The complete larval development of the crab *Pilumnus spinifer* (Brachyura: Xanthoidea: Pilumnidae) reared in the laboratory

GUILLERMO GUERAO¹, PERE ABELLÒ², & DAVID DÍAZ²

¹Departament de Biologia Animal (Artròpodes), Facultat de Biologia (U.B.), Barcelona, Spain, and ²Institut de Ciències del Mar (CSIC), Barcelona, Spain

(Accepted 11 July 2005)

Abstract
The complete larval development of the crab *Pilumnus spinifer* from the western Mediterranean was obtained in the laboratory. All four zoeal stages and the megalopa are described and illustrated. The morphological characters of the larvae of *Pilumnus spinifer* are compared with those of other known larvae of the genus. The zoeae of *P. spinifer* show the rostral spine longer than the antennule (excluding aesthetascs); short lateral spines present on the carapace, and the mediolateral processes are present only in abdominal somites 2 and 3. The megalopa is similar to that of other Pilumnidae species. The morphology of the larval stages shows very similar characteristics to that of those of *P. hirtellus* and *P. dasypodus*, among the described stages of the family.

Keywords: Brachyura, Decapoda, larval development, megalopa, Pilumnidae, Pilumnus spinifer, Xanthoidea, zoea

Introduction

*Pilumnus spinifer* H. Milne Edwards, 1834 is a pilumnid crab recorded along the western coasts of Africa and Europe from Mauritania to the Bay of Biscay, including the Azores, Madeira and Canary Islands and throughout the Mediterranean Sea (Monod 1956; Zariquey-Álvarez 1968; Manning and Holthuis 1981; d’Udekem d’Acoz 1999). This species has been recorded from the shallow subtidal down to 188 m, but is most frequent between around 20 and 100 m (e.g. Relini et al. 1986; Abelló et al. 1988, 2002; Stevic 1990; d’Udekem d’Acoz 1992; Pipitone and Tumbiolo 1993). It has been recorded as a characteristic species of “coralligenous” and “detrictic” bottoms, sandy and boulder areas, sandy and seagrass bottoms, etc. (Spanò 1994; González Pérez 1995). It has often been found associated with sponges (Koukouras et al. 1985; Stevic 1990; d’Udekem d’Acoz 1992; Voultsaidou-Koukoura and Koukouras 1993; González Pérez 1995).
The taxonomy and systematics of the species of the genus Pilumnus are still problematic (d’Udekem d’Acoz 1999; Clark and Ng 2004a). Five species are usually recognized in north-eastern Atlantic and Mediterranean waters (Zariquiey-Álvarez 1968), with one or two Indo-Pacific lessepsian immigrants into the Mediterranean (d’Udekem d’Acoz 1999; Galil et al. 2002), one Indo-Pacific isolated record in the north-eastern Atlantic and one yet undescribed new species (d’Udekem d’Acoz 1999).

Within the genus Pilumnus Leach 1815, the larval development is known for P. dasypodus Kingsley, 1879, P. hirtellus (Linnaeus, 1761), P. vestitus Haswell, 1882, P. kempi Deb, 1987, P. lumperinus Bennett, 1964, P. minutus De Haan, 1835, P. novaeezalandiae Filhol, 1885, P. reticulatus Stimpson, 1860, P. sayi Rathbun, 1923, P. scabriusculus Abams and White, 1849, P. vespertilio (Fabricius, 1793), P. sluiteri De Man, 1892, and P. limosus Smith, 1869 (Lebour 1928; Hale 1931; Wear 1967; Sandifer 1974; Bookhout and Costlow 1979; Lim and Tan 1981; Salman 1982; Ingle 1983; Terada 1984, 1990; Montú et al. 1989; Siddiqui and Tirmizi 1992; Ko 1994a; Spivak and Rodríguez 2002; Clark and Paula 2003; Clark and Ng 2004a; García-Guerrero et al. 2005). The first zoetal stage is known for P. longicornis Hilgendorf, 1878 (Clark and Paula 2003). Rice and Williamson (1977) described a zoea III of the genus Pilumnus from a plankton sample which the authors considered could belong to P. inermis A. Milne-Edwards and Bouvier, 1894. The first zoetal stage of P. spinifer has been previously reported from Marseille Gulf by Gourret (1884), who figured a lateral view of this stage, plus the antennula, antenna and telson.

The present study aims to describe the morphology of the complete larval development of Pilumnus spinifer, in larvae hatched from an ovigerous female captured in the western Mediterranean, and to compare its larval features with those known for other species of Pilumnus. This constitutes the second larval development description, after that of P. hirtellus (Lebour 1928; Salman 1982; Ingle 1983) for a species of Pilumnus in north-eastern Atlantic and Mediterranean waters.

Materials and methods

A single Pilumnus spinifer ovigerous female was obtained, associated with a large soft-bodied sponge, by bottom trawling on muddy bottoms of the continental shelf off Punta Entinas (Almería) in the western Mediterranean (36°38.1′N, 2°46.9′W), from a depth of 53–58 m on 10 May 2004. Sampling was performed within the frame of the EU demersal fisheries research programme “MEDITS” on board B/O Cornide de Saavedra.

The crab was placed in a thermally insulated plastic container (60 × 35 × 30 cm) on board the ship, containing well-aerated filtered sea water, changed daily. The ovigerous crab was transferred to the laboratory on land on 24 May 2004. The incubation and larval rearing was carried out in the laboratory at a salinity of approximately 37.5 and kept at 25 ± 1°C and an artificial 12 h light: 12 h dark cycle. The larvae were fed freshly hatched nauplii of Artemia sp. Water and food were changed daily. Exuviae and specimens of each developmental stage were preserved in 70% alcohol.

A binocular microscope equipped with an ocular micrometer was used for the dissection and measurements of individuals (5–10 individuals of each larval stage were measured). A microscope was used for the determination of the setal formula and measurements of the appendages. The following measurements were taken: rostro-dorsal length (RDL) as the distance between the tips of the dorsal and rostral spines; carapace length (CL) from the base of the rostral spine to the posterolateral carapace margin; distance between the tips of the lateral spines (CW); furcal length (FL) from an imaginary line across the base of the
outer lateral spine of the telson to the furcal tip; length of the outer lateral spine of the telson (OLS); length of the outer minute lateral spine of the telson (OLM); length of the telson dorsal spine (DS). For the megalopa, carapace length (CL) was measured as the distance from the frontal margin to the posterior margin of the carapace; carapace width (CW) as the greatest distance across the carapace.

