

Larval Development of *Pagurus japonicus* (Stimpson) (Decapoda: Anomura: Paguridae) Reared in the Laboratory

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Abstract: The complete larval development of *Pagurus japonicus* (Stimpson) is described, based on laboratory rearing. The species has four zoeal stages and a megalopa. The larvae are described and illustrated, and detailed comparisons with other pagurid larvae in the Korean coast are made.

Key words: larval development, *Pagurus japonicus*, Paguridae, Decapoda, Anomura

Pagurus japonicus (Stimpson, 1858) frequently inhabits the Turban shell, *Turbo cornutus* (Lightfoot, 1786), and sometimes *Thais bronni* (Dunker, 1860). These species are usually observed at depths of 10 to 300 m on rocky and/or boulder bottoms along the Korean coasts, and their geographic distribution is limited to Korea, Japan, and China (Kim, 1973; Miyake, 1978).

Along coasts of Korea, 24 species of Paguridae, representing four genera, have been reported by Kim (1973), Oh (1997) and Kim and Son (2006), but complete larval development has been described for only 12 species of *Pagurus*, i.e., *Pagurus lanuginosus* De Haan, 1849, *P. similis* (Ortmann, 1892), *P. dubius* (Ortmann, 1892), *P. brachiomastus* (Thallwitz, 1892), *P. geminus* McLaughlin, 1876, *P. middendorffii* Brandt, 1851, *P. ochotensis* Brandt, 1851, *P. trigonocheirus* (Stimpson, 1858), *P. constans* (Stimpson, 1858), *P. pectinatus* (Stimpson, 1858), *P. simulans* (Komai, 2000), *P. gracilipes* (Stimpson, 1858) (cf., respectively, Hong, 1969, 1981; Lee and Hong, 1970; Kurata, 1968; Quintana and Iwata, 1987; Konish and Quintana, 1987, 1988; McLaughlin et al., 1992; Hong and

Kim, 2002; Kim and Hong, 2005; Kim et al., 2007; Kornienko and Korn, 2007).

The first zoeal stage of *P. japonicus* was described by Ko and Yang (2003), but subsequent larval stages were as yet unknown. The purpose of the present study is to describe the complete series of zoeal stages as well as a megalopa of *P. japonicus* reared in the laboratory, and to compare these with other known pagurid larvae.

MATERIAL AND METHODS

Berried females of *Pagurus japonicus* were caught by SCUBA diving from a depth of 5-10 m in the vicinity of Maemuldo (34°30'60"N 128°30'15"E) on 13 August 2000. The specimens were brought to the laboratory and kept in a container filled with aerated natural seawater (34-35‰) at 18-20 until their eggs hatched. About 15 larvae hatched from a *P. japonicus* female on 25 August 2000, and these were reared individually in 50 ml glass bottles filled with filtered seawater. The glass bottles were placed in an incubator (34.2±0.1‰, 18±1°C) on a 13:11 light-dark cycle.

Larvae were fed with newly hatched *Artemia* nauplii. Moulting and mortality were checked daily. After checking, the larvae were transferred to freshly prepared bottles. At each developmental stage, dead larvae and exuviae were fixed and preserved with 3% neutralized formalin solution. Each stage was dissected in ethylene glycol for microscopic observation. Drawings were made with the aid of drawing tubes attached to a dissecting microscope.

Measurements taken were: carapace length (CL), from the tip of the rostrum to the posterior midpoint of the carapace; shield length (SL), from the tip of the rostrum to the midpoint of the cervical groove; total length (TL), from the tip of the rostrum to the midpoint of the telson, excluding telson processes.

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RESULTS

Pagurus japonicus passed through four zoeal stages and a megalopa. Of the 15 larvae reared individually, 6 moulted to the megalopa stage within 15-19 days.

First zoea (Fig. 1)

Size: CL=1.9 mm; TL=4.2 mm.

Duration: 5-6 days.

Carapace (Fig. 1A, B). Rostrum well-developed, directed downward between antennules; carapace with mid-dorsal ridge in lateral profile and slight, concave depression above eyes, posterolateral part of carapace rounded; eyes sessile.

Abdomen (Fig. 1A, B). Five somites plus telson; posterodorsal margins of somites as follows: somites 1-2 unarmed, somites 3-5 each with 2 pairs of spines, outermost pair smaller, spine pairs progressively increasing in size posteriorly; posterolateral margins of somites 2-4 each with a pair of small spines; posterolateral margins of somite 5 with a pair of strong, moderately elongate spines.

Telson (Fig. 1K). Elongate, fan-shaped, somewhat dorsoventrally swollen; posterior margin distinctly convex with a shallow median cleft and 7+7 processes, outermost a fused, naked spine; second an anomuran hair, third through seventh all plumodenticulate processes, fourth of which being the longest; very minute marginal setae between processes and on median cleft.

Antennule (Fig. 1C). Conical, indistinctly bilobed, slightly shorter than antenna; exopod with 1 or 2 large and 4 small aesthetascs; 1 long plumose terminal seta on rudimentary endopodal bud.

Antenna (Fig. 1D). Scaphocerite with strong distolateral spine, outer margin unarmed; inner margin convex, with 10 plumose setae; endopod approximately two-thirds length of scaphocerite, with 2 terminal plumose setae; 1 strong protopodal spine at base of endopodal junction, armed with marginal spinules.

Mandible (Fig. 1E). Asymmetrically dentate; incisor process with strong teeth and a few smaller teeth; molar process with a few strong teeth and acute small teeth; no palp bud.

