Journal of Plankton Research Vol.19 no.1 pp.29–41, 1997

Larval and postlarval development of *Pisa tetraodon* (Pennant, 1777) (Decapoda: Majidae) reared in the laboratory

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Abstract. The larval and first crab stages of *Pisa tetraodon* (Pennant, 1777) were reared in the laboratory from an ovigerous crab collected in the Gulf of Cádiz (Spain). The morphology of the larvae and first crab is described, and compared with those of *Pisa armata* (Latreille), the only other species of the same genus for which a complete description of the larval stages is presently available.

Introduction

The genus *Pisa* is represented in Iberian waters by six species: *P.muscosa*, *P.armata*, *P.carinimana*, *P.corallina*, *P.nodipes* and *P.tetraodon* (Zariquiey-Alvarez, 1968; Garcia-Raso, 1984). The spider crab, *P.tetraodon*, is established in shallow water down to ~100 m, from England to Cabo Blanco (Mauritania) and in the Mediterranean (Monod, 1956; Zariquiey-Alvarez, 1968). The complete larval development has been described only for *P.armata* (Ingle and Clark, 1980; Ingle, 1992). Previous descriptions of the larval development of *P.tetraodon* and *P.nodipes* (Bourdillon-Casanova, 1960; Heegaard, 1963) are incomplete and inaccurate for detailed comparative studies. In this study, the larval stages of *P.tetraodon* are described and compared with those of *P.armata*.

Method

An ovigerous crab of *P.tetraodon*, with a carapace length of 22.5 mm and carrying eggs in an advanced state of development, was collected from Chato beach (Cádiz) on 26 May 1990. The female was transported to the laboratory and placed in a container with running seawater. Larvae hatched within 24 h and a total of 2245 zoea I larvae were collected. The larvae were reared using two 2 l plastic buckets, each stocked with ~1000 larvae. The seawater was maintained gently aerated at 23°C and the average salinity was 33 ± 1‰. Larvae were subjected to a 16 h light:8 h dark artificial light regimen. The food offered was *Artemia* nauplii, and the containers were checked daily for exuviae and to remove dead larvae. The water was changed daily and newly hatched *Artemia* nauplii supplied. Specimens and moults were fixed in buffered 5% formaldehyde.

All measurements were made with an ocular micrometer on a binocular microscope, and were recorded from 20 specimens of each stage. The rostro-dorsal length (TT) for the zoeal stages was measured from the tip of the rostral spine to the tip of the dorsal spine; carapace length (CL) from the base of the rostrum between the eyes to the posterio-lateral carapace margin; for the megalopa, CL was measured from the rostral apex and for the first crab from the rostral base. At least 10 specimens were dissected of each larval stage. Drawings of the entire

larvae and dissected appendages were made using a Wild M-5 stereomicroscope and a Zeiss compound microscope with Nomarski interference contrast, both with a camera lucida. Micropreparations were mounted in CMC 10 (Turtox Ltd) and lignin pink. Setal counts are proximal to distal. Some megalopa larvae and first crabs of *P.armata* donated by the Natural History Museum were also dissected and studied for comparison with those of *P.tetraodon*.

Results

The diameter of the eggs before hatching was 980 ± 40 μm. The larvae passed through two zoeal stages and one megalopal stage before the metamorphosis to first crab stage 10 days later after hatching. The first day of appearance and the mean duration of each stage at 23°C, and measurement of TT and CL are shown in Table I. Survival was 21% from zoea I to first crab.

Description

Pisa tetraodon (Pennant, 1777) (Figures 1–5). *Pisa tetraodon*, Bourdillon-Casanova (1960): 211, Figure 70a and b; Heegaard (1963): 478, Figures 91–97.

Zoea I

Carapace (Figure 1A and B). Dorsal spine strongly curved distally; rostral spine small and acute; lateral spines absent; a prominent antero-median elevation; one pair of antero-dorsal and postero-dorsal setae; each ventral margin with a majid seta + 6 setae; eyes sessile.

Antennule (Figure 2A). Endopod absent; exopod unsegmented with six unequal terminal aesthetascs.

Antenna (Figure 2E). Spinous process distally spinulate; endopod less than one-third the size of spinous process; exopod with two unequal subterminal setae.

Mandible (Figure 2I). Endopod palp absent; incisor and molar processes well developed.