All drawings were made with the aid of a camera lucida and microscope photography. The long aesthetasc of the antennules and the long plumose setae on the distal exopod of the maxillipeds and pleopods are not fully illustrated and are drawn truncated instead. Larval descriptions followed the basic malacostracan body pattern, and setal armature on appendages is described from proximal to distal segments and from endopod to exopod according to Clark et al. (1998). When the type of seta is stated, terminology has followed Ingle (1992) and Garm (2004).

The female from which these larvae hatched plus samples of all larval stages have been deposited in the Biological Collections of Reference of the Institut de Ciències del Mar (CSIC) in Barcelona (codes: ICMD 2/2005 for the female; ICMD 3–6/2005 for the zoeal stages; ICMD 7/2005 for the megalopae).

Results

The larval development of *Pilumnus spinifer* consisted of four zoeal stages and one megalopa. The development through the zoea I stage lasted (mean ± SD; initial n = 100) 4 ± 0.8 days, the zoea II stage took 3.9 ± 1.1 days, the zoea III 4.1 ± 0.9 days, and the zoea IV 4.2 ± 0.8 days. The first zoeal stage is described in detail, while in subsequent stages only differences and changes are described.

Description

*Pilumnus spinifer* H. Milne Edwards, 1834

(Figures 1–17)

Gourret 1884, p. 17, Plate 2, Figures 8–11, zoea I.

**First zoea**

*Size.* RDL: 0.87–0.90 mm; CL: 0.50–0.55 mm; CW: 0.50–0.57 mm.

*Carapace (Figure 1A, B).* Globose, smooth, without tubercles. Dorsal spine present, well-developed, markedly curved posteriorly, with sparsely minute protuberances (Figure 1A1). Rostral spine smooth, thin and shorter than dorsal spine, longer than antennule (excluded aesthetasc) and shorter than antenna (Figure 1B). A single thin and short lateral spine. A pair of simple setae on posterodorsal region. Posterior and ventral margin without setae. Posterolateral margin of carapace with numerous acute small spines (Figure 1A2). Eyes sessile.

*Antennule (Figure 3A).* Uniramous. Endopod absent. Exopod unsegmented with four terminal aesthetasc and one terminal minute seta.

*Antenna (Figure 4A).* Longer than rostral spine. Protopodal process and exopod approximately equal in length. Protopodal process with two rows of spines of different
Figure 1. *Pilumnus spinifer* H. Milne Edwards, 1834. Zoea I: (A) carapace, lateral view; (A₁) detail of the dorsal spine; (A₂) detail of the posterior-ventral margin of the carapace; (B) carapace, frontal view. Zoea II: (C) carapace, lateral view. Zoea III: (D) carapace, lateral view. Scale bars: 0.2 mm.
size along distal half. Exopod unsegmented with one long and one smaller seta arising near mid-length and two rows of spines of different size along distal half. Endopod absent.

*Mandible.* Incisor and molar processes differentiated. Endopod palp absent.

Figure 2. *Pilumnus spinifer* H. Milne Edwards, 1834. Zoea IV: (A) carapace, lateral view; (B) carapace, frontal view. Megalopa: (C) carapace, dorsal view; (D) carapace, lateral view. Scale bars: 0.2 mm.
Figure 3. *Pilumnus spinifer* H. Milne Edwards, 1834. Antennule: (A) zoea I; (B) zoea II; (C) zoea III; (D) zoea IV; (E) megalopa. Scale bars: 0.1 mm.
Figure 4. *Pilumnus spinifer* H. Milne Edwards, 1834. Antenna: (A) zoea I; (B) zoea II; (C) zoea III; (D) zoea IV; (E) megalopa. Scale bars: 0.1 mm.
Maxillule (Figure 6A). Exopod and epipod seta absent. Coxal endite with seven setae. Basial endite with five setae. Endopod two-segmented, with one seta on proximal segment and six setae on distal segment (arranged as 2+2+2).

Maxilla (Figure 7A). Coxal endite bilobed, with 5+4 setae. Basial endite bilobed with 5+4 setae. Endopod unsegmented, bilobed, with three long setae on proximal and five (two subterminal and three terminal) on distal lobe. Scaphognathite (exopod) with four plumose marginal setae and a long distal stout process.

First maxilliped (Figure 9A). Coxa without seta. Basis with 10 medial setae arranged 2+2+3+3 on inner side. Endopod five-segmented, with 3, 2, 1, 2, 5 (one subterminal and four terminal) setae. Exopod two-segmented; distal segment with four long plumose natatory setae.

Second maxilliped (Figure 10A). Coxa without setae. Basis with four medial setae arranged 1+1+1+1. Endopod three-segmented, with 1, 1, 6 setae. Exopod two-segmented; distal segment with four long plumose natatory setae.

Third maxilliped. Present as bilobed small bud.

First pereiopod. Present as small bud.

Abdomen (Figures 14A, B, 15A). Five somites. Somites 2 and 3 with one pair of dorsolateral processes. Dorsolateral process on somite 2 stout and blunt, with tip directed anteriorly; process on somite 3 sharp, with posteriorly pointed tip, with relative size decreasing throughout the stages. Somites 3–5 with short posterolateral processes. Somites 2–5 with one pair of posterodorsal simple setae. Posterior margin of somites 2–5 spinulate.

Pleopods. Pleopod buds absent.

Telson (Figures 14A, C, 15A). With two lateral spines (one large and one very small), and one dorsomedial spine. Furca large, with a medial V-shaped cleft on posterior margin; with three pairs of serrate setae on posterior margin. Furca and large lateral spine strongly spinulated. F/OLS=3.3; F/DS=6.8; F/OLM=18.8.
Figure 6. *Pilumnus spinifer* H. Milne Edwards, 1834. Maxillule: (A) zoea I; (B) zoea II; (C) zoea III; (D) zoea IV; (E) megalopa. Scale bars: 0.05 mm.
Second zoea

Size. RDL: 1.05–1.07 mm; CL: 0.67–0.7 mm; CW: 0.62–0.65 mm.

Carapace (Figure 1C). Two pairs of anterodorsal setae. Each lateroventral margin with three setae. Eyes stalked.

Antennule (Figure 3B). Exopod with five aesthetascs and one minute seta.
Antenna (Figure 4B). Endopod bud present.

Mandible. Unchanged.

Maxillule (Figure 6B). Basial endite with eight \((1 + 7)\) setae. Exopod plumose seta and epipod seta present.

Maxilla (Figure 7B). Basial endite with \(6 + 5\) setae. Scaphognathite with 10–11 plumose marginal setae, and without the long setose posterior process present in zoea I.

First maxilliped. Exopod distal segment with six long plumose natatory setae.