Maxillule (Fig. 1F). Coxal endite with 1 simple and 4 plumose setae marginally and 2 small simple setae submarginally; basal endite with 2 strong, elongate, spine-like teeth armed with minute denticles, and 2 simple setae submarginally; endopod 3-segmented with 1, 1, 3 setae.

Maxilla (Fig. 1G). Coxal and basal endites distinctly bilobed; coxal endite with 7+1 setae on proximal lobe, 2+1 setae on distal lobe; basal endite with 3+1 setae on proximal lobe, 3+1 setae on distal lobe; scaphognathite posteriorly fused to protopod, distal lobe with 5 short, marginal plumose setae; endopod weakly bilobed with 3

marginal plumose setae on proximal lobe and 3 marginal plumose setae on distal lobe.

First maxilliped (Fig. 1H). Coxa without setae; basis with 2, 1, 1, 3, 3 setae; endopod 5-segmented with 3, 2, 1, 2, 4+1 setae and additional fine setae on lateral margins of segments 1-3; exopod approximately one-half of endopod with 4 plumose natatory setae.

Second maxilliped (Fig. 1I). Coxa without setae; basis with 1 simple marginal seta in distal half, 2 plumose setae at distal angle; endopod 4-segmented, segments 1-3 with 2, 2, 2 setae, respectively, distal segment with 4+1 plumose setae and additional fine setae on lateral margins of segments 2-3; exopod with 4 plumose natatory setae.

Third maxilliped (Fig. 1J). Exopod a 2-segmented bud.

Colour. Overall transparent with red chromatophores as follows: on telson dorsally, above second, third somites of the abdomen, and at bases of mandible and maxilla; corneas black.

Second zoea (Fig. 2)

Size: CL=2.5 mm; TL=5.5 mm.

Duration: 4-5 days.

Carapace (Fig. 2A, B). Carapace depression on middorsal ridge more prominent; rostrum slightly shorter than or equal to length of antenna; eyes stalked.

Abdomen (Fig. 2A, B). Little change from stage I.

Telson (Fig. 2K). Posterior margin with 8+8 processes, with addition of short median pair of spines; median cleft obsolescent or absent.

Antennule (Fig. 2C). Still weakly bilobed; endopod bud with 1 terminal plumose seta; exopod with 3 large and 4 small aesthetascs; protopod usually with 2 small setae at exopodal margin.

Antenna (Fig. 2D). Unchanged from stage I.

Mandible (Fig. 2E). Larger, but generally unchanged from stage I.

Maxillule (Fig. 2F). Coxal endite unchanged from stage I; basal endite with 4 strong teeth, each with minute denticles, and 2 simple submarginal setae; endopod 3-segmented with 2, 1, 3 setae.

Maxilla (Fig. 2G). Coxal endite with 7+1 setae on proximal lobe, 3+1 setae on distal lobe; basal endite with 4+1 setae on proximal lobe, 3+1 setae on distal lobe; scaphognathite now with 7 short, marginal plumose setae; endopod unchanged from stage I.

First maxilliped (Fig. 2H). Coxa and basis setation unchanged from stage I; endopod now with 3+1, 2+1, 1+1, 2, 4+1 setae; exopod now with 7 plumose natatory setae.

Second maxilliped (Fig. 2I). Coxa and basis setation unchanged from stage I; endopod now with 2, 2+1, 2+1, 4+1 setae; exopod now with 7 plumose natatory setae.