Table I. Mean size and standard deviation in millimetres of the distance between the tips of dorsal and rostral spines (TT) and carapace length (CL); days to appearance and mean duration of the larval and postlarval stages of *P.tetraodon* reared in the laboratory at 23°C

Stage	TT	CL	First day to appear	Mean duration
Zoea I	1.2 ± 0.1	0.8 ± 0.1	0	3
Zoea II	1.3 ± 0.2	1.05 ± 0.2	3	2.5
Megalopa	–	1.2–1.4	6	7
First crab	–	1.5–1.7	10	–

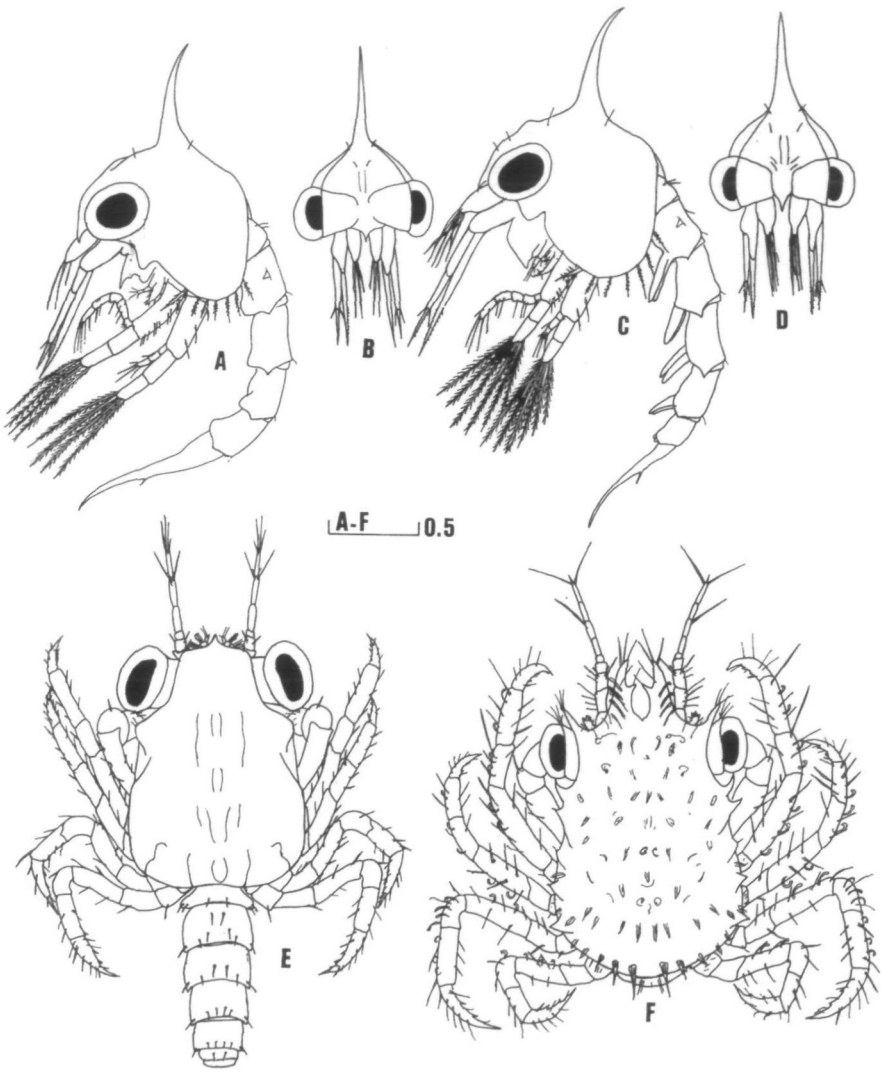

Fig. 1. *Pisa tetraodon*: zoea I, lateral (**A**) and frontal (**B**) view; zoea II, lateral (**C**) and frontal (**D**) view; megalopa (**E**) and first crab (**F**) dorsal view. Scale bar is in millimetres.

Maxillule (Figure 3A). Coxal endite with seven setae/spines; basial endite with seven processes on dorsal and inner margin, single seta absent from outer margin; endopod 2-segmented, proximal segment with one seta; distal segment with two subterminal and four terminal setae.

Maxilla (Figure 3E). Coxal endite bilobed with 5 + 4 setae; basial endite bilobed with 5 + 4 setae; endopod with five terminal setae; scaphognathite (exopod) margin with 11–13 plumose setae plus one distal stout process.