Second maxilliped. Exopod distal segment with six long plumose natatory setae.

Third maxilliped. Biramous.

Pereiopods (Figure 12A). All present, unsegmented. First pereiopod distally bilobed.

Abdomen (Figures 14D, 15B). First somite with two long mid-dorsal setae.

Pleopods. Absent.
Telson (Figures 14D, 15B). $F/OLS = 3.1$; $F/DS = 9.7$; $F/OLM = 46.5$.

Third zoea

Size. RDL: 1.25–1.30 mm; CL: 0.75–0.76 mm; CW: 0.70–0.72 mm.

Carapace (Figure 1D). Two pairs of anterodorsal setae. Dorsal spine with two pairs of setae. Each lateroventral margin with six setae.

Antennule (Figure 3C). Small endopod bud present. Exopod with one additional subterminal aesthetasc.

Antenna (Figure 4C). Endopod bud elongated, approximately half the length of exopod.

Mandible. Unchanged.

Maxillule (Figure 6C). Basial endite with nine ($1 + 8$) setae.

Maxilla (Figure 7C). Basial endite with $6 + 6$ setae. Scaphognathite with 18 plumose marginal setae.
First maxilliped (Figure 9B). Endopod distal segment with six setae. Exopod distal segment with eight long plumose natatory setae.

Second maxilliped. Exopod distal segment with eight long plumose natatory setae.

Third maxilliped (Figure 11A). Biramous, unsegmented; epipod present, rudimentary.

Pereiopods (Figure 12B). Unsegmented. Chelipeds bilobed, extending beneath carapace.

Abdomen (Figures 14E, 15C). Somite 6 now present, without setae. First somite with four dorsomedial setae and one medial posterodorsal seta.

Pleopods (Figure 15C). Present as buds on somites 2–5, endopods absent.

Telson (Figures 14E, 15C). F/OLS=2.8; F/DS=12.5; F/OLM=53.5.
Fourth zoea

Size. RDL: 1.45–1.47 mm; CL: 0.87–0.90 mm; CW: 0.80–0.82 mm.

Carapace (Figure 2A, B). Three pairs of anterodorsal setae. Dorsal spine with three pairs of setae. Each lateroventral margin with nine setae.

Antennule (Figure 3D). Biramous, endopod bud developed without setae. Exopod with proximal minute seta, and five (1 + 4) subterminal and five terminal aesthetascs.

Antenna (Figure 4D). Endopod approximately three-quarters length of exopod, extending beyond the exopod setae.
Mandible (Figure 5A). Palp bud present.

Maxillule (Figure 6D). Coxal endite with eight to nine setae. Basial endite with 10–11 setae.

Maxilla (Figure 7D). Scaphognathite with 21–22 plumose marginal setae.

First maxilliped. Exopod distal segment with 10 long plumose natatory setae.

Second maxilliped (Figure 10B). Exopod distal segment with 10 long plumose natatory setae.

Third maxilliped (Figure 11B). Endopod and exopod slightly segmented.

Pereiopods (Figure 12C). Incipient segmentation.

Abdomen (Figures 14F, 16A). Unchanged.
Pleopods (Figure 16A). Pleopod buds elongated, endopods present.

Telson (Figures 14F, G, 16A). With two dorsal setae. F/OLS = 2.8; F/DS = 14.2; F/OLM = 64.
Figure 14. *Pilumnus spinifer* H. Milne Edwards, 1834. Abdomen, dorsal view: (A) zoea I; (B) zoea I, enlarged details of the somites 2–5; (C) zoea I, detail of the furca; (D) zoea II; (E) zoea III; (F) zoea IV; (G) zoea IV, detail of the furca; (H) megalopa. Scale bars: 0.1 mm.
Figure 15. *Pilumnus spinifer* H. Milne Edwards, 1834. Abdomen, lateral view: (A) zoea I; (B) zoea II; (C) zoea III. Scale bars: 0.1 mm.
Figure 16. *Pilumnus spinifer* H. Milne Edwards, 1834. Abdomen, lateral view: (A) zoea IV; (B) megalopa. Scale bars: 0.1 mm.
Megalopa

Size. CL: 1.20–1.25 mm; CW: 0.85–0.87 mm.

Carapace (Figure 2C, D). Longer than broad. Rostrum deflected obliquely downwards; frontal region moderately broadened with margins expanded and slightly acute. Without spines or tubercles. Setal arrangement as figured.

Antennule (Figure 3E). Peduncle three-segmented, with 4, 2, 0 setae, respectively. Endopod unsegmented with two subterminal and four terminal setae. Exopod four-segmented, with 0, 6–7, 6, 4 aesthetascs and 0, 0, 3, 2 (one subterminal and one terminal) setae.

Antenna (Figure 4E). Peduncle three-segmented, with 2, 1, 1–2 setae. Flagellum seven-segmented, with 0, 0, 0, 5, 0, 3, 4 setae.

Mandible (Figure 5B). Palp two-segmented, with seven setae on distal segment.

Maxillule (Figure 6E). Coxal endite with 14 setae. Basial endite with 18 (16+2) setae. Endopod three-segmented, with 1, 1, 3 setae.

Maxilla (Figure 8). Coxal endite bilobed, with 8+4 setae. Basial endite bilobed with 7+7–8 setae. Endopod unsegmented, with two setae on outer basal margin. Scaphognathite with 38–39 plumose marginal setae and four lateral setae.

First maxilliped (Figure 9C). Epipod with five long setae. Coxal endite with seven to eight setae. Basial endite with 14 setae. Endopod unsegmented with two subterminal and two

Figure 17. *Pilumnus spinifer* H. Milne Edwards, 1834. Megalopa: (A) pleopod 1; (B) pleopod 4; (C) uropod. Scale bars: 0.1 mm.
terminal setae. Exopod three-segmented, proximal segment with two distal setae, distal segment with five long terminal plumose setae.

Second maxilliped (Figure 10C). Epipod rudimentary. Coxa and basis not differentiated, with one seta. Endopod four-segmented with 2, 1–2, 5, 7 setae. Exopod three-segmented; proximal segment with one medial seta, distal segment with five terminal plumose setae.

Third maxilliped (Figure 11C). Epipod with 13 setae (five pappose setae + eight long simple setae). Coxa with 14 setae. Basis with four setae. Endopod five-segmented, with 12–14, 10, 6, 10, 6 setae. Exopod two-segmented; proximal segment with one seta and distal segment with three to four long terminal plumose setae.