Third maxilliped (Fig. 2J). Protopod naked; endopod bud

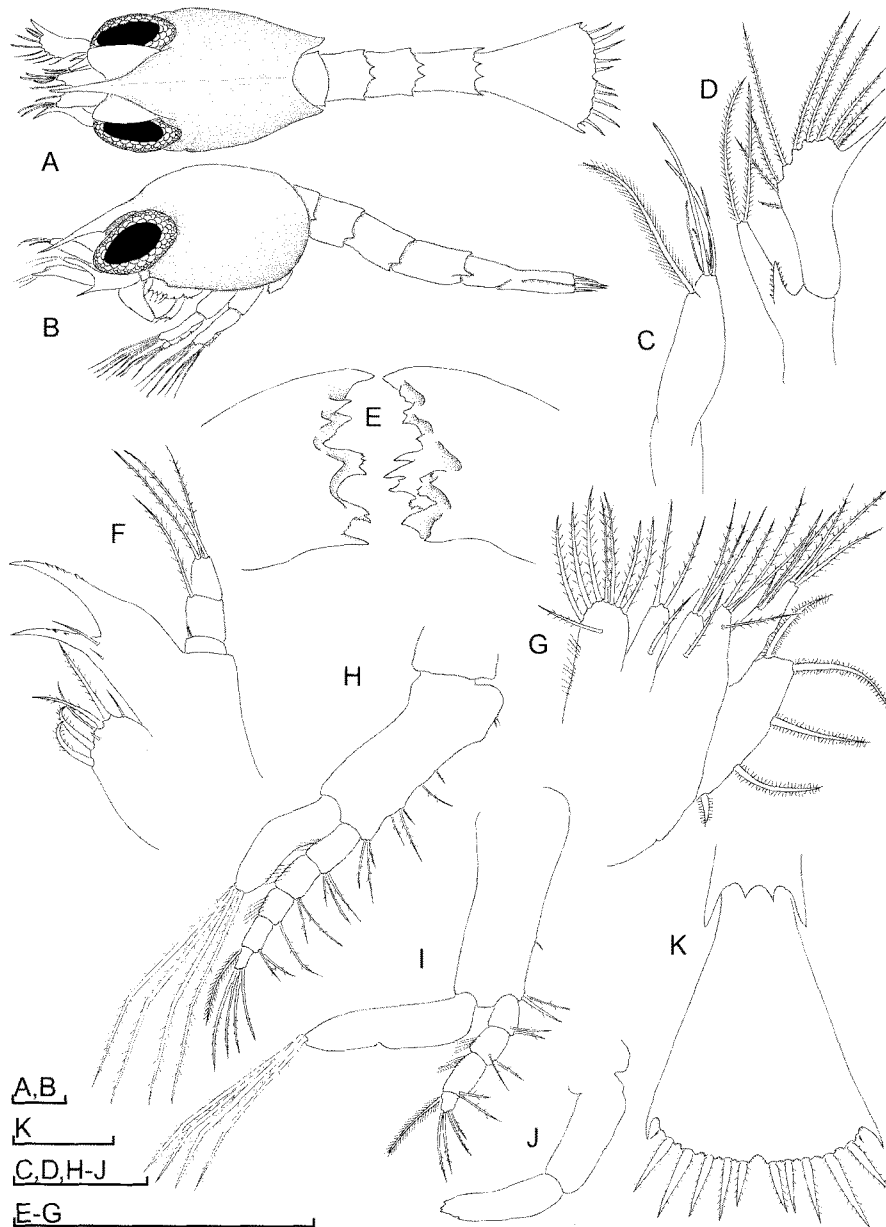


Fig. 1. *Pagurus japonicus* (Stimpson, 1858). First zoea. A, dorsal view; B, lateral view; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla; H, telson. Scale bars=0.4 mm.

with 1 plumose and 1 simple setae; exopod with 6 plumose natatory setae.

Pereopods. Distinct buds present.

Third zoea (Fig. 3)

Size: CL=3.0 mm; TL=6.4 mm.

Duration: 4-5 days.

Carapace (Fig. 3A, B). Larger, but generally unchanged from stage II; rostrum now shorter than antenna.

Abdomen (Fig. 3A, B). Sixth somite now delineated, armed with a pair of small ventrolateral spines and 1 dorsomedial spine on posterior margin; uropods weakly

biramous, not separated from protopod; endopods naked; inner margins of exopods each with 6 plumodenticulate setae.

Telson (Fig. 3K). Posterior margin with 8+8 process, fourth now fused and short.

Antennule (Fig. 3C). Endopod bud apparent, with 1 terminal plumose seta; exopod with 3-5 large and 2 small terminal aesthetascs and 2 subterminal aesthetascs; protopod with 2 plumose setae at endopodal junction.

Antenna (Fig. 3D). Margin of scaphocerite unchanged from stage II; endopod more elongate, tapering to acute tip, with 1 subterminal seta; protopodal junction still with strong denticulate spine at endopodal junction and now

