 © 2003 Balaban

Redescription of the larval stages of *Upobebia pusilla* (Petagna, 1792) (Thalassinidea, Upogebiidae) from laboratory-reared material

ANTONINA DOS SANTOS[1*] and JOSÉ PAULA[2]
[1]*Instituto de Investigação das Pescas e do Mar (IPIMAR), Av. de Brasília, s/n. 1449-006 Lisboa, Portugal*
Tel. +351 (21) 302-7194; Fax +351 (21) 302-5948; email: antonina@ipimar.pt
[2]*IMAR–Laboratório Marítimo da Guia, Faculdade de Ciências, Universidade de Lisboa,*
Estrada do Guincho, 2750-642 Cascais, Portugal

Received 21 November 2001; Accepted 9 December 2002

Summary

The complete larval development of *Upogebia pusilla* (Petagna, 1792) was reared under laboratory conditions and the development comprised four zoeal stages and a megalop. The morphological features were described, illustrated and compared with other known larvae of *Upogebia*.

Key words: Larval development, *Upogebia pusilla*, Upogebiidae, Decapoda, zoeal stages, megalopal stage

Introduction

Upogebia pusilla (Petagna, 1792) is a common species on estuaries in Portugal and occurs from the English Channel to Mauritania and the Canary Islands, the Mediterranean, Black Sea and Suez Canal (d'Udekem d'Acoz, 1999). Besides *U. pusilla*, the Upogebiidae family has five other species occurring in European waters: *Gebiacantha talismani* (Bouvier), *Upogebia deltaura* (Leach), *U. mediterranea* Noël, *U. stellata* (Montagu) and *U. tipica* (Nardo).

Upogebiidae larvae are known for a number of European species only; *Gebia littoralis* (either *Upogebia pusilla* or *U. tipica* according to Williamson, 1967) by Cano, 1861 [three zoeal stages and post-larva]; *Upogebia deltaura* and *U. stellata* by Webb, 1919 from plankton and reared material [four zoeal stages and post-larva]; *U. pusilla* (originally as *U. littoralis*) by Dolgopolskaia, 1954 and 1969 [four zoeal stages and post-larva] and *U. deltaura* and *U. pusilla* (as *U. littoralis*) by Heegaard, 1963 [first stage zoea]. Although these studies gave some indication of general form, appendage morphology and chromatophore patterns, the descriptions do not meet with modern day standards.

With regard to *U. pusilla*, Dolgopolskaia (1954) has described four zoeas and one megalop (as post-larval stage) from plankton material caught in the Black Sea as *U. littoralis*. This description was re-published in 1969 as *U. pusilla* syn. *U. littoralis* (Dolgopolskaia, 1969). Both references present the descriptions of the

*Corresponding author.

appendages but are lacking the accurate number and position of setal processes. Thus, the morphological features of all zoeal stages and megalop remain incomplete.

The purpose of this study is to complete the description of the larval stages of *U. pusilla* based on larvae reared from eggs to megalop in order to facilitate the identification of the different stages and to distinguish them from other species of the genus *Upogebia* from plankton samples.

Materials and Methods

Several ovigerous females of *U. pusilla* were collected with a Yabby pump from their burrows in May, 1989, in the intertidal muddy sand of the mid-Mira Estuary, southwestern Portugal. Females were kept individually in 500 ml bowls, bottoms covered with plastic tubes, to simulate the burrow structure and decrease stress conditions. The water was at a salinity of 35 and at room temperature, and females were kept unfed until hatching. The first stage zoea hatched on 1, 5 and 9 June.

Cultures used 1 l tanks, with an initial average of five larvae per ml, with the same salinity and temperature as for females, and were gently aerated. Clean water and newly-hatched *Artemia* spp. nauplii as food were added every second day. The light–dark period was natural. Periodic observation of larvae was made, and a number of specimens of each larval stage were preserved in buffered 4% formaldehyde.

Drawings and measurements were made with the aid of a camera lucida on a binocular Wild M8. Setal observations and drawings were made using a Zeiss microscope with camera lucida. The preparation of slides with appendages was temporary. The long aesthetascs on the antennules and the long plumose setae on distal exopod segments are drawn truncated, and setal counts refer proximal to distal sequence. Measurements taken were: total length (TL) from tip of rostrum and posterior end of telson, and carapace length (CL) from tip of rostrum to posterior margin of carapace. The spent females and complete larval series have been deposited in the Instituto de Investigação das Pescas e do Mar (IPIMAR) in Lisbon, Portugal (number AdS 08/1993).

Results

Rearing data

Under laboratory conditions, *U. pusilla* hatches as zoea; it passes through four zoeal stages to megalopa. *U. pusilla* reaches the megalopal stage after 12–15 days of rearing.