First maxilliped (Figure 4A). Basis with 10 setae arranged 2,2,3,3; endopod 5-segmented with 3,2,1,2,5 setae, respectively; exopod 2-segmented, distal segment with four terminal plumose natatory setae.

Second maxilliped (Figure 4E and K). Basis with three setae; endopod 3-segmented, with 0,1,5 setae, respectively; exopod 2-segmented, distal segment with four terminal plumose natatory setae.

Third maxilliped. Represented as a small bilobed bud.

Pereiopods. Represented as small finger-like projections.

Abdomen (Figure 5A). With five somites; somite 2 with one pair of dorso-lateral processes; somites 3–5 with short postero-lateral processes; somite one with a pair of dorso-medial setae; somites 2–5 with one pair of postero-dorsal setae; pleopod buds present.

Telson (Figure 5B). Forks long, curved and spinulate with a lateral spine, posterior margin with three pairs of stout spinulate setae.

Zoea II

Carapace (Figure 1C and D). Anterio-median region elevated, with three pairs of anterio-dorsal setae, eyes freely movable on stalks. Otherwise unchanged.

Antennule (Figure 2B). Endopod bud developed; exopod with eight aesthetascs.

Antenna (Figure 2F). Endopod slightly more than one-third the length of spinous process. Otherwise unchanged.

Mandible (Figure 2J). Endopod bud present.

Maxillule (Figure 3B). Coxal endite with eight setae/spines; basial endite with nine setae/spines and outer margin with a plumose seta. Endopod unchanged.

Maxilla (Figure 3F). Coxal endite unchanged, basial endite with 5 + 5 setae; endopod unchanged; scaphognathite (exopod) margin with 21–23 plumose setae, distal stout process now reduced.

First and second maxilliped (Figure 4B and F). Distal segment of exopod with six terminal plumose natatory setae. Otherwise unchanged.

Third maxilliped. More prominent than in first stage and with exopod bud longer than endopod.

Pereiopods. First pair conspicuously chelate, 2nd–5th longer than in first zoeal stage.

Fig. 2. *Pisa tetraodon*: antennule, zoea I (**A**), zoea II (**B**), megalopa (**C**), first crab (**D**); antenna, zoea I (**E**), zoea II (**F**), megalopa (**G**), first crab (**H**); mandible, zoea I (**I**), zoea II (**J**), megalopa (**K**), first crab (**L**). Scale bar is in millimetres.

Abdomen (Figures 1C and 5C). With six somites; 2nd somite with additional pair of dorsal medial setae; somites 2–5 with well-developed pleopod buds.