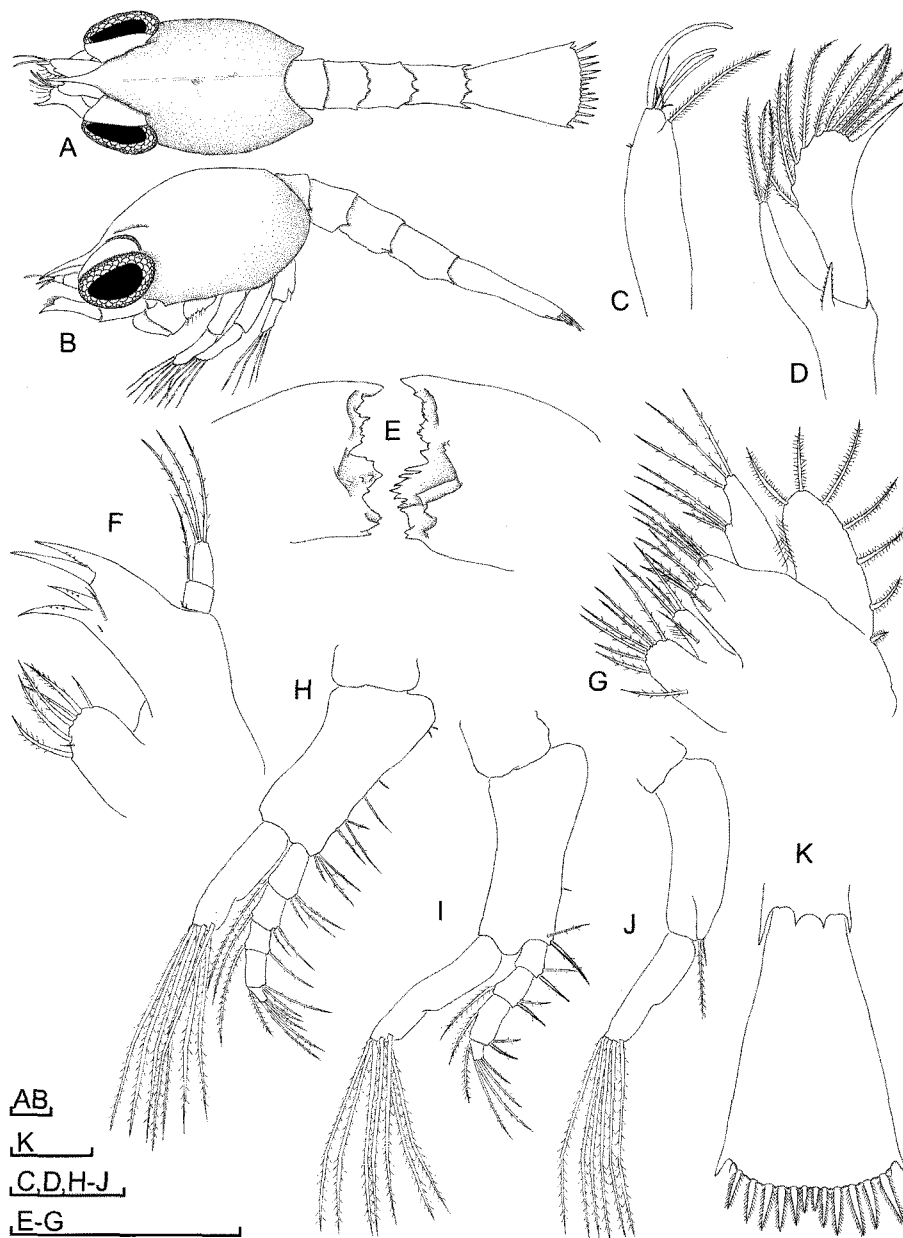


Fig. 2. *Pagurus japonicus* (Stimpson, 1858). Second zoea. A, dorsal view; B, lateral view; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped; J, third maxilliped; K, telson. Scale bars=0.4 mm.

with additional small unarmed spine at base of scaphocerite.

Mandible (Fig. 3E). Larger and with more acute teeth and denticles, but unchanged from stage II.

Maxillule (Fig. 3F). Unchanged from stage II.

Maxilla (Fig. 3G). Setation of endites and endopod unchanged from stage II; scaphognathite now with 9 short, marginal plumose setae.

First maxilliped (Fig. 3H). Basis and endopod unchanged from stage II; exopod with 8 plumose natatory setae.

Second maxilliped (Fig. 3I). Basis and endopod unchanged from stage II; exopod with 8 plumose natatory setae.

Third maxilliped (Fig. 3J). Endopod enlarged but still

with 1 plumose and 1 simple setae; exopod now with 7 plumose natatory setae.

Pereopods. Cheliped bud with dactyl distinguishable; no gill buds.

Fourth zoea (Fig. 4)

Size: CL=3.1 mm; TL=6.9 mm.

Duration: 5-6 days.

Carapace (Fig. 4A, B). Larger but essentially unchanged from stage III.

Abdomen (Fig. 4A, B). Somites 2-5 with pleopod buds;

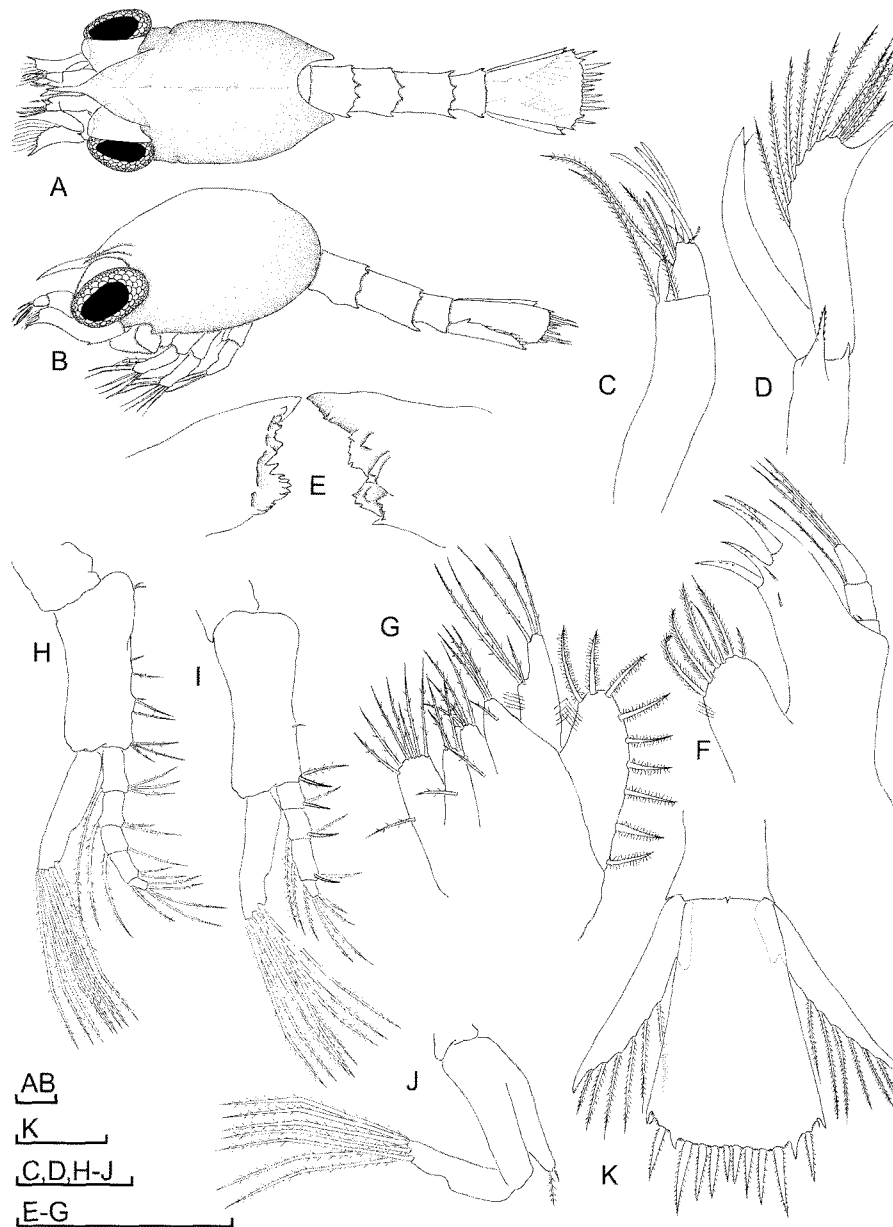


Fig. 3. *Pagurus japonicus* (Stimpson, 1858). Third zoea. A, dorsal view; B, lateral view; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped; J, third maxilliped; K, telson. Scale bars=0.4 mm.

uropodal exopods now separated from protopods, inner margins each with 6 plumose, marginal setae and 1 short, simple seta; endopods fused to protopods, each with 2 short setae.