Description — *Upogebia pusilla* (Petagna, 1792) (Figs. 1–6)

- *Upogebia littoralis* (Dolgopolskaia, 1954:198–209, Figs. 10–14, four zoeal stages and post-larva).
- *Upogebia pusilla* (Dolgopolskaia, 1969: Plates XXVIII–XXX, four zoeal stages and post-larva).

Zoea I

Dimension: TL = 2.10–2.38 mm; CL = 0.77–0.87 mm.

Carapace (Fig. 1A): longer than broad with a pointed rostral spine reaching the tip of antennules; eyes fused with the anterior portion of carapace.

Antennule (Fig. 1B): uniramous unsegmented process with one long plumose seta subterminally and one long thick and four thin aesthetascs, and one seta terminally. Endopod absent.

Antenna (Fig. 1C): protopod with one short serrated spine near the base of exopod; endopod with three apical plumose setae; tip of exopod pointed, bearing nine plumose setae on its inner margin.

Mandible (Fig. 1D): incisor process smaller than molar process; palp absent.

Maxillule (Fig. 1E): coxal endite with eight setae; basial endite with four stout spines and two setae; endopod unsegmented with 2+2+4 setae.

Maxilla (Fig. 1F): coxal endite bilobed with 8+5 setae; basial endite bilobed with 5+4 setae; endopod unsegmented and bilobed with 3+3 distal setae; scaphognathite with 10 marginal plumose setae.

First maxilliped (Fig. 1G): coxa with one seta; basis with 9 (2+3+2+2) setae; endopod 5-segmented with 3, 2+1, 1, 2+1, four setae; exopod 2-segmented, bearing four long setae terminally.

Second maxilliped (Fig. 1H): coxa without setae; basis with 1+1 setae; endopod 4-segmented with 2, 2, 2+1, four setae respectively; exopod 2-segmented, bearing four long setae terminally.

Third maxilliped (Fig. 1I): biramous bud.

Pereiopods (Fig. 1I): rudimentary buds.

Abdomen (Fig. 1A): Six somites without lateral spine on somites, being the sixth fused with telson; anal spine present.

Pleopods: absent.

Uropod: absent.

Telson (Fig. 1A): with median cleft and 7+7 processes posteriorly; outermost immovable spine, second reduced to a very thin seta situated near the base of process 3; processes 3–7 with plumose setae.

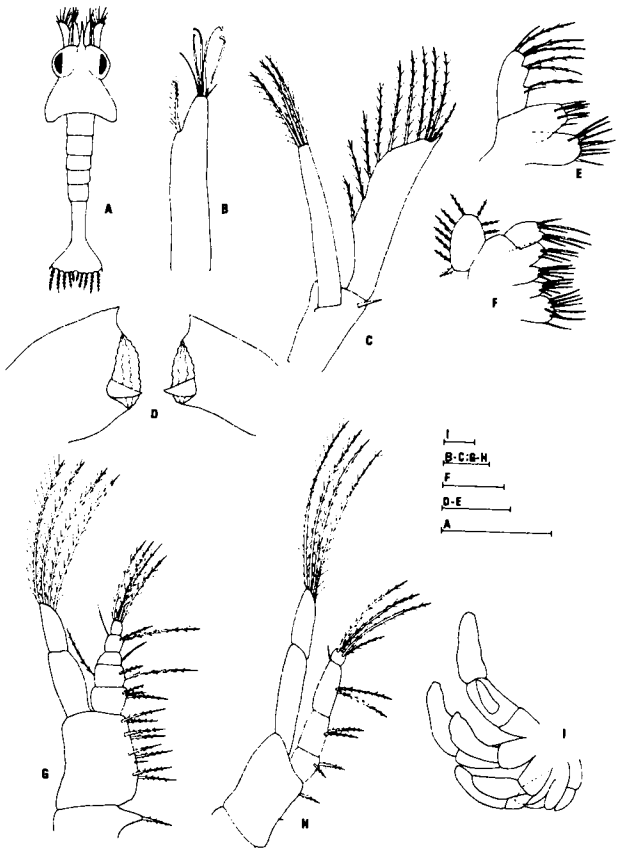

Fig. 1. *Upogebia pusilla*. Zoea I. A: dorsal view; B: antennule; C: antenna; D: mandible; E: maxilule; F: maxilla; G: first maxilliped; H: second maxilliped; I: (from left to right) third maxilliped and pereiopods. Scale bar: 1 mm (A); 100 μm (B–I).