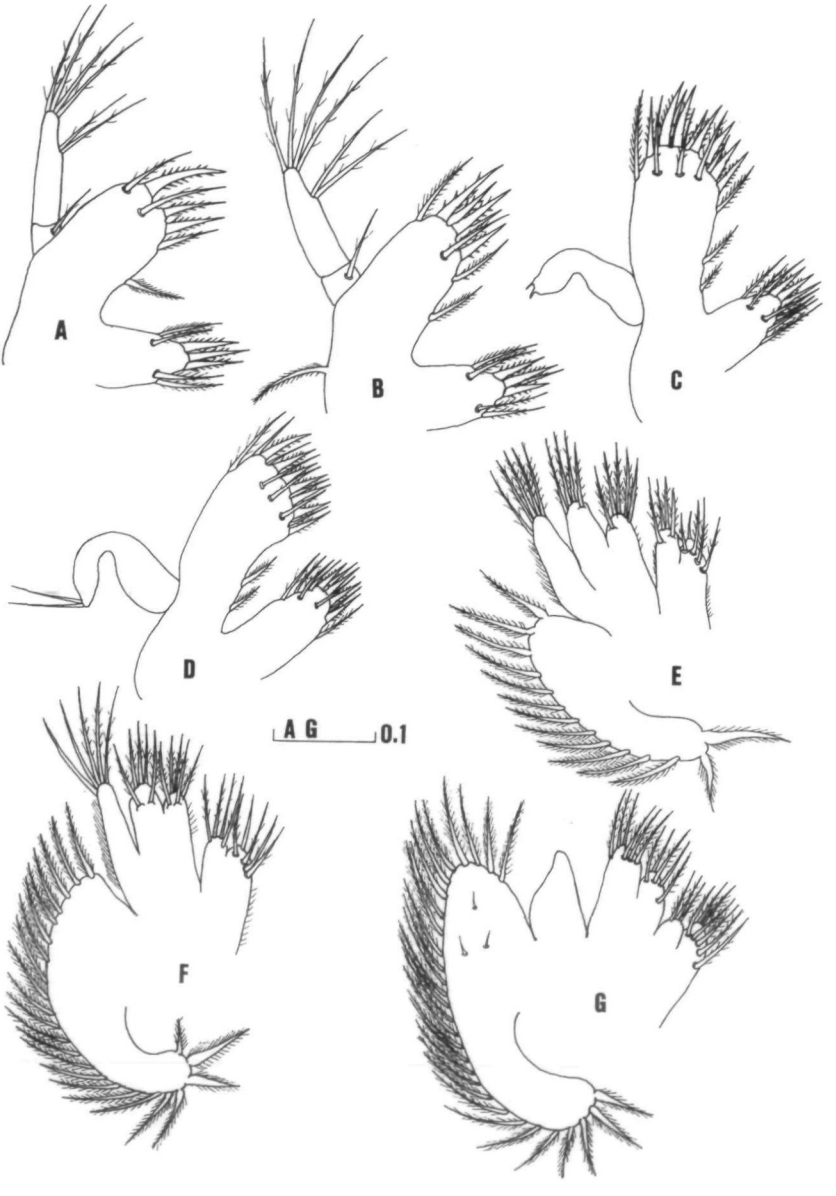

Fig. 3. *Pisa tetraodon*: maxillule, zoea I (**A**), zoea II (**B**), megalopa (**C**), first crab (**D**); maxilla, zoea I (**E**), zoea II (**F**), megalopa (**G**). Scale bar is in millimetres.

Megalopa

Carapace (Figure 1E). Longer than broad, without spines; rostrum short, directed slightly downward; hepatic region broadly inflated, margin of frontal region gently rounded; an obtuse cardiac tubercle, a pair of epigastric and mesogastric carinae,

a pair of protuberances on metabranchial region and a tubercle on intestinal region. Eyes with cornea well developed.

Antennule (Figure 2C). Peduncle 3-segmented with 0,1,1 setae, respectively; endopod 2-segmented with 0,3 setae; exopod 3-segmented with 6,4,0 aesthetascs and 1,0,1 setae, respectively.

Antenna (Figure 2G). Peduncle 3-segmented with 0,2,3 setae, respectively, segment 1 with a prominent obtuse distal process; flagellum 4-segmented with 0,0,4,4, setae, respectively.

Mandible (Figure 2K). Molar process well developed, palp 2-segmented, distal segment with five setae.

Maxillule (Figure 3C). Coxal endite with nine setae/spines; basial endite with 15 setae/spines in dorsal margin and two setae on inner margin; endopod unsegmented with two incipient setae.

Maxilla (Figure 3G). Coxal endite with 7 + 3 setae; basial endite with 5 + 6 setae; endopod reduced to a terminal subacute process without setae; scaphognathite (exopod) with 30–32 marginal plumose setae and three setae on dorsal surface.

First maxilliped (Figure 4C). Coxal endite with seven setae; basial endite with 11 setae; endopod curved, unsegmented without setae; exopod stout, 2-segmented, the proximal segment long with a disto-external plumose seta, distal segment short with four terminal setae; epipodite long with one proximal and five distal gill-grooming setae.

Second maxilliped (Figure 4G). Coxal and basal segment not differentiated; endopod 4-segmented with 0,1,3,6 setae/spines, respectively; exopod long and stout, 2-segmented with five long plumose setae on distal segment.

Third maxilliped (Figure 4I). Coxa and basis not differentiated with six setae; endopod 5-segmented with 11,9,6,6,4 setae/spines, respectively, the ischium with inner margin spinosed or crenulate; exopod 2-segmented with 0,4 + 1 setae; epipodite with one pair of setae and seven long gill-grooming setae.

Pereiopods (Figure 5). Cheliped (F), setosed as shown, propodus swollen, dactylus curved; pereiopod 2 (G), with an ischial spine obtuse; pereiopods 3 and 4 same (H), pereiopod 5 (I); dactylus of pereiopods 2–5 long and stout, terminally thin, with two spines on inner margin (G–I).