Pereiopods (Figure 13A–H). All articles well differentiated. Pereiopod 1 (cheliped) without coxal spine, with two ischial spines (one minute) and one meral spine (Figure 13A); pereiopods 2–3 with one coxal and one ischial spine (Figure 13 B, C); pereiopod 4 with one coxal spine (Figure 13D). Dactylus of pereiopods 2–4 with three strong serrated spines (Figure 13B–D, F, G) on inner margin. Dactylus of pereiopod 5 with two long subterminal setae of different size (Figure 13H). Setation as figured.

Sternum (Figure 13I). Maxillipeds and cheliped sternites fused with six setae plus one pair of small processes. All sternal sutures are interrupted medially.

Abdomen (Figures 14H, 16B). Six somites present; somite 1 with 12 setae; somite 2 with 10 setae; somites 3 and 4 with 12 setae; somite 5 with 14 setae; somite 6 with four setae. Posterolateral processes of somites 3–5 acute; processes of somite 5 overlapping with somite 6.

Pleopods (Figure 17A, B). Somites 2–5 each with one pair of biramous pleopods. Endopod unsegmented with 3, 2, 2, 2 subterminal hooks on internal margin; exopod unsegmented with 13, 13, 12, 10 long marginal plumose natatory setae, respectively, for each pair of pleopods.

Uropods (Figure 17C). Uropods two-segmented on somite 6, proximal segment with one, and distal segment with six long plumose setae.

Telson (Figures 14H, 16B). Posterior margin rounded, with two dorsal and two ventral setae.

Discussion

The zoeal morphology of the species of the family Pilumnidae is more variable than in other Xanthoidea families (Rice 1980; Ko 1994a, 1994b, 1995; Clark and Ng 2004a). Characters that are usually not very variable within a family show in the Pilumnidae a great variability between genera and even within species of the same genus, such as number of zoeal stages (zero to four), presence or absence of the carapace lateral spines, presence or absence of the dorsolateral abdominal processes on somites 4–5, and length of the carapace rostral spine (long, short, or vestigial) (Lim and Tam 1981; Martin 1984; Ko 1994a, 1994b, 1995; Spivak and Rodriguez 2002; Ko and Yang 2003). This has given rise to the
consideration that a revision of the genus *Pilumnus* is necessary, since based on larval characteristics, such as number of zoeal stages, among others, there appear to be reasons to reassign species to different, new genera (Clark and Ng 2004a).

The main characteristics present in all the described zoeae of the family Pilumnidae are: (1) the exopod of the antenna is more or less equal in length to the spinous process of the protopod; it is distally bilaterally spinulated with one long and one smaller seta arising near mid-length; (2) the endopod of the maxillule always bears 1, 6 setae; and (3) telson with three pairs of spines. Additionally, some rather constant characteristics are: (4) the endopod of the maxilla with eight setae (*Pilumnopeus makiana*); (5) setation of endopod of first maxilliped is 3, 2, 1, 2, 5 in zoea 1 (3, 2, 1, 2, 6 in *Benthopanope eucratoides* (Stimpson, 1858) (Rice 1980; Martin 1984; Ko 1994a, 1994b, 1997; Ko and Yang 2003; Clark and Paula 2003).

Ko (1994b, 1997) assigned the Pilumnidae zoeae to five groups based on the characteristics of the carapace spines and abdominal dorsolateral processes: (1) the genus *Heteropanope*, (2) *Heteropilumnus* and *Pilumnopeus*, (3) *Actumnus* and *Pilumnus*, (4) *Parapilumnus*, and (5) *Benthopanope* (see Ko 1994b; Ko and Yang 2003). The group 3 species (*Pilumnus* and *Actumnus*) share the following characteristics: (1) carapace with lateral spines; (2) carapace with curved (hook-like or slightly) dorsal spine; (3) a 0, 1, 6 setation of the second maxilliped endopod, and (4) rostral spine between 0.5 and 2.0 times the length of antennula, excluding aesthetascs (Sandifer 1974; Ko 1994b, 1997; Spivak and Rodriguez 2002). The zoeal morphology of *Pilumnus spinifer* herein described completely fits the characteristics of Ko’s group 3.

Table I compares the morphological and meristic characters that may differ between the different larval stages of the known larval stages described for the species of the genus *Pilumnus*. Unfortunately, some of the descriptions do not show the sufficient level of detail or accuracy to compare with total reliability all the necessary characters, and therefore some of these characters, such as the setation of the zoeal carapace which sometimes is present in the figures but not in the descriptive text, are not shown in Table I. The zoeal morphology of *P. sayi* is similar to that of *P. dasypodus*, but is somewhat confused and therefore the characters of this species are not shown in the table; however an important difference has been described for the zoeae of these species: a pair of dorsolateral spines is present on abdominal segments 4 and 5 in the zoeal stages of *P. sayi*, which are absent in the zoeal stages of *P. dasypodus* (Bookhout and Costlow 1979).

The zoeae of *Pilumnus spinifer* resemble those of *P. hirtellus, P. dasypodus, P. scabriusculus*, and *P. limosus* by having four zoeal stages and by showing mediolateral processes only on abdominal somites 2–3 (Table I). The zoeae of *P. reticulatus, P. minutus*, and *P. sayi* can be clearly differentiated from those of *P. spinifer* by presenting mediolateral processes on abdominal somites 2–5 (Table I). *Pilumnus minutus* and *P. vespertilio* can be well differentiated from *P. spinifer* by the reduced length of the rostral spine, which is shorter than the antennule (Lim and Tan 1981; Ko 1994a, 1994b, 1997; Spivak and Rodriguez 2002).