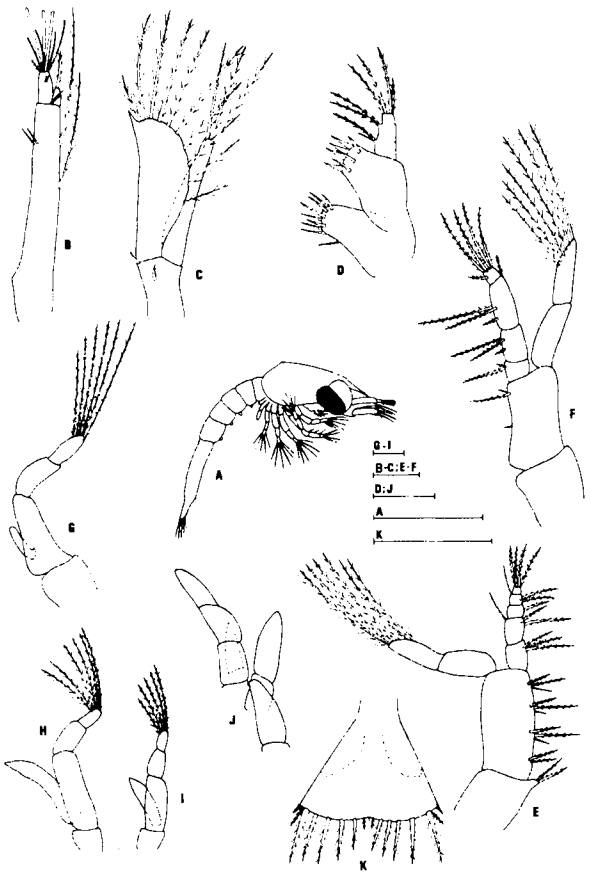

Fig. 2. *Upogebia pusilla*. Zoea II. A: lateral view; B: antennule; C: antenna; D: maxilule; E: first maxilliped; F: second maxilliped; G: third maxilliped; H: first pereiopod; I: second pereiopod; J: third to fifth pereiopods; K: telson. Scale bar: 1 mm (A); 500 μm (K) and 100 μm (B–J).

Zoea II

Dimension: TL = 2.40–2.62 mm; CL = 0.88–0.92 mm.

Carapace (Fig. 2A): eyes stalked; otherwise unchanged.

Antennule (Fig. 2B): biramous. Protopod with two inner long plumose setae and two outer short setae; two simple small setae on distal end; endopod bearing one terminal long plumose seta; exopod with four thick and three thin aesthetascs, one thin seta terminally and two small simple setae sub-terminally.

Antenna (Fig. 2C): protopod with two serrated spines; endopod with three apical plumose setae; exopod with 10 inner plumose setae.

Mandible: unchanged.

Maxillule (Fig. 2D): coxal endite with six setae; basial endite with four stout spines and three plumose setae; endopod with 2+2+4 setae.

Maxilla: unchanged.

First maxilliped (Fig. 2E): unchanged.

Second maxilliped (Fig. 2F): coxa without setae; basis with 1+2 setae; endopod 4-segmented with 2,2+1, 3+1, five setae; exopod 2-segmented, bearing six long setae terminally.

Third maxilliped (Fig. 2G): coxa and basis without setae; endopod as bud without setae and unsegmented; exopod 2-segmented with 6 natatory setae terminally.

First pereiopod (Fig. 2H): biramous; endopod as bud; exopod 2-segmented, distal one with six plumose setae.

Second pereiopod (Fig. 2I): biramous; endopod as bud; exopod segmented, distal one with five plumose setae.

Third to fifth pereiopods (Fig. 2J): pereiopod 3 biramous; pereiopod 4 and 5 uniramous with endopod buds absent and without setae.

Abdomen (Fig. 2A): unchanged.

Pleopods (Fig. 2A): rudimentary buds in abdominal somites 2–5.

Uropod: absent.

Telson (Fig. 2K): with small median process and 8+8 lateral processes posteriorly.

Zoea III

Dimension: TL = 2.64–2.88 mm; CL = 0.88–0.98 mm.

Carapace (Fig. 3A): larger, otherwise unchanged.

Antennule (Fig. 3B): protopod with eight long plumose setae and four outer short and thin setae subterminally and another four on distal end; endopod with two fine subterminal setae; exopod with three large aesthetascs, two long and three very thin setae.

Antenna (Fig. 3C): endopod with two thin and simple setae; otherwise unchanged.

Mandible: unchanged.

Maxillule: unchanged.

Maxilla (Fig. 3D): coxal endite with 7–8+5 setae; basial endite with 5+7 setae; scaphognathite with 12 plumose setae; otherwise unchanged.

First maxilliped (Fig. 3E): endopod 5-segmented with 3, 3+1, 0, 2, 4+1 setae on each segment; exopod distinctly 2-segmented bearing seven long setae terminally; otherwise unchanged.

Second maxilliped (Fig. 3F): basis with 1+1+2 setae; endopod 4-segmented with 3, 3, 3+1, 5 setae respectively; otherwise unchanged.

Third maxilliped (Fig. 3G): unchanged.

First and second pereiopod (Fig. 3H,I): endopod longer than exopod with a 2-segmented exopod, distal segment with seven terminal plumose setae.

Third pereiopod (Fig. 3J): exopod slightly segmented, distal segment with four plumose setae.