Abdomen (Figure 5D). Six-segmented, setosed as shown, 6th somite without setae; telson with a pair of median setae, sometime with distal protuberances, probably from vestiges of zoea caudal furca. Pleopods present on segments 2–6; 1st and 2nd same (J), 3rd (K) and 4th (L), with exopods stout 2-segmented with

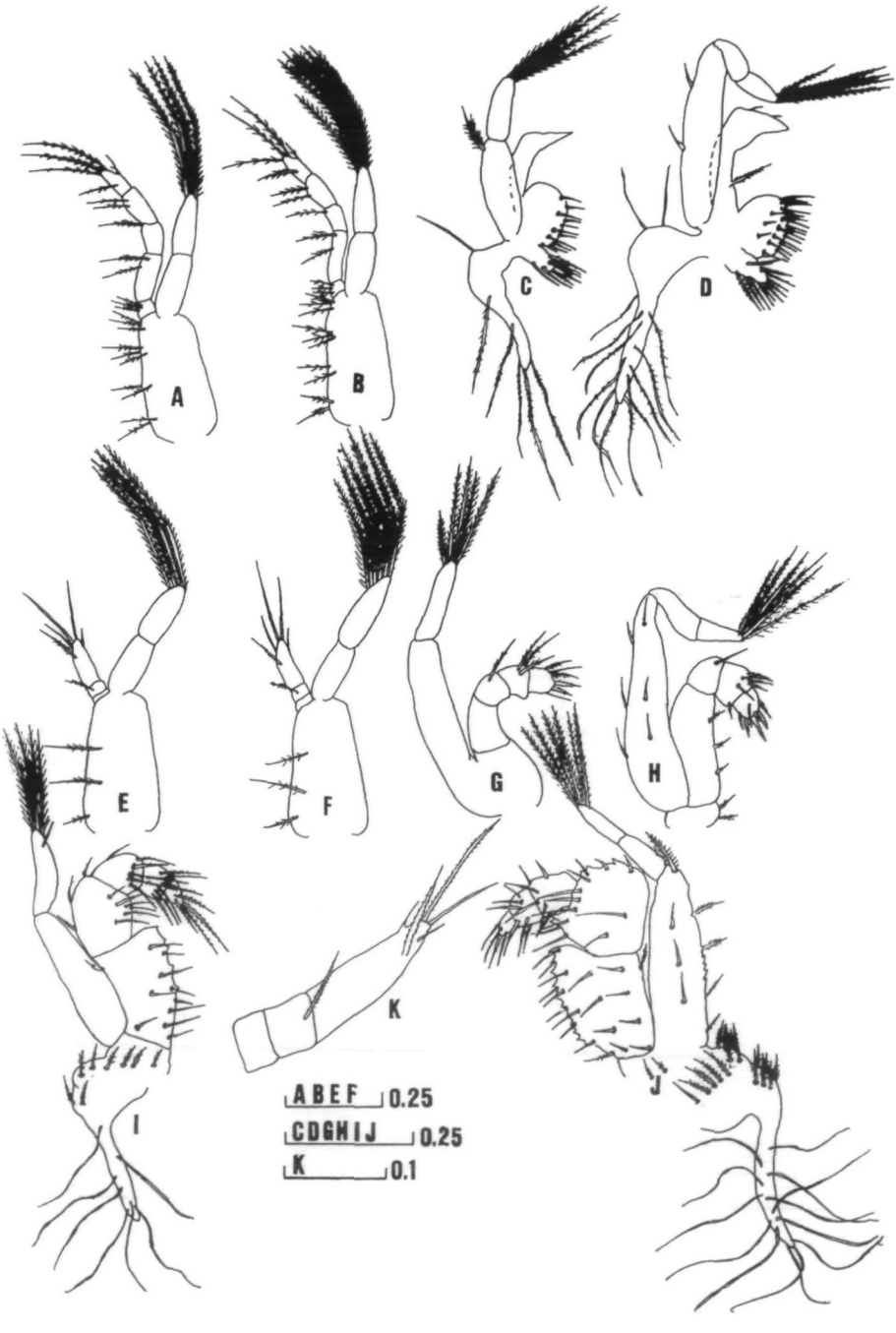

Fig. 4. *Pisa tetraodon*: first maxilliped, zoea I (**A**), zoea II (**B**), megalopa (**C**), first crab (**D**); second maxilliped, zoea I (**E**), zoea II (**F**), megalopa (**G**), first crab (**H**); endopod of second maxillipeds of zoea I (**K**); third maxilliped, megalopa (**I**), first crab (**J**). Scale bar is in millimetres.