Telson (Fig. 4K). Unchanged from stage III.

Antennule (Fig. 4C). Endopod bud approximately of equal length to exopod, naked; aesthetascs of exopod progressing distally 2, 2 or 3, 3 or 4 large and 2 small aesthetascs; protopod with 3 setae at endopodal junction.

Antenna (Fig. 4D). Scaphocerite with 8 or 9 plumose setae on inner margin, distolateral spine still well developed; endopod segmented, of approximately equal length of

scaphocerite, inner margin with 1 short subterminal seta; protopod unchanged from stage III.

Mandible (Fig. 4E). Enlarged; tiny palp bud apparent or absent.

Maxillule (Fig. 4F). Coxal endite now with 1 simple and 6 plumose setae marginally and 1 short simple seta submarginally; basal endite with 5 strong teeth each armed with minute denticles, and 2 simple submarginal setae; endopod unchanged from stage III.

Maxilla (Fig. 4G). Setation of endites and endopod unchanged from stage III; scaphognathite with 14 marginal plumose setae on distal lobe.

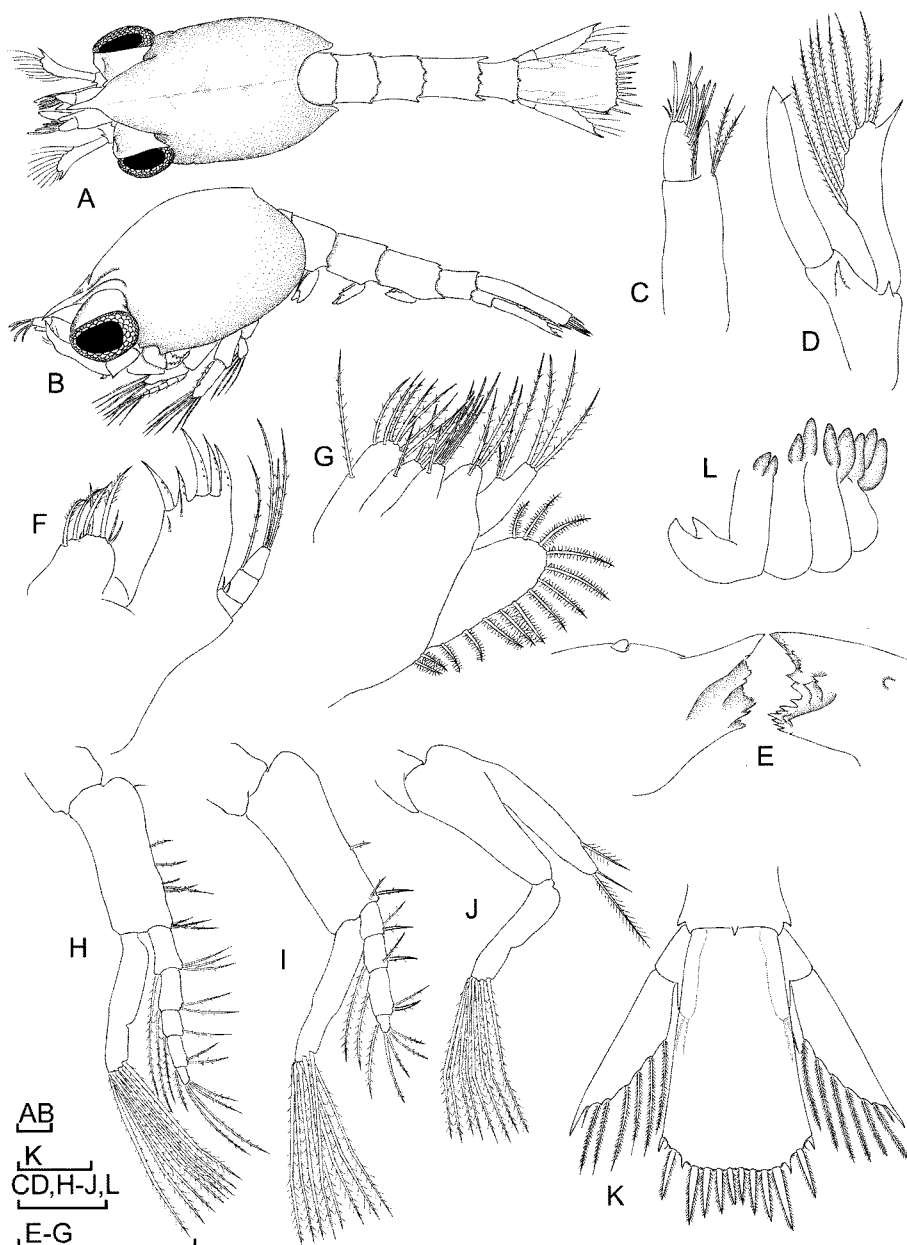


Fig. 4. *Pagurus japonicus* (Stimpson, 1858). Fourth zoea. A, dorsal view; B, lateral view; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped; J, third maxilliped; K, telson; L, pereopods and gills. Scale bars=0.4 mm.