Fourth and fifth pereiopods (Fig. 3K): more elongated, otherwise unchanged.

Abdomen (Fig. 3A): now with the sixth somite separated from telson; pleopods more elongated and biramous; uropods present and biramous; otherwise unchanged.

Uropod (Fig. 3L): endopod and exopod with eight and 10 marginal plumose setae, respectively.

Telson (Fig. 3L): subquadrate with 9+9 lateral processes, process 4 the longest.

Zoea IV

Dimension: TL = 2.77–3.26 mm; CL = 1.00–1.18 mm.

Carapace (Fig. 4A): unchanged.

Antennule (Fig. 4B): unchanged.

Antenna (Fig. 4C): endopod without setae; exopod with 15 inner plumose setae.

Mandible: unchanged.

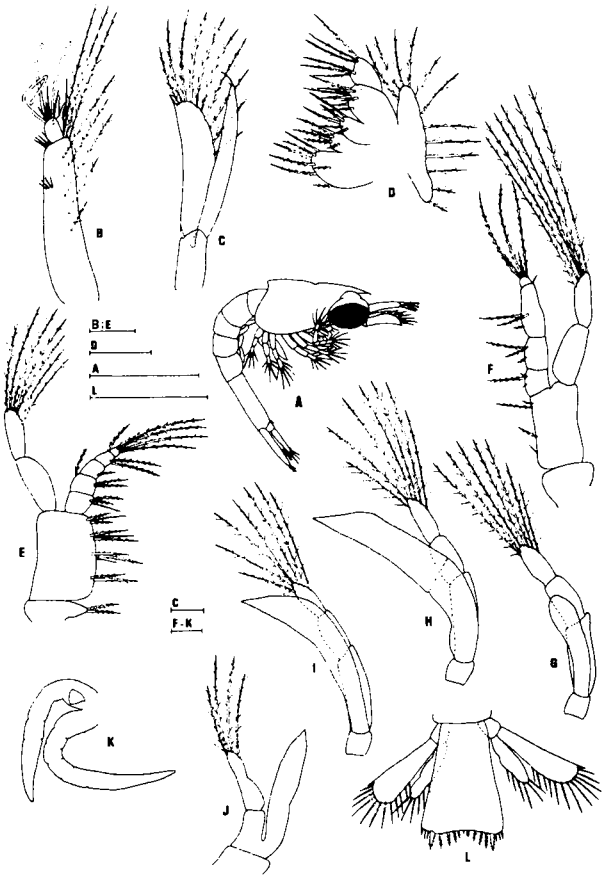

Fig. 3. *Upogebia pusilla*. Zoea III. A: lateral view; B: antennule; C: antenna; D: maxilla; E: first maxilliped; F: second maxilliped; G: third maxilliped; H: first pereiopod; I: second pereiopod; J: third pereiopod; K: fourth to fifth pereiopods; L: telson and uropods. Scale Bar: 1 mm (A); 500 μm (L); 100 μm (B–K).

Maxillule (Fig. 4D): coxal endite with nine setae; basial endite with four stout spines and three plumose setae; endopod 2-semented with 2, 2+4 setae terminally; otherwise unchanged.

Maxilla (Fig. 4E): coxal endite with 9+5 setae; basial endite with 3+6–7 setae; endopod unsegmented with 3+2 plumose setae; scaphognathite with 16 plumose setae and a long posterior lobe.

First maxilliped: unchanged.

Second maxilliped (Fig. 4F): exopod with seven setae; otherwise unchanged.

Third maxilliped (Fig. 4G): endopod elongated; exopod with seven setae; otherwise unchanged.

First pereiopod (Figs 4H): endopod 3-segmented and longer than exopod; exopod with six plumose setae.

Second to third pereiopod (Fig. 4I,J): endopod 2-segmented, longer than exopod; exopod with six plumose setae.