12,12,11,9 natatory setae, respectively, and with prominent endopod bearing two coupling hooks; pleopod 5 (uropod), protopod without setae and exopod with five setae (M).

First crab

Carapace (Figure 1F). Longer than broad, dorsal surface with numerous papillate and hooked setae. Rostrum broadly bifid, inner margin of each half with a stout acute process; orbital spine large with three terminal setae; hepatic region with acute bifid process; epi-meso-metabranchial regions each with a stout spine. Eyes large, broad, with well-developed cornea.

Antennule (Figure 2D). Peduncle 3-segmented, with 5,1,3 setae, respectively; endopod 3-segmented with 0,2,3 setae, respectively; exopod 4-segmented with 0,6,5,0 aesthetascs and 0,1,0,3 setae, respectively.

Antenna (Figure 2H). Peduncle 3-segmented with 5,4,5 setae, respectively, the 1st segment with an inner broad terminally bifid process; flagellum 6-segmented with 0,0,1,0,2,2 setae, respectively.

Mandible (Figure 2L). Palp 3-segmented with two subterminal and three terminal setae on distal segment, molar process broad.

Maxillule (Figure 3D). Coxal margin with 12 setae/spines. Distal margin of basis with 17 setae/spines, inner margin with two setae. Endopod unsegmented with two distal long setae.

Maxilla. Unchanged from previous stage.

First maxilliped (Figure 4D). Coxal endite with 11 setae, basial endite with 19 setae; endopod curved with a long seta on proximal and two small setae on distal margin; exopod 3-segmented, the 1st longest, with 2,0,5 setae, respectively; epipodite long with two proximal and 10–11 distal gill-grooming setae.

Second maxilliped (Figure 4H). Undifferentiated coxa and basis with two setae; endopod 4-segmented with 3,1,6,7 setae/spines, respectively; exopod long, 3-segmented, with 6,0,6 setae, respectively.

Third maxilliped (Figure 4J). Undifferentiated coxa and basis with 12 setae; endopod 5-segmented, ischium with inner margin strongly crenulate and 18–19 setae, merus with 12 setae, carpus with six setae, propodus with six setae and dactylus with four terminal setae; exopod 3-segmented, with 8,0,6 setae, respectively; epipod long with six proximal plumose setae and 13 distal gill-grooming setae.

Pereiopods (Figure 1F). Invested with numerous hooked and simple setae; merus of cheliped with four and two spines on outer and inner margin, respectively; inner