Some of the variability reported in some zoeal characteristics may not be so since recent descriptions have shown that some characters may have been overlooked due to observation difficulties. Thus, Lim and Tan (1981) did not observe the occurrence of the minute lateral spines on the base of the telson of *P. vespertilio*, which were however observed by both Terada (1990) and Clark and Paula (2003), and showed the occurrence of nine setae on the basis and of two setae on the first endopod segment of the first maxilliped. The works of Terada (1990) and Clark and Paula (2003) showed in this species
| Table I. Morphological differences among described zoeal stages of the genus *Pilumnus*. |
|---------------------------------------------------------------|
| *Pilumnus spinifer*   | *Pilumnus hirtellus* | *Pilumnus reticulatus* | *Pilumnus minutus* | *Pilumnus dasyopus* | *Pilumnus scabriusculus* | *Pilumnus limosus* | *Pilumnus vespertilio* | *Pilumnus sluteri* | *Pilumnus kempi* | *Pilumnus longicomis* |
| Number of stages | 4 | 4 | 4 | 4 | 4 | 4 | 3 | 2 | 2 | 2 | nd |
| Zoea I |
| RDL (mm) | 0.9 | 1.5 (1.2)<sup>b</sup> | 1.02 | 0.71 | 1.2<sup>c</sup> | 0.77 | 0.91 | 1.78 (0.98)<sup>d</sup> | nd | nd | nd |
| Carapace |
| Anterodorsal s | 0 | 0 | 0 | 0 | 0 | nd | 2 | 0 | 2 | nd | 0 |
| S on ventral margin | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1<sup>f</sup> | 0 |
| Antennule (a, s) | 4, 1 | 4, 2 | 4, 1 | 3, 3 | 4, 1 | nd | 4, 1 | 3, 2 (4, 2)<sup>e</sup> | 5, 2 | 7, 1 | 4, 2 |
| Endopod | Absent | Absent | Absent | Absent | Absent | Absent | Absent | Present<sup>d</sup> | Present | Present | Absent |
| Maxilla |
| S on coxal end. | 5+4 | 5+4 (4+4)<sup>b</sup> | 5+4 | 6+4 | 5+4 | 6+4 | 5+4 | 4+3 (6+4)<sup>e</sup> | 6+4 | 5+4 | 6+4 |
| S on basial end. | 5+4 | 5+4 | 5+4 | 5+4 | 5+4 | 5+4 | 5+4 | 6+4 | 5+4 | 5+4 | 5+4 |
| Maxilliped I |
| S on basis | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 9 (10)<sup>d,e</sup> | 10 | 11 (10)<sup>f</sup> | 10 |
| S on end. | 3, 2, 1, 2, 5 | 3, 2, 1, 2, 5 | 3, 2, 1 | 3, 2, 1 | 3, 2, 1, 2, 5 | 3, 2, 1 | 3, 2, 1, 2, 5 | 3, 2, 1 | 3, 2, 1, 2, 5 | 3, 2, 1 | 2nd–3rd |
| Pleon |
| Dorsomedial s (so1) | 0 | 0 | 0 | 0 | nd | 2 | 0 | 0 | 1 | 0<sup>f</sup> | 0 |
| Posteroberodorsal s (so1) | 0 | 0 | 0 | 0 | nd | 0 | 0 | 0 | 1 | 0<sup>f</sup> | 0 |
| Lateral processes<sup>g</sup> | 2nd–3rd | 2nd–3rd | 2nd–5th | 2nd–5th | 2nd–3rd | 2nd–3rd | 2nd–3rd | 2nd–3rd | 2nd–5th | 2nd–3rd | 2nd–3rd |
| Zoea II |
| RDL (mm) | 1.06 | 1.7 (1.3)<sup>b</sup> | 1.16 | 0.86 | 1.33<sup>c</sup> | 0.85 | 1.11 | 2.42 (1.02)<sup>d</sup> | nd | nd | nd |
| Carapace |
| Anterodorsal s | 4 | 4 | 4 | nd | nd | nd | 4 | nd | 4 | 4<sup>f</sup> | nd |
| S on ventral margin | 3 | 2<sup>b</sup> | 2 | 2 | nd | nd | 2 | nd | 8 | 12<sup>f</sup> | nd |
| Antennule (a, s) | 5, 1 | 5, 1 | 6, 1 | 4, 2 | 4, 1 (4, 3)<sup>c</sup> | 4, 2 | 6, 1 | 4, 1–2 | 14, 3 | 10 (11)<sup>f</sup> | nd |
| Proximal s | Absent | Absent | Absent | Absent | Absent | Absent | Absent | Absent | Present | Present<sup>f</sup> | nd |
| Maxillule |
| S on coxal end. | 7 | 7 | 7 | 7 | 7 | 7 | 9 | 9 | nd | 9 | 9 |
| S on basial end. | 8 | 8 (7)<sup>b</sup> | 8 | 8 | 10 | 8 | 8 | 10 (9)<sup>d</sup> | 9 | 9 | nd |
|                     | Pilumnus spinifer | Pilumnus hirtellus | Pilumnus reticulatus | Pilumnus minutus | Pilumnus dasypodus | Pilumnus scabriasculus | Pilumnus limosus | Pilumnus spectabilis | Pilumnus sluiteri | Pilumnus kempi | Pilumnus longicomis |
|---------------------|------------------|-------------------|---------------------|-----------------|------------------|------------------------|----------------|---------------------|------------------|----------------|---------------------|
| **Epipod seta**     |                  |                   |                     |                 |                  |                        |                |                     |                  |                |
| Maxilla             | Present          | nd                | Absent              | Present         | Present          | Absent                 | nd             | Absent              | Present          | nd             | Present             |
| **S on coxal end.** | 5 + 4            | 5 + 4             | 5 + 4              | 6 + 4           | 5 + 4            | 6 + 4                  | 5 + 4          | 6 + 4               | 6 + 4            | 6 + 4          |
| **S on scaphognath.** | 11               | 10–11             | 10                 | 11              | 11–12            | 11                     | 9              | 14 (12–15)d         | 19               | 23             |
| **Pleon**           |                  |                   |                     |                 |                  |                        |                |                     |                  |                |
| Dorsomedial s (so1) | 2                | 2 (1)a            | 1                  | 1               | nd               | 2                      | 1             | nd                  | 3               | 5f             |
| Posterodorsal s (so1) | 0               | 0                 | 0                  | 0               | nd               | 0                      | 0             | nd                  | 1               | 1f             |
| **Zoea III**        |                  |                   |                     |                 |                  |                        |                |                     |                  |                |
| RDL (mm)            | 1.25–1.30        | 2.1 (1.6)b        | 1.44               | 1.0             | 1.74c            | 0.9                    | 1.42           | 2.53                |                  |                |
| Carapace            |                  |                   |                     |                 |                  |                        |                |                     |                  |                |
| **S on dorsal spine** | Present       | Present           | Absent             | Absent          | Absent           | nd                     | Absent        | Absent              | Absent           |                |
| **S on ventral margin** | 6               | 6b                | 6                  | 3               | nd               | 6                      | nd            |                     | nd               |                |
| Antennule (a, s)    | 6                | 6, 1              | 7, 1               | 4, 1            | 5, 2             | nd                     | 8, 1          | 8, 1                |                  |                |
| Maxillule           |                  |                   |                     |                 |                  |                        |                |                     |                  |                |
| **S on coxal end.** | 5 + 4            | 5 + 4             | 5 + 4              | 6 + 4           | 5 + 4            | 6 + 4                  | 5 + 4          | 6 + 4               | 6 + 4            |
| **S on scaphognath.** | 18              | 17–18             | 19–20              | 19              | 18–20            | 19–20                  | 19            | 20 (22–23)d         |                  |                |
| Maxilliped 1        |                  |                   |                     |                 |                  |                        |                |                     |                  |                |
| **S on endopod**    | 3, 2, 1,         | 3, 2, 1,          | 3, 2, 1,           | 3, 2, 1,        | 3, 2, 1,         | nd                     | 3, 2, 1,       | 2 (3)d, 2         | nd               |                |
| **Pleon**           |                  |                   |                     |                 |                  |                        |                |                     |                  |                |
| Dorsomedial s (so1) | 4                | 4 (2)a            | 3                  | 3               | 4                | 2                      | 3             | 3                   |                  |                |
| Posterodorsal s (so1) | 1               | 1                 | 0                  | 0               | 0                | 0                      | 0             | 1                   |                  |                |
| **Telson**          |                  |                   |                     |                 |                  |                        |                |                     |                  |                |
| **S on posterior margin** | 6               | 6                 | 6                  | 6               | 6                | 6                      | 6             | 8                   |                  |                |
Table I. (Continued).