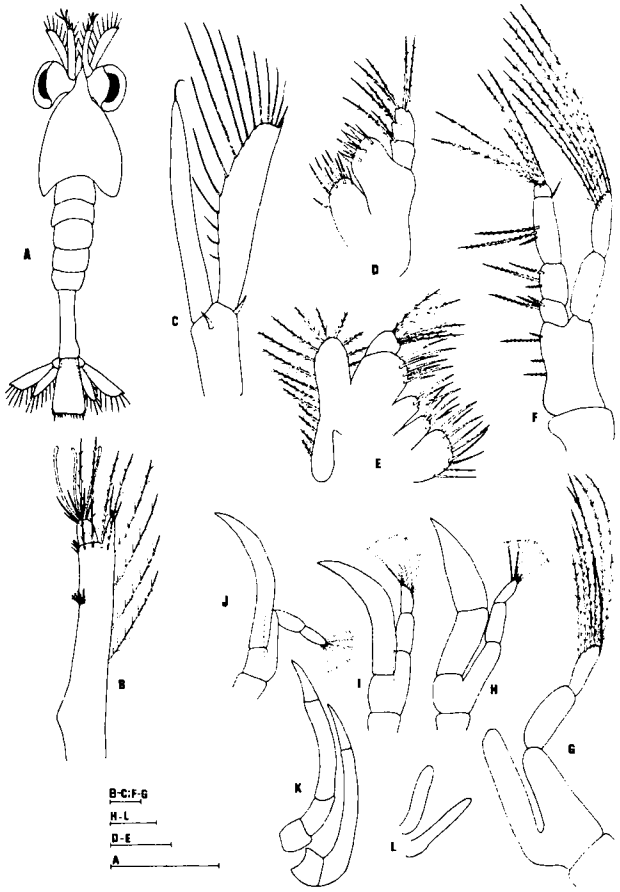

Fig. 4. *Upogebia pusilla*. Zoea IV. A: dorsal view; B: antennule; C: antenna; D: maxilule; E: maxilla; F: second maxilliped; G: third maxilliped; H: first pereiopod; I: second pereiopod; J: third pereiopod; K: fourth and fifth pereiopods; L: first pleopods. Scale bar: 1 mm (A); 100 µm (B–L).

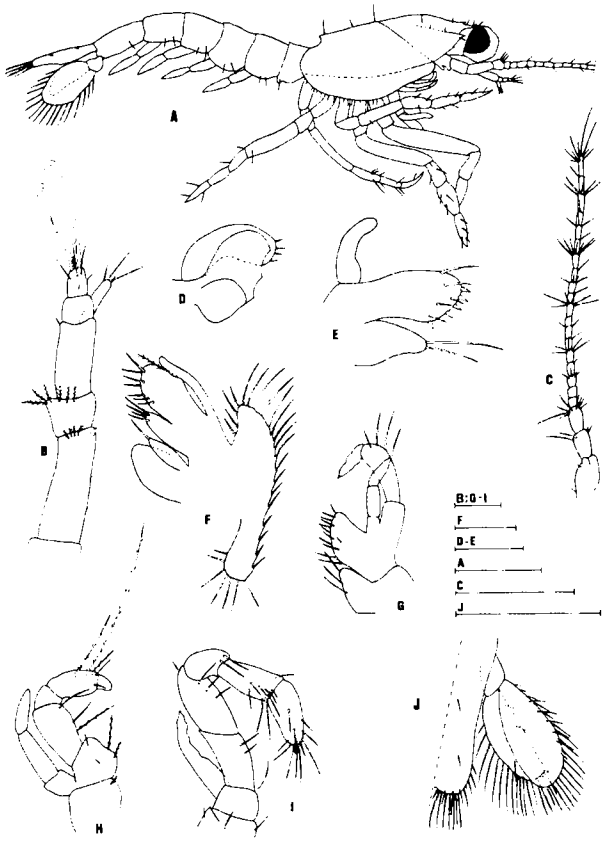

Fig. 5. *Upogebia pusilla*. Megalopa. A: lateral view; B: antennule; C: antenna; D: mandible; E: maxilule; F: maxilla; G: first maxilliped; H: second maxilliped; I: third maxilliped; J: telson and uropods. Scale bar: 500 µm (A and J); 100 µm (B–I).

Fourth pereiopod (Fig. 4K): uniramous, 4-segmented.

Fifth pereiopod (Fig. 4K): uniramous, 3-segmented.

Abdomen (Fig. 4A): unchanged.

Pleopods (Fig. 4L): more elongated, otherwise unchanged.

Uropod (Fig. 4A): more elongated, otherwise unchanged.

Telson (Fig. 4A): unchanged.

Megalop

Dimension: TL = 2.74–2.85 mm; CL = 0.98–1.02 mm.

Carapace (Fig. 5A): rostral spine present and very minute; "linea thalassinica" not evident at this stage.

Antennule (Fig. 5B): peduncle 3-segmented with a stout spine and several simple thin spines, six thin plumose setae on penultimate segment and one thin seta on distal segment; endopod unsegmented, with four setae terminally; exopod 2-segmented with three aesthetascs and six thin setae on distal segment.

Antenna (Fig. 5C): peduncle 3-segmented; flagellum composed of 19 segments, each with 0–7 setae on distal margin, arranged as figured, except for the distal segment with four terminal and five subterminal setae; a rudimentary exopod present on the proximal peduncular segment.

Mandible (Fig. 5D): palp unsegmented with four short setae distally.

Maxillule (Fig. 5E): coxal endite with two setae; basial endite with five stout spines and five setae; endopod unilobed and unarmed.

Maxilla (Fig. 5F): coxal endite with 0+1 simple seta; basial endite with four and seven setae on each lobe; endopod reduced, with a subterminal plumose seta; scaphognathite with 28 plumose setae.