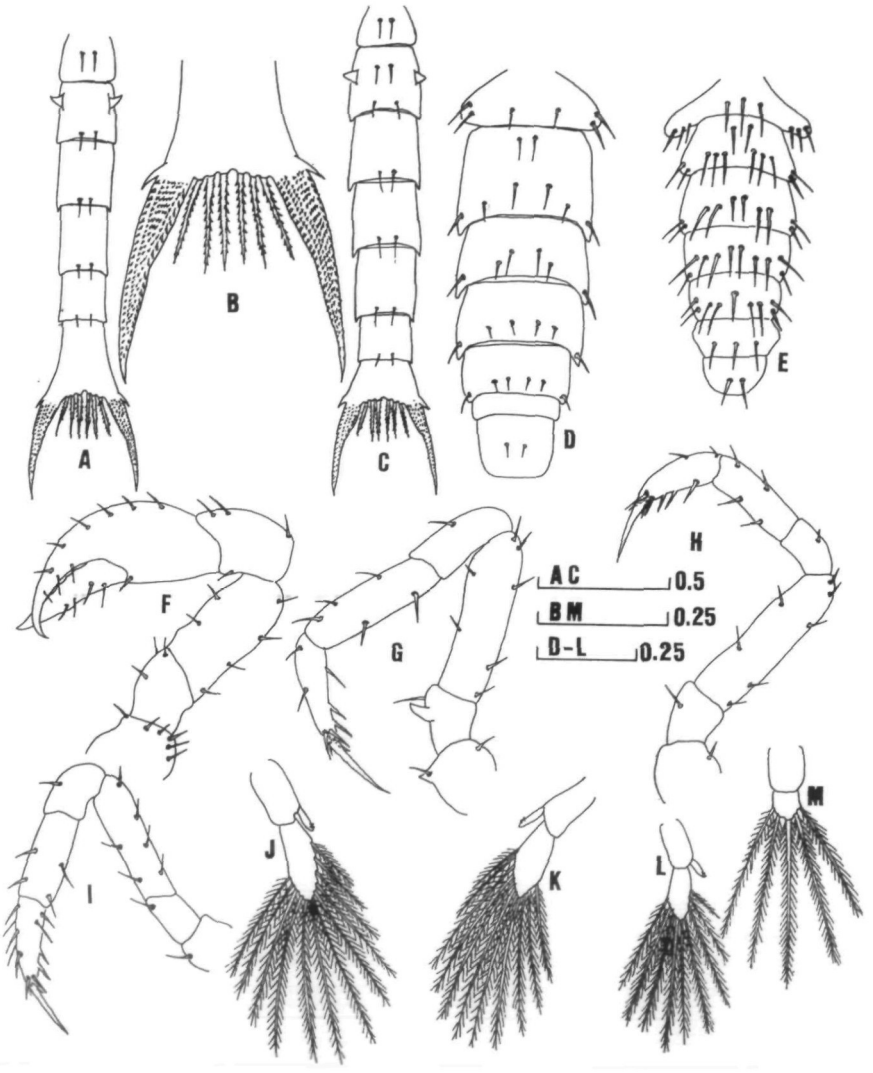

Fig. 5. *Pisa tetraodon*: abdomen, zoea I (**A**), zoea II (**C**), megalopa (**D**), first crab (**E**); furca of zoea I and II (**B**); pereiopod of megalopa, cheliped (**F**), second (**G**), third and fourth (**H**), fifth (**I**); pleopods of megalopa, first (**J**), second and third (**K**), fourth (**L**), fifth (uropod) (**M**). Scale bar is in millimetres.

margin of dactylus of 2nd pereiopod with a small spine and of pereiopods 3–5 with two stout spines.

Abdomen (Figure 5E). With numerous setae as shown; pleopods reduced to buds.

Discussion

The first stages of two *Pisa* species, designated as *Pisa* sp. (A) and *Pisa* sp. (B), were described and figured by Bourdillon-Casanova (1960), who suggested that

they may have belonged to *P.tetraodon* and *P.nodipes*, but they were incompletely described. Heegaard (1963) found short spines on abdominal segments 2–4 of zoea I stage attributed by him to *P.tetraodon*. For these specimens, he described the endopod of the maxillule as 3-segmented, with 0,2,3 setae, respectively; the endopod of the maxilla with four setae; maxilliped 1 with a 5-segmented endopod with 0,0,1,2,4 setae, respectively, and maxilliped 2 with a 2-segmented endopod. The zoea I stage in this study has the maxillule endopod 2-segmented with 1,2 + 4 setae; the maxilla endopod with five setae; maxilliped 1, endopod 5-segmented with 3,2,1,2,5 setae, respectively, and maxilliped 2 with a 3-segmented endopod. These discrepancies in the various accounts of the first zoeal stages of *P.tetraodon* may be due to descriptive errors by Heegaard. The larval descriptions in this study only agree with his account in having a short or moderate sized lateral process on the abdominal segment. Salman (1982) provided a key to the first zoeal stage of the subfamily Pisinae in which he included *P.tetraodon*, but the features for this species were presumably based on those given by Heegaard (1963). The first zoeal stage described by Paula (1987) taken from plankton samples in S. Torpes Bay (SW Portugal) as Pisinae S8, has the scaphognathite armed with 11 marginal plumose setae, and the proximal segment of maxilliped 2 endopod unarmed, as noted for *P.tetraodon* and *P.armata*, but his description is also incomplete.

The present larval features of *P.tetraodon* reared in the laboratory are compared with those of *P.armata* in Table II.

The zoeae of *P.tetraodon* show many affinities to those of *P.armata*. They are of similar size, the rostrum of both is extremely short, carapace lateral spines are absent and the posterio-lateral margin has six submarginal setae and a majid seta. Also, the antennule of both has six (zoea I) and eight (zoea II) aesthetascs; the antennal spinous process is distally spinulated, the exopod has two unequal subterminal setae/spines and the distal process is spinulated, reaching the tip of the spinous processes as a 'barbed lance' type of exopod described by Kurata (1969); the maxillule endopod is 2-segmented with 1,2 + 4 setae and the second maxilliped endopod 3-segmented. The zoeae I and II of *P.armata* and *P.tetraodon* cannot be satisfactorily separated on setal armature. Only the lateral spines on abdominal segments 2–5 seem larger in *P.armata* [Figures 5g and h of Ingle and Clark (1980), and Figure 1A and C of this study].