First maxilliped (Fig. 4H). Unchanged from stage III.

Second maxilliped (Fig. 4I). Unchanged from stage III.

Third maxilliped (Fig. 4J). Endopod with 1 terminal, 1 subterminal plumose setae and 1 terminal simple short seta; exopod with 8 natatory setae.

Pereopods (Fig. 4L). Cheliped with chela enlarged, dactyl distinct; ambulatory legs moderately elongate.

Gills (Fig. 4L). Pereopods 1-4 each with a pair of arthrobranch buds, fourth also with 1 pleurobranch bud.

Megalopa (Figs. 5, 6)

Size: SL=1.1 mm; TL=4.9 mm.

Carapace (Fig. 5A, B). Smooth, shield approximately one-half total carapace length; as broad as long; rostrum moderately slender, rounded or subacute, and occasionally with small acute tip or spinule, not overreaching moderately developed ocular acicles. Ocular peduncles moderately short, corneas slightly dilated.

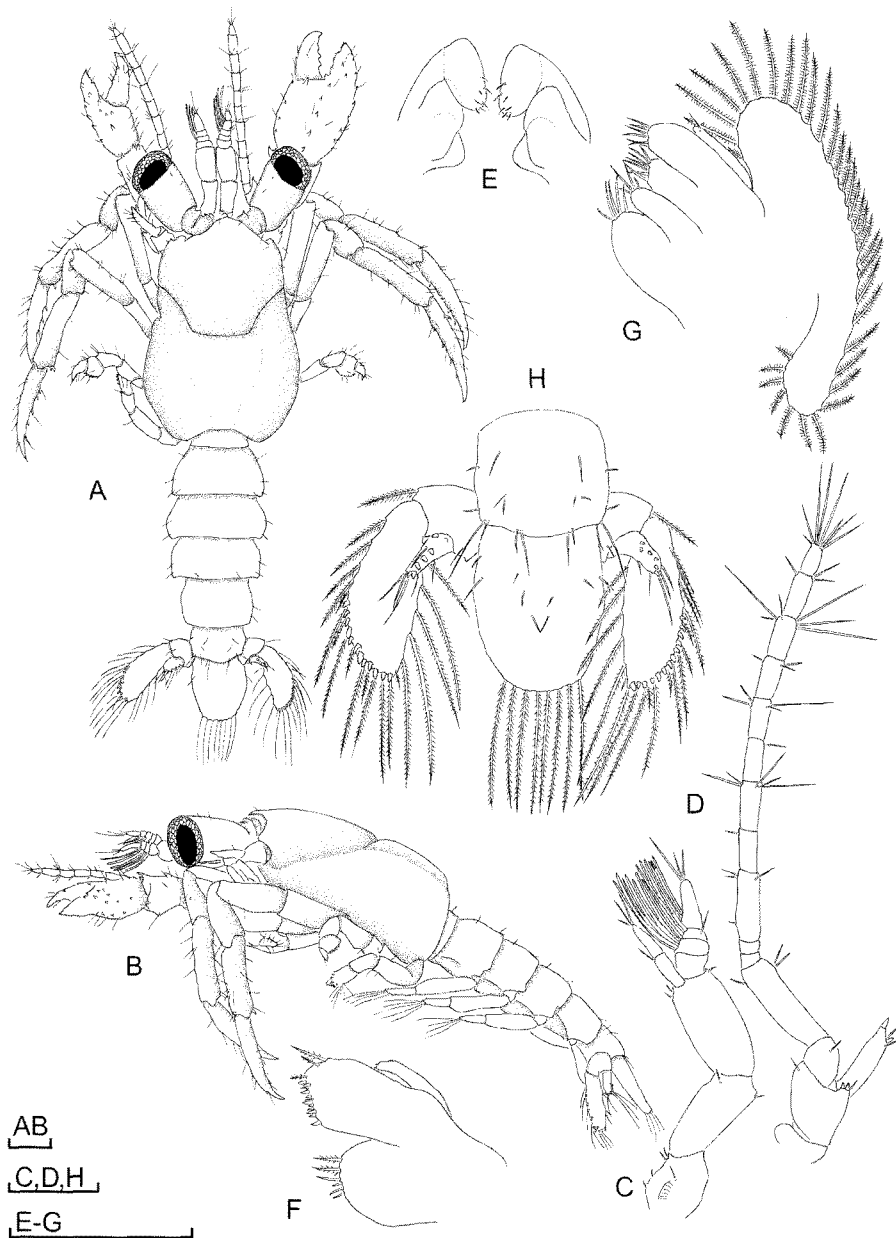


Fig. 5. *Pagurus japonicus* (Stimpson, 1858). Megalopa. A, dorsal view; B, lateral view; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla; H, telson. Scale bars=0.4 mm.

Abdomen (Fig. 5A, B). With six somites, all unarmed but with scattered short setae on dorsal and lateral surfaces; symmetrical biramous pleopods (Fig. 6K) on somites 2-5; exopod well developed, each with 8-10 marginal, plumose setae; endopods each with appendix interna consisting of 2 apical hooks.

Tail fan (Fig. 5H). Telson with numerous scattered setae on dorsal and lateral surface; posterior margin slightly convex and with 4+4 long plumose setae; uropods symmetrical, biramous, protopods with 1 seta on posterolateral surface; exopods with 12-13 scale-like processes posterolaterally and 19-20 simple or plumose

setae; endopods very short, one-fifth to one-fourth length of exopods, each with 5 or 7 setae and 6 scale-like processes.