|         | Pilumnus spinifer | Pilumnus hirtellus | Pilumnus reticulatus | Pilumnus minutus | Pilumnus dasypodus | Pilumnus scabriusculus | Pilumnus limosus | Pilumnus vespertilio | Pilumnus sluiteri | Pilumnus kempi | Pilumnus longicornis |
|---------|-------------------|--------------------|----------------------|-----------------|-------------------|-----------------------|------------------|---------------------|-------------------|-----------------|----------------------|
| Zoa IV  |                   |                    |                      |                 |                   |                       |                  |                     |                   |                 |                      |
| RDL (mm)| 1.45–1.47         | 2.7 (1.7)          | 1.48                 | 1.18            | 2.09c             | 1.18                  | 1.46             | Not present         | Not present       | Not present | nd                   |
| Carapace| Present           | Present            | Absent               | Absent          | Present           | nd                    | Absent           | nd                  |                   |                 | nd                   |
| S on dorsal spine | Present       | Present (Absent)b | Absent               | Absent          | Present           | nd                    | Absent           | nd                  |                   |                 | nd                   |
| S on ventral margin | 9            | 9b                 | 11                   | nd              | nd                | nd                    | 9                |                     |                   |                 | nd                   |
| Antennule (a, s) | 10–11, 1       | 12–13              | 9, 1                 | 9, 1            | 10–11             | nd                    | 12, 2            |                     |                   |                 | nd                   |
| Maxillule|                   |                    |                      |                 |                   |                       |                  |                     |                   |                 | nd                   |
| S on coxal end. | 8–9            | 7–8                | 8                    | 7               | 9–10 (8)c         | 8                    | 8                |                     |                   |                 | nd                   |
| S on basial end. | 10             | 10–12              | 10                   | 11              | 10                | 10–11                 | 10              |                     |                   |                 | nd                   |
| Maxilla |                   |                    |                      |                 |                   |                       |                  |                     |                   |                 | nd                   |
| S on coxal end. | 5 + 4          | (6)b               | 5 + 4                | 6 + 4           | 5 + 4 (6 + 4)c     | 6 + 4                 | 5 + 5            |                     |                   |                 | nd                   |
| S on basial end. | 6–7 + 6       | 6 + 6              | 6 + 6                | 6 + 6           | 6–7 + 6           | 5–6 + 5–6            | 6 + 6            |                     |                   |                 | nd                   |
| S on scaphog. | 21–22          | 21–25              | 25–27                | 21              | 26–28             | 23–26                 | 21              |                     |                   |                 | nd                   |
| Pleon   |                   |                    |                      |                 |                   |                       |                  |                     |                   |                 | nd                   |
| Dorsomedial s (s01) | 4              | 4                  | 4                    | 4               | 4                 | 2                    | 4               |                     |                   |                 | nd                   |
| Posterodorsal s (s01) | 1              | 1                  | 0                    | 0               | 1                 | 0                    | 0               |                     |                   |                 | nd                   |

a, aesthetasc; end., endopod; nd, not described; s/S, setae; scaphog., scaphognathite; so, somite; Sp, spine.

References: Pilumnus spinifer, this study; Pilumnus hirtellus, Salmon 1982, Ingle 1983b, Ingle 1992b; Pilumnus reticulatus, Spivak and Rodrı´guez 2002; Pilumnus minutus, Ko 1994a; Pilumnus dasypodus, Sandifer 1974, Bookhout and Costlow 1979c; Pilumnus scabriusculus, Terada 1990; Pilumnus limosus, Garcia-Guerrero et al. 2005; Pilumnus vespertilio, Lim and Tam 1981, Terada 1990d, Clark and Paula 2003e; Pilumnus sluiteri, Clark and Ng 2004a, Pilumnus kempi, Siddiqui and Tirmizi 1992, Clark and Ng 2004a; Pilumnus longicornis, Clark and Paula 2003. *In all zoal stages.
the characteristic setation of the genus (10 and three setae, respectively). Additionally, in the original description of \textit{P. kempi}, a species with abbreviated development, the zoea 1 shows 11 setae on the basis of the first maxilliped; however, the figure corresponding to zoea 2 showed 10 setae. The recent redescription of \textit{P. kempi} by Clark and Ng (2004a) shows 10 setae in the two zoeal stages.

Spivak and Rodriguez (2002) mention that the presence of the posteromarginal minute spines on abdominal somites 2 to 5–6 may be important in the identification of \textit{Pilumnus} zoeae (according to these authors, present only in \textit{P. reticulatus}, \textit{P. kempi}, and \textit{P. hirtellus}). However, it is probable that this character may be present in all the species of the genus. This character has been described in \textit{P. hirtellus}, \textit{P. reticulatus}, \textit{P. kempi}, \textit{P. dasypodus}, \textit{P. spinifer}, \textit{P. longicornis}, \textit{P. sluieri}, and \textit{P. limosus} (Sandifer 1974; Salman 1982; Siddiqui and Tirmizi 1992; Spivak and Rodriguez 2002; Clark and Paula 2003; Clark and Ng 2004a; Garcia-Guerrero et al. 2005). In \textit{P. minutus}, it is not reported in the text, but it is clearly present in the figures (see Ko 1994a, Figures 1I, 2F, 3G). In \textit{P. vespertilio} and \textit{P. sayi} it is not described by Lim and Tan (1981) but Clark and Paula (2003) reported the occurrence of this character in the zoea 1 of \textit{P. vespertilio}. Additionally, this character also occurs in other genera of the family Pilumnidae, such as in \textit{Parapilumnus trispinosus} Sakai, 1965, \textit{Benthopanope indica} (De Man, 1887), \textit{Pilumnopeus granulatus} Balss, 1933, \textit{Eurycarcinus natalensis} (Krauss, 1843), and \textit{Actumnus setifer} (De Haan, 1835) (Ko 1994b, 1995, 1997; Clark and Paula 2003; Clark and Ng 2004b).