Ingle and Clark (1980) made descriptive errors in their paper on *Pisa*, some were corrected later in Clark and Webber (1991) and Ingle (1992), although in these accounts some previous errors were not still corrected and others are probably due to typographical errors.

The systematic relationships within the Majoidea were discussed by Rice (1988) and Clark and Webber (1991). The latter authors proposed a new familiar classification *(sensu* Guinot, 1978), based on characters of larval zoeae from 10 majid genera, Oregonidae, Machrocheiridae, Majidae and Inachidae, and in which *Pisa* was assigned to the Inachidae. However, with the exception of *P.armata* and *P.tetraodon*, the basal antennal article of all megalopas of inachid described carries a well-developed spine. This character was noted by Rice (1988) as a feature which may help to resolve phylogenetic relationships in majid crabs at a variety of taxonomic levels. Furthermore, the proximal segment of the maxillule endopod of all

Table II. Differences in larval stages and first crab of *P.armata* (Ingle and Clark, 1980; Ingle, 1992; this study) and *P.tetraodon* (this study). Numbers are setal and spine counts

Stages	*P.armata*			*P.tetraodon*
	Ingle and Clark, 1980	Ingle, 1992	This study	This study
Zoea I				
Maxilla:				
coxa	6+4	5+4	–	5+4
basis	4+4	5+4	–	5+4
scaphognathite	11	10–12	–	12–14
Maxilliped-2:				
endopod	1,2,3	0,1,5[a]	–	0,1,5
Zoea II				
Maxilla:				
coxa	6+4	5+4	–	5+4
basis	5+4	5+5	–	5+4
Megalopa				
Antennule:				
peduncle	0,1,1	–	0,2,1	0,2,1
Maxillule:				
basis	17	18	18	17
Maxilla:				
coxa	7+3	7+3	7–8+3	7+3
basis	4+6	5+6	5+6	5+6
scaphognathite	30	30[b]	30	30–32
Maxilliped-1:				
coxa	7–8	–	7	7
basis	16	–	13–14	9
endopod	4	–	4	2
exopod	1,5	–	1,4	1,4
epipod	5	–	6	6
Maxilliped-2:				
endopod	0,1,3,6	0,1,4,6[c]	0,1,3,6	0,1,3,6
Maxilliped-3:				
endopod	12,8,5,6,4	12,8,5,5,3[d]	11,9,5,6,4	11,9,5,6,4
Abdomen:				
exopod of pleopod				
1st to 5th	12,12,12,12,5	10,10,10,10,5	12,12,11,9,5	12,12,11,9,5
telson	2	2+2	2+2	2
1st crab				
Antennule:				
peduncles	0,4,3	–	6,2,3	5,2,3
exopod	0,7,5,4	–	0,7,5,4	0,7,4,3
Maxillule:				
coxa	11	–	11	12
basis	19	–	20	17
Maxilla:				
coxa	7+3	–	7–8+3	7+3
scaphognathite	7,30–32	–	6,30–32	3,30–32
Maxilliped-1:				
coxa	12	–	11	2+10–11
basis	27–30	–	24	18
endopod	9–10	–	9–10	1+2
epipod	10	–	10	12
Maxilliped-2:				
basis/coxa	3	–	3	2
endopod	2,1,5,8	–	2,1,5,8	3,1,6,7
exopod	8,0,5	–	8,0,5	6,0,6
Maxilliped-3:				
endopod	19–20,12–13,9,6–7,4	–	21,14,9,7,4	18–19,12,6,6,4

[a]On p. 30 described 0,1,4+1, but on p. 174 described as 1,1,4+1.
[b]On p. 101, figured with 21 setae, but on p. 175 described with 30.
[c]On p. 101, the propodus is drawn with four setae, but is described with three.
[d]On p. 109, propodus and dactylus are drawn with five and three setae, respectively, but are described with six and four.

zoeal stages of *Inachus* is unarmed, whereas a seta is present in this region of the endopod in *P.armata* and *P.tetraodon*, and other Inachinae studied.

Acknowledgements

I am very grateful to Paul Clark (Natural History Museum), who kindly donated some megalopa larvae and first crabs of *P.armata*, and for his critical review of the manuscript.

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Received on May 16, 1995; accepted on July 22, 1996