First maxilliped (Fig. 5G): coxa and basis with three and 12 setae, respectively; endopod 3-segmented without setae; exopod 2-segmented with 4 lateral setae on outer side and one terminal, respectively.

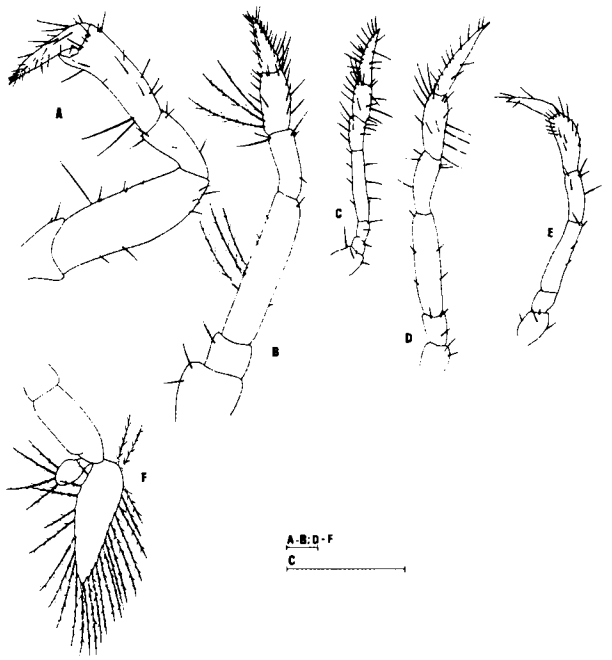

Fig. 6. *Upogebia pusilla*. Megalopa. A: first pereiopod; B: second pereiopod; C: third pereiopod; D: fourth pereiopod; E: fifth pereiopod; F: first pleopod. Scale bar: 500 µm (C); 100 µm (A,B and D–F).

Second maxilliped (Fig. 5H): coxa and basis with one and four setae, respectively; endopod 4-segmented with 3, 0, 4+1 and 0 setae, respectively; exopod 3-segmented without setae.

Third maxilliped (5I): coxa and basis with four and one setae, respectively; endopod 5-segmented with 2, 3+1, 2, 10 and 10 setae; exopod unsegmented unarmed.

First pereiopod (Fig. 6A): all segments well differentiated and setose as figured; propodus with a stout distal spine, forming subchelate shape with two inner teeth.

Two to fifth pereiopod (Fig. 6B–E): all segments well differentiated and setose as figured; propodus not subchelate.

Abdomen (Fig. 5A): Six somites; somite 1 and 6 with a pair of lateral seta, second to fifth with two pairs of lateral seta as shown.

Pleopods (Fig. 6F): Four pairs on second to fifth somites; well developed; biramous; margin of endopod and exopod with four and 24–25 long plumose setae, respectively.

Uropod (Fig. 5J): endopod with a spine, 13 plumose setae marginally and seven setae sub-marginally; exopod with a spine and five sub-marginal simple setae on the outer side and 30 plumose setae marginally.

Telson (Fig. 5J): posterior margin bearing 16 setae terminally, three sub-terminal, one lateral tooth and two pairs of setae on dorsal surface.

Discussion

Upogebia pusilla larvae have the characters typically attributed to *Upogebia* species: second telson spine represented by a very fine seta, posterio-lateral margin of carapace rounded, abdominal segments without dorso-lateral spines and, telson with a posterior margin slightly convex and with a median spine from second zoeal stage.

Besides the description by Dolgopolskaia (1954) of the zoeal and megalopal stages from plankton samples collected in the Black Sea, Heegaard (1963) has also presented a short description for the first zoeal stage of *U. pusilla* from laboratory-hatched material. These descriptions, nevertheless, are insufficient for accurate specimen identification. Regarding the description by Cano (1891) of *Gebia litoralis* Risso, which Dworschak (1988) has ascribed to *U. pusilla*, it can be said that this description differs widely from the present work. Cano (1891) describes only three zoeal stages (as two zoeae and one mysis) and one megalop (as post-larval stage), but the description shows a larva with abbreviated development as described by Rabalais and Gore (1985). The first zoeal stage of Cano's description is considerably more developed than other descriptions (present work; Heegaard, 1963; Dolgopolskaia, 1954), namely the antennule (see Plate I, Fig. 2a) that presents the development similar to the zoea II in the present work (see Fig. 2A–K). These differences permit us to agree with Williamson (1967); Cano was probably dealing with other species (most likely *U. tipica*) instead of *U. pusilla*.