Several other differences among \textit{Pilumnus} zoeae were observed regarding the setation formulae (Table I). In general, differences in setation are small, except for \textit{P. vespertilio}, \textit{P. kempi}, and \textit{P. sluieri} which present an abbreviated larval development (three, two and two zoecal stages, respectively; see discussion by Clark and Ng 2004a). The heterochronic processes linked to the reduction of stages need to be taken into account when comparing the morphology of stages among species with different numbers of larval stages.

Concerning the megalopae, there is no single character or group of characters that can be used to clearly differentiate \textit{Pilumnus} megalopae from those of other Pilumnidae genera. The megalopal morphology of the known species of the genus \textit{Pilumnus} is similar (see Table II), except for \textit{P. novaezealandiae} and \textit{P. lumpinus}, which have not been included in Table II since most of the setation reported in these species is figured but not specifically described in the text. However, the larval development of these species is abbreviated: the megalopa hatches directly from the egg and the carapace and appendices show important differences from the rest of species shown in Table II (Wear 1967; Martin 1988).

In the north-eastern Atlantic and Mediterranean waters, the zoeal morphology of species of the genus \textit{Pilumnus} is only known for \textit{P. hirtellus} (Salman 1982; Ingle 1983, 1992) and \textit{P. spinifer}, but at least five species are recognized to occur in this biogeographical area (Zariquiey-Alvarez 1968; d’Udekem d’Acoz 1999). The only useful characteristics to distinguish the zoeae of \textit{P. spinifer} from those of \textit{P. hirtellus} is the length of the rostral spine. The rostral spine of \textit{P. spinifer} does not clearly reach the aesthetascs and the ratio length of rostral spine/length of antennule (excluding aesthetascs) is approximately 1.6–1.7. The rostral spine of \textit{P. hirtellus} clearly surpasses the aesthetascs and the ratio reaches values of around 2.0. Also, rostro-dorsal length (RDL) is greater in \textit{P. hirtellus} than in \textit{P. spinifer} (see Table I).

A character that may be useful to differentiate the megalopae of some species is the armature of the pereiopods. This feature is very similar in the megalopae of \textit{P. hirtellus} and \textit{P. spinifer}. \textit{Pilumnus hirtellus} has a spine on the ischium and merus of the first pereiopod, a spine on the ischium of the second and third pereiopods, and a spine on the coxa of the second, third and fourth pereiopods. \textit{Pilumnus spinifer} presents an additional minute spine
Table II. Morphological differences among described megalopae of the genus *Pilumnus*.

|                  | *Pilumnus spinifer* | *Pilumnus hirtellus* | *Pilumnus reticulatus* | *Pilumnus minutus* | *Pilumnus dasypodus* | *Pilumnus limorus* | *Pilumnus vespertilio* | *Pilumnus sluiteri* | *Pilumnus kempi* |
|------------------|---------------------|-----------------------|------------------------|-------------------|----------------------|---------------------|-----------------------|-------------------|-----------------|
| **CL (mm)**      | 1.2–1.25            | 1.3                   | 1.05                   | 1.11              | 1.03                 | 1.01                | 0.94                  | 1.3               | nd              |
| **CW (mm)**      | 0.85–0.87           | nd                    | 0.88                   | 0.91              | 0.88                 | 0.83                | 0.79                  | 1.2               | nd              |
| **Antennule**    |                     |                       |                        |                   |                      |                     |                       |                   |                 |
| S on peduncle    | 4, 2, 0             | 4, 1, 0               | 3, 2, 0                | 0, 1, 0           | 0, 1, 1              | 2, 3, 0             | 0, 1, 0               | 1, 2, 1           | 0, 0, 0         |
| A on exopod      | 0, 6–7, 6, 4        | 0, 6, 7, 4            | 0, 6, 4, 4             | 18                | 0, 8, 6, 4           | 0, 6, 6, 4          | 0, 3, 3, 3            | 0, 8, 7, 4        | 12              |
| S on exopod      | 0, 0, 3, 2          | 0, 0, 3, 2            | 0, 0, 3, 2             | 3                 | 0, 0, 3, 3           | 0, 0, 2, 2          | 0, 0, 0, 2            | 0, 0, 2, 2        | 0, 0, 1, 2      |
| S on end         | 2+4                 | 2+4                   | 2+4                    | 2+4               | 2+4                 | 2+4                 | 1+4                   | 2+4               | 2+3             |
| **Antenna**      |                     |                       |                        |                   |                      |                     |                       |                   |                 |
| S on peduncle    | 2, 1, 1–2           | 2, 1, 1               | 2, 1, 1                | 2, 1, 1           | 2, 1, 1              | 2, 1, 1             | 2, 1, 1               | 2, 1, 1           | 1, 1, 1          |
| S on flagellum   | 0, 0, 0, 5          | 0, 0, 0, 4            | 0, 0, 0, 4             | 0, 0, 0, 5        | 0, 0, 0, 4           | 0, 0, 0, 4          | 0, 4, 0, 3, 4         | 0, 0, 0, 5        | 1, 1, 1          |
| Mandible         |                     |                       |                        |                   |                      |                     |                       |                   |                 |
| S on end         | 7                   | 9                     | 8–9                    | 8                 | 9                    | 9                   | 8                      | 5                 | 8               |
| Maxillule        |                     |                       |                        |                   |                      |                     |                       |                   |                 |
| S on coxal end.  | 14                  | 13–14                 | 13                     | 15                | 9–11 (14)c           | 15                  | 9                      | 12               | 9               |
| S on basial end. | 18                  | 18 (19)b              | 19                     | 19                | 16–18                | 18                  | 16                     | 18               | 15              |
| Maxilla          |                     |                       |                        |                   |                      |                     |                       |                   |                 |
| S on coxal end.  | 8+4                 | (8)b 5–7+4            | 8+4                    | 8+6               | 6–8+4–5              | 7+5                 | 11                     | 8+4              | 7+3             |
| S on basial end. | 7+7–8               | 6 (7)b + 9 (8)b       | 6+8                    | 6+9               | 7–8 (9)c + 8–10      | 6+8                 | 13                     | 8+9              | 4+5             |
| Scaphog          |                     |                       |                        |                   |                      |                     |                       |                   |                 |
| S on margin      | 38–39               | 34–36                 | 40–45                  | 41                | 34–39                | 50–52               | 34                     | 37               | 33              |
| S on surface     | 4                   | nd                    | 5                      | 4                 | nd                   | 4                   | nd                     | 3                | nd              |
| Maxilliped 1     |                     |                       |                        |                   |                      |                     |                       |                   |                 |
| S on coxal end.  | 9                   | 9                     | 9                      | 9                 | 6–8 (11)c            | 9                   | 5–7                    | 9                | 7               |
| S on basial end. | 14                  | 12                    | 13                     | 16                | 12–16 (23)c          | 13                  | 12–13                  | 19               | 10              |
| S on end         | 4                   | 3                     | 5                      | 3                 | 11 (10)c             | 5                   | 5                      | 6                | 0               |
| S on exopod      | 2, 0, 4             | 2, 5                   | 2, 5                   | 2, 0, 5           | 2, 0, 5–7            | 2, 5                 | 2, 0, 5                | 2, 5              | 1, 0, 4         |
| S on epipod      | 5                   | 8                     | 6                      | 7                 | 4–7c                 | 5                   | 4                      | 8                | 7               |
| Maxilliped 2     |                     |                       |                        |                   |                      |                     |                       |                   |                 |
| S on end         | 1, 1–2,             | 2, 1,                  | 2, 1, 5, 7             | 1, 1, 5, 7        | 1–2, 1, 5–6,         | 2, 1, 5, 7          | 1, 1, 5, 7             | 0, 1, 1           | 1, 1, 5, 6      |
| S on exopod      | 1, 0, 5             | 1, 5                   | 1, 5                   | 1, 0, 4           | 1, 0, 5–6            | 1, 5                 | 0, 0, 4                | 1, 5              | 1, 5            |