Antennule (Fig. 5C). Biramous, considerably overreaching ocular peduncles; peduncle 3-segmented, each segment with a few setae, basal segment with statocyst apparent; exopod 4-segmented, first segment without aesthetascs or setae, second with 6 aesthetascs, third with 4 aesthetascs and 1 short simple seta, fourth elongate with 3 aesthetascs and 3 short simple setae distally; endopod 2-segmented, with 1 short seta on basal segment and 3 terminal setae on distal segment.

Antenna (Fig. 5D). With supernumerary segment

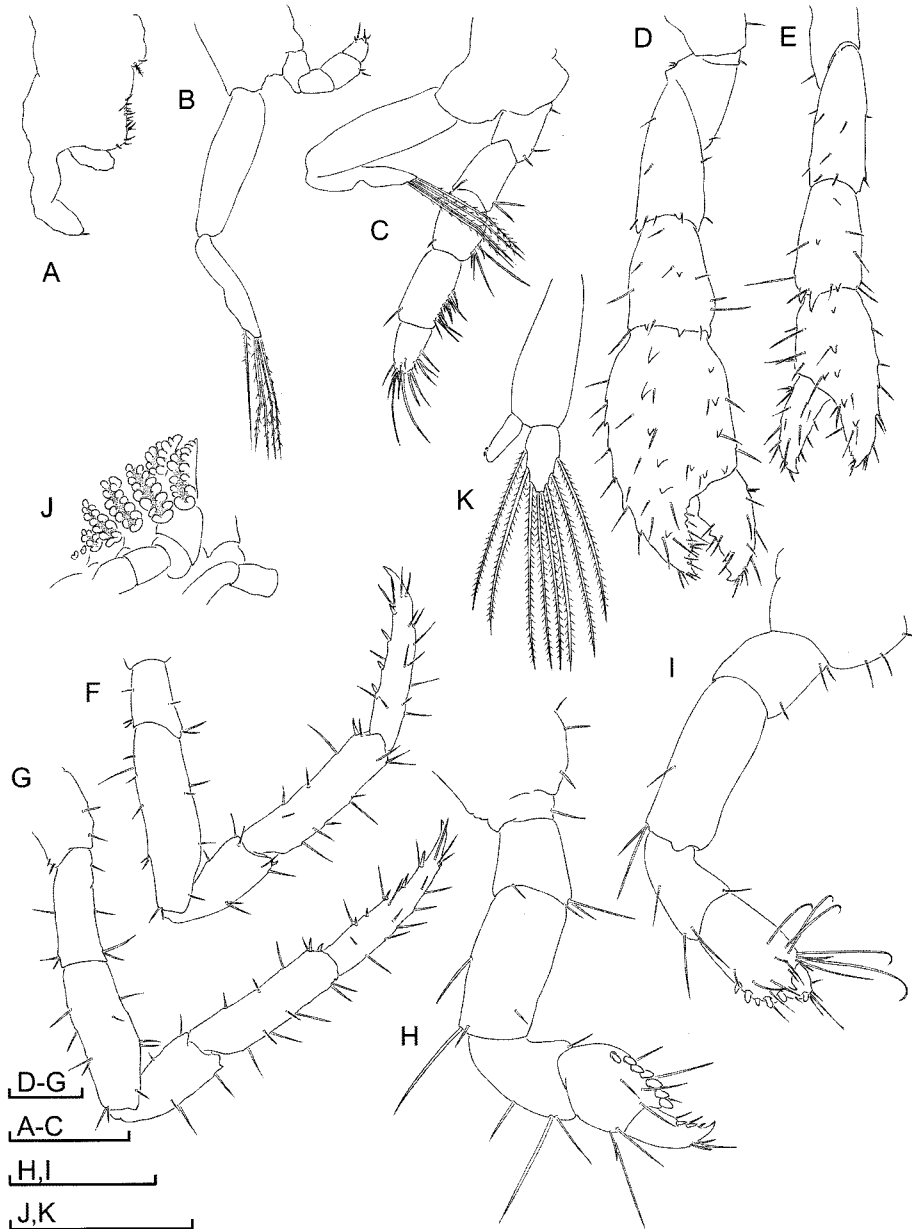


Fig. 6. *Pagurus japonicus* (Stimpson, 1858). Megalopa. A, first maxilliped; B, second maxilliped; C, third maxilliped; D, right cheliped; E, left cheliped; F, second pereopod; G, third pereopod; H, fourth pereopod; I, fifth pereopod; J, gills; K, pleopod. Scale bars=0.4 mm.

apparent; acicle with 2 scale-like processes and several scattered short setae; flagellum usually with 10 articles, setal formula variable.

Mandible (Fig. 5E). Reduced and simplified; palp incompletely 2-segmented, terminal segment with 5-7 small marginal setae.

Maxillule (Fig. 5F). Coxal endite with 7 marginal setae; basal endite with 3 marginal plumose setae and 2 incomplete rows of small teeth; endopod unsegmented, with 2 small setae.

Maxilla (Fig. 5G). Coxal and basal endites still bilobed, coxal endite with 4-5 and 4 marginal plumose setae on proximal and distal lobes, respectively; basal endite with 7

and 6-8 plumose marginal setae on proximal and distal lobes, respectively; scaphognathite with 33-34 moderately short, marginal plumose setae; endopod unsegmented with 1 naked seta.

First maxilliped (Fig. 6A). Coxal endite with 2 simple or weakly plumose setae marginally; basal endite broad, with 13 marginal simple or weakly plumose setae; endopod unsegmented, and with short submarginal bristles; exopod incompletely 2-segmented, distal segment with 1 simple seta.