Comparing the first zoeal stage and the megalop of *U. pusilla* with other larvae of *Upogebia* species, restricted to those previously described from laboratory-reared material [*U. edulis*, *U. darwini*, *U. quddusiae*, *U. major* and *U. kempi* (see Table 1 for references], *U. pusilla* has the smallest larvae (for *U. kempi* there are no available length measurements), and the largest larvae belong to *U. edulis*, which has only two larval stages. However, in all the *Upogebia* larvae, the most striking differences between the first zoeal stages are in the endopod of antenna and maxillule. *U. kempi* has the endopod of antenna 2-segmented and *U. quddusiae* has it partially 2-segmented while in all the others this appendage is unsegmented. Although the endopod of maxillule is unsegmented in *U. edulis* and *U. pusilla*, it is 3-segmented in all the others. In the

Table 1. Selected morphological features in the first zoea and megalop of *Upogebia pusilla* and co-generic species

Features	*Upogebia edulis* (Shy and Chan, 1996)	*Upogebia darwini* (Ngoc-Ho, 1977)	*Upogebia quddusiae* (Siddiqui and Tirmizi, 1995)	*Upogebia major* (Konishi, 1989)	*Upogebia pusilla* (Present work)	*Upogebia kempi* (Shenoy, 1967)
Number of stages	2 zoea+1 megalop	3 zoea+1 megalop	3 zoea+1 megalop	3 zoea+1 megalop	4 zoea+1 megalop	4 zoea+2 megalop
First zoea:						
Total length, mm	3.56	2.5–2.8	2.55–2.8	Not mentioned	2.1–2.38	Not mentioned
Carapace cervical groove	Absent	Present	Absent	Present	Absent	Absent
Antennule, long plumose seta:	Absent	Present	Present	Present	Present	Present
Antenna:						
Endopod, terminal seta	4	3	3	3	3	3
Endopod segments	Unsegmented	Unsegmented	Partially 2-segmented	Unsegmented	Unsegmented	2-segmented
Maxillule endopod	Unsegmented	3-segmented	3-segmented	3-segmented	Unsegmented	3-segmented
Maxilla, no. of scaphognatithe setae	9	8	9-12	7	10	5
First maxilliped, endopod segment (setation)	2 (without seta)	5 (3,2,1,2,5)	5 (3,2+1,1+1,2+1,4)	5 (3,2,1,2,4+1)	5 (3,2+1,1,2+1,4)	5 (2,2,1,2,5)
Second maxilliped, endopod segment (setation)	3 (without seta)	4 (2,2,2,5)	4 (2-3,3,2-3+1,4)	4 (2,2,2,4+1)	4 (2,2,2+1,4)	4 (2,2,1,4)
Third maxilliped	Fairly large biramous	Fairly large biramous	Rudiment	Rudiment	Rudiment	Rudiment
Pereiopods	Fairly large	Fairly large	Rudiments	Rudiments	Rudiments	Rudiments
Pleopods	Buds	Buds	Absent	Buds	Absent	Absent
Telson, posterior margin:						
Processes	6+6	7+7	7+7	7+7	7+7	7+7
Process 2	Spine	Very thin seta	Very thin seta	Very thin seta	Very thin seta	Very thin seta
Megalop:						
Total length, mm	3–5	3.0–3.2	2.8–3.0	Not mentioned	2.74–2.85	Not mentioned
Antennule:						
Endopod	Unsegmented	2-segmented	2-segmented	Unsegmented	Unsegmented	Unsegmented
Exopod	Unsegmented	3-segmented	3-segmented	2-segmented	2-segmented	3-segmented
Antenna, vestige of scale	Absent	Absent	Present	Absent	Absent	Present
Mandible palp	Unsegmented	3-segmented	3-segmented	3-segmented	Unsegmented	Unsegmented
Maxillule endopod	Unsegmented, unarmed	Unsegmented, unarmed	Unsegmented, unarmed	Unsegmented, unarmed	Unsegmented, unarmed	3-segmented, 8 setae
First maxilliped endopod	unsegmented	Unsegmented	Unsegmented	Unsegmented	3-segmented	5-segmented
Second maxilliped endopod	5-segmented	5-segmented	5-segmented	4-segmented	4-segmented	5-segmented
Third maxilliped, setae on endopod	Dense	Thick fringe	Thick fringe	Numerous	28	Sparse
Exopods of pereiopods:	Vestigial	Absent	Absent	Absent	Absent	Present
Pleopods, no. of setae on endopod	Numerous	6	Not mentioned	10–11	4	4–5

megalopal stage the most characteristic difference is on the antennule. The endopod of antennule is 2-segmented in *U. darwini* and *U. quddusiae*, whereas the others species have an unsegmented endopod. The exopod of antennule is unsegmented in *U. edulis*, 2-segmented in *U. major* and *U. pusilla* and 3-segmented in *U. darwini*, *U. quddusiae* and *U. kempi*. Another significant difference is the setal formula of the endopod of pleopods. While in *U. pusilla*, *U. kempi* and *U. darwini* have from four to six setae on the endopod, *U. major* has 10–11 and *U. edulis* numerous (see Table 1).