Larval development of *Pilumnus spinifer*
Table II. (Continued).

|                | Pilumnus spinifer | Pilumnus hirtellus | Pilumnus reticulatus | Pilumnus minutus | Pilumnus dasypodus | Pilumnus limosus | Pilumnus vespertilio | Pilumnus sluiteri | Pilumnus kempi |
|----------------|------------------|-------------------|----------------------|-----------------|-------------------|-----------------|----------------------|-----------------|----------------|
| Maxilliped 3   |                  |                   |                      |                 |                   |                 |                      |                 |               |
| S on end.      | 12–14, 10, 6     | 14–15, 9, 5, 6    | 14, 10, 7, 9, 7      | 15, 9, 5, 7     | 12–15, 10, 8     | 13, 8, 8, 8     | 9, 8, 6, 7, 4, 8   | 10, 9, 6, 7    | 11, 6, 3, 6   |
| S on exopod    | 1, 4             | 1, 5              | 1, 5                 | 1, 0, 5         | 1, 0, 6           | 1, 5            | 0, 0, 6              | 1, 6            | 1, 5          |
| S on epipod    | 8                | 9                 | 14                   | 9               | 8                 | 17              | 10                   | 13              | nd            |
| Pereiopod 1    |                  |                   |                      |                 |                   |                 |                      |                 |               |
| Sp on ischium  | 2                | 1                 | 0                    | nd              | 3                 | 0               | nd                   | 1               | 1             |
| Sp on merus    | 1                | 1                 | nd                   | nd              | 1                 | 0               | nd                   | 0               | 1             |
| Pereiopod 2    |                  |                   |                      |                 |                   |                 |                      |                 |               |
| Sp on coxa     | 1                | 1                 | nd                   | nd              | 1                 | 0               | nd                   | 1               | 1             |
| Sp on ischium  | 1                | 1                 | nd                   | nd              | 1                 | 0               | nd                   | 1               | 1             |
| Sternum (s)    | 6                | nd                | nd                   | nd              | nd                | nd              | nd                   | 6               | nd            |
| Pleopod:       |                  |                   |                      |                 |                   |                 |                      |                 |               |
| Hooks on end.  | 3, 2, 2, 2       | 3, 3, 3, 3        | 3–4, 3, 3, 2         | nd              | 3–2 (2, 2, 2, 2)c | 3, 3, 3, 3    | nd                   | 2, 2, 2         | nd            |
| S on exopod    | 13, 13           | 14, 12–14         | 13, 13, 11, 11       | 13, 12–13, 11–12, 9–10 | 13, 13, 11, 12, 14–14, 11, 10 | 13, 13 | 13, 11, 12, 15, 10, nd | 12, 10          |               |
| Uropod         |                  |                   |                      |                 |                   |                 |                      |                 |               |
| S on exopod    | 1, 6             | 1, 5–8            | 1, 6                 | nd, 6           | 1, 6              | 1, 6            | 1, 7                 | 1, 7            | nd            |
| Telson         |                  |                   |                      |                 |                   |                 |                      |                 |               |
| Dorsal, ventral s | 2, 2             | 2, 2              | 3, 2                 | 2, nd           | 2, 2              | 2, 2            | 2, nd                | 2, 2            | nd            |

A, aesthetasc; end., endopod; nd, not described; s/S, setae; scaphog., scaphognathite; Sp, spine.

References: Pilumnus spinifer, this study; P. hirtellus, Salman 1982, Ingle 1983b, Ingle 1992b; P. reticulatus, Spivak and Rodriguez 2002; P. minutus, Ko 1994a; P. dasypodus, Sandifer 1974, Bookhout and Costlow 1979; P. scabriusculus, Terada 1990; P. limosus, Garcia-Guerrero et al. 2005; P. vespertilio, Lim and Tam 1981, Terada 1990d, Clark and Paula 2003c; P. sluiteri, Clark and Ng 2004a, P. kempi, Siddiqui and Tirmizi 1992, Clark and Ng 2004a; P. longicornis, Clark and Paula 2003.
on the ischium of the first pereiopod (see figure 11D). However, in most of the published descriptions, this information is not available or is incomplete (see Table II). The megalopa of *P. spinifer* can be differentiated from that of *P. hirtellus* in the morphology of the posterolateral processes of the abdomen of somite 5, which overlaps somite 6 in *P. spinifer*, whereas in *P. hirtellus* the margin is rounded and does not overlap with abdominal somite 6 (Ingle 1983, 1992).

**Acknowledgements**

We wish to thank all participants in the cruise MEDITS_ES-0600 on board B/O *Cornide de Saavedra*. This research was performed within the frame of the research programme “MEDITS-DEMERMED”. We also wish to thank Dr J. A. Cuesta for his help in locating key references and for helpful comments.

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