Second maxilliped (Fig. 6B). Endopod 4-segmented, basal and second segments naked, penultimate segment with 2 short simple setae, ultimate segment with 5 terminal

Table 1. Comparison of morphological characters of the zoeal stages of *Pagurus japonicus* and *Pagurus similis*

	<i>Pagurus japonicus</i> (present study)	<i>Pagurus similis</i> (Lee & Hong, 1970)
Zoea I		
Maxilla		
coxal endite	bilobed	not separate
coxal endite (n)	7+1, 2+1	7+3
basial endite (n)	3+1, 3+1	5, 4
Maxilliped II		
setal formula of endopod	2, 2, 2, 4+1	2, 2+1, 2+1, 4+1
Zoea II		
Antennule		
submarginal setae of Endopod (n)	2	absent
Zoea III		
Maxilla		
scaphognathite (n)	9	10
Maxilliped I		
exopod (n)	7	8
Zoea IV		
Uropodal exopod (n)	7	6
Mandibular palp	small bud present	absent
Maxilla		
scaphognathite (n)	14	11
Megalopa		
Maxilla		
endopod (n)	1	0
scaphognathite (n)	33-34	29

(n): number of the setae

simple setae; exopod 2-segmented, distal segment with 5 plumose setae.

Third maxilliped (Fig. 6C). Endopod 5-segmented, all segments with numerous setae, those of ultimate and penultimate segments often serrated or barbed; exopod 2-segmented, distal segment with 4 terminal plumose setae.

Pereopods (Fig. 6D-I). Chelipeds unequal, right one somewhat larger. Cutting edges of dactylus and fixed finger of right cheliped with 6 or 7 strong calcareous teeth, terminating in corneous claws; palm with 6 well-developed spines on dorsomesial margin, 4 slightly smaller spines on dorsolateral margin and occasionally 1-2 small spinules on dorsal surface, and scattered setae; carpus with 3 spines on distal angle and occasionally 1 or 2 small spinules on dorsal surface. Cutting edges of dactylus and fixed finger of left one with 1 or 2 strong calcareous teeth, terminating in corneous claws; palm usually with 5 strong spines in dorsal midline and 1 or 2 on dorsolateral margin; carpus with 3 spines on distal angle and usually also 1 or 2 on dorsal surface. All segments of both chelae with scattered setae and a few stiff bristles (Fig. 6D, E). Ambulatory legs moderately long; dactyli each with a row of small spinules

on ventral margin, all segments with scattered setae (Fig. 6F, G). Fourth pereopod with protopodal rasp of corneous scales, dactylus with 3 corneous spines on ventral margin; all segments with scattered setae (Fig. 6H). Fifth pereopods with 5 corneous scales on outer surface and margin of propodus, ventrodiscal angle with several long, curved, thick setae; dactylus with 1 corneous scale on outer surface; carpus and merus also with scattered short simple setae (Fig. 6I).

Gills (Fig. 6J). Arthrobranches of chelipeds slightly larger than in stage IV; arthrobranches of second-fourth and pleurobranch of fourth pereopods becoming lobular.

DISCUSSION

The first zoeal stage of *P. japonicus* was described by Ko and Yang (2003), there is agreement with our descriptions. The subsequent larval stages including the first zoeal stage of the *P. japonicus* as observed in the present study are very similar to those of *P. similis* as described by Lee and Hong (1970), albeit with minor differences (Table 1). It is noted that larvae of the *P. japonicus* have a bilobed coxal endites of the maxilla while those of the *P. similis* have not separated coxal endites of the maxilla. In the first zoeal stage, the endopod setal formula of the second maxilliped in *P. japonicus* is 2, 2, 2, 4+1, while that of *P. similis* is 2, 2+1, 2+1, 4+1. Differences in the setal formulae of the maxillules, maxillae, and maxillipeds are also found between the two species. However, the most significant difference is found in the development of a rudimentary mandibular palp in the fourth zoeal stage. Larvae of *P. japonicus* have a rudimentary mandibular palp in the fourth zoeal stage whereas those of *P. similis* do not. A rudimentary mandibular palp in the fourth zoeal stage was, until now, only reported in *Pagurus brevidactylus* (cf. Negreiros-Fransozo, 1984). The presence or absence of the mandibular palp in the fourth zoeal stage is a significant datum from the standpoint of larval phylogenetic groupings and has given rise to phylogenetic polarities (McLaughlin and Gore, 1988). The presence or absence of the mandibular palp in the fourth zoeal stage, as McLaughlin and Gore (1988) suggested, has proven to phylogenetic polarities that compression of postlarval features back into the larval stage (apomorphy) or an ontogenetic sequence arising in the late zoeal stages is carried over into the megalopa (plesiomorphy).

It is noted that the larvae of *P. japonicus* are distinguished from other known *Pagurus* larvae by the in carapace morphology. *P. japonicus* has a rounded posterolateral margin of the carapace, which has only been found in the carapace of *P. similis*, until now (Lee and Hong, 1970). The carapace morphology of *P. japonicus* resembles that of some Diogenidae and Coenobitidae, in

that these also lack posterolateral spines. The lack of posterolateral spines on the carapace is regarded as an apomorphic character state. If the presence of the mandibular palp in a late zoeal stage, and the lack of posterolateral spines on the carapace both would imply apomorphic states, we may presume that *P. japonicus* is, in these respects, more advanced than the other *Pagurus* species, at least those of which the development has been described until now.

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