The other larvae of the genus *Upogebia* that can occur in the same study area described by Webb (1919) from plankton material are *U. deltaura*. When compared with the *U. pusilla* larvae, they are not obviously separated. *U. deltaura* has, in all zoeal stages, two setae on the endopod of the first maxilliped second segment and *U. pusilla* has one more seta on the same segment.

The number of zoeal stages of *Upogebia* species ranges from two (e.g., *U. edulis*) to four stages (e.g., *U. pusilla* and *U. kempi*). When rearing larvae with the objective of describing morphology, most authors use constant conditions such as fixed temperature and salinity. It has been shown however, that variation of these factors may induce abbreviation or expansion of the larval series [for instance *U. africana* larval series may be constituted by three or four zoeal stages according to temperature and salinity conditions (see Paula et al., 2001)]. It is not clear, at the present state of knowledge, if all these stages occur in the natural environment, or if they represent culture-induced moults. It may be that the number of stages shown by the different authors describing *Upogebia* larvae may be different in varying rearing conditions. Moreover, Strasser and Felder (2000) have shown that other factors, such as settlement cues, may affect development including number of stages in other thalassinid larvae.

Acknowledgements

The authors wish to thank to Dr. Álvaro Peliz of the IPIMAR for the Russian to Portuguese translation of the Dolgopolskaia works and to Dr. Maria Thessalou-Legaki who made these papers available.

References

Cano, G., Sviluppo postembrionale della Gebia, Axius, Callianassa e Calliaxis; morfologia dei Thalassinidi. Boll. Soc. Nat. Napoli, 5 (1891) 5–30.

Dolgopolskaia, M.A., Métamorphose des Crustacés de la mer Noire. 2. Callianassidae. Tr. Sevastopol biol. Stn., 8 (1954) 178–213.

Dolgopolskaia, M.A., Larvae of Decapoda Macrura and Anomura. In: Mordukhai-Boltovskoi, F.D. (ed.), Keys to the Fauna of Black and Azov Seas, 2 (1969) 307–362.

D'UDekem D'Acoz, C., Inventaire et distribution des crustacés décapodes de l'Atlantique nord-oriental, de la Méditerranée et des eaux continentales adjacentes au nord de 25°N. Patrimoines naturels (MNHN/SPN), 40 (1999) 1–383.

Dworschak, P.C., The Biology of *Upogebia pusilla* (Petagna) (Decapoda, Thalassinidea). III. Growth and production. Mar. Ecol., 9 (1988) 51–77.

González-Gordillo, J.I., Dos Santos, A. and Rodríguez, A., Checklist and annotated bibliography of decapod Crustacea larvae from the Southwestern European coast (Gibraltar Strait area). Sci. Mar., 65 (2001) 275–305.

Heegaard, P., Decapod larvae from the Gulf of Napoli hatched in captivity. Videnk. Medd. Fra Dank naturli. Foren., 125 (1963) 449–493.

Konishi, K., Larval development of the mud shrimp *Upogebia* (Upogebia) major (De Haan) (Crustacea: Thalassinidea: Upogebiidae) under laboratory conditions, with comments on larval characters of thalassinid families. Bull. Natl. Res. Inst. Aquaculture, 15 (1989) 1–17.

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

Paula, J., Nogueira Mendes, R., Paci, S., McLaughlin, P., Gherardi, F. and Emmerson, W., Combined effects of temperature and salinity on the larval development of the estuarine mud prawn *Upogebia africana* (Crustacea, Thalassinidea). Hydrobiologia, 449 (2001) 141–148.

Petagna, V., Institutiones entomologicae (1792) i–xii+ 1–718+pl. 1–10.

Rabalais, N.N. and Gore, R.H., Abbreviated development in decapods. Crust. Iss., Larval Growth, 2 (1985) 67–126.

Shenoy, S., Studies on larval development in *Anomura* (Crustacea, Decapoda). II. Proc. Symp. Crust., Part II (1967) 777–804.

Shy, J.-Y. and Chan, T.-Y., Complete larval development of edible mud shrimp *Upogebia edulis* Ngoc-Ho and Chan, 1992 (Decapoda, Thalassinidea, Upogebiidae) reared in the laboratory. Crustaceana, 69 (1996) 175–186.

Siddiqui, F.A. and Tirmizi, N.M., Laboratory rearing of *Upogebia quddusiae* Tirmizi and Ghani, 1978 (Decapoda, Thalassinidea) from ovigerous female to postlarva. Crustaceana, 68 (1995) 445–460.

Strasser, K.M. and Felder, D.L., Larval development of the ghost shrimp *Callichirus islagrande* (Decapoda: Thalassinidea: Callianassidae) under laboratory conditions. J. Crust. Biol., 20 (2000) 1000–1117.

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

Williamson, D.I., On a collection of planktonic Decapoda and Stomatopoda (Crustacea) from the Mediterranean coast of Israel. Bull. Sea Fish. Res. Sta. Haifa, 45 (1967) 32–64.