

LARVAL DEVELOPMENT OF *PARAPAGURODES CONSTANS* (DECAPODA: ANOMURA: PAGURIDAE) REARED IN THE LABORATORY

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ABSTRACT

The complete larval development of *Parapagurodes constans* is described, based on laboratory rearing. The species has four zoeal stages plus the megalopa. Each stage is described and illustrated, and detailed comparisons are made with other pagurid larvae in closely related species of *Parapagurodes* and other pagurid genera.

Parapagurodes constans (Stimpson, 1858) is known to inhabit gastropod shells that are frequently overgrown by the hydroid *Hydrissa sodalis* (Stimpson) and occasionally by the sponge *Suberites* sp. This hermit crab usually lives on muddy-sand bottoms, 5–150 m in depth, with a geographic distribution limited to Korea, Japan, and China (Makarov, 1938, 1962; Kim, 1973; Miyake, 1978).

Stimpson (1858) described *Pagurus constans* (as *Eupagurus*) from Hakodate Bay, Japan, and it has since been reported by several carcinologists from Korea and adjacent waters (e.g., Makarov, 1938, 1962; Miyake, 1960; Kim, 1973; Okutani, 1994). However, in a recent study, Komai (1999) found the characteristics of the genus *Parapagurodes* McLaughlin and Haig, 1973, in *Pagurus constans* and transferred *Pagurus constans* to *Parapagurodes*.

At present, the genus *Parapagurodes* includes six species: *P. constans*; *P. makarovi* McLaughlin and Haig, 1973; *P. laurentae* McLaughlin and Haig, 1973; *P. hartae* McLaughlin and Jensen, 1996; *P. gracilipes* (Stimpson, 1858); and *P. nipponensis* (Yokoya, 1933) (cf. McLaughlin and Haig, 1973; McLaughlin and Jensen, 1996; Komai, 1998, 1999). Of these species, however, larval development is partially known only from the descriptions of the first zoeal telsons of *P. makarovi* and *P. laurentae* by McLaughlin and Haig (1973) and first zoea of *P. hartae* by McLaughlin and Jensen (1996).

In order to examine the larval morphology of *Parapagurodes constans*, we have described the complete zoeal stages and the megalopa of

P. constans reared in the laboratory and have compared these with larvae of other species of *Parapagurodes* and other paguridean species.

MATERIALS AND METHODS

Four berried females of *Parapagurodes constans* were caught with a beam trawl from the depth of 25 to 30 m in the vicinity of Tongyong (128°40'E, 34°30'N), Korea, on 22 April 2000. The females were brought to the laboratory of the Department of Marine Biology, Pukyong National University, Pusan, and kept in a container filled with aerated natural sea water (34‰ to 35‰ salinity) at 15° to 17°C until larvae hatched. One of the females released about 80 larvae on 23 April 2000, and these were reared in an incubator (34‰ ± 2‰, 15° ± 2°C) on a 13:11 light and dark cycle. Forty larvae were reared individually in 50 ml glass bottles filled with filtered sea water, and mass cultures of the remainder were made in glass beakers (1 l). Larvae were fed with newly hatched brine shrimp nauplii. Molting and mortality were checked daily. After being checked, the larvae were transferred to freshly prepared bottles and beakers. At each developmental stage, dead larvae and exuviae were fixed and preserved with 3% neutralized Formalin solution. At least five specimens of each stage were dissected in ethylene glycol for microscopic observation. Drawings were made with the aid of a drawing tube attached to a dissecting microscope.

Measurements taken were as follows: carapace length (CL), from the tip of the rostrum to the posterodorsal margin of carapace in the midline; 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. At least five specimens of each stage were measured using a calibrated ocular micrometer.

RESULTS

Development and Duration of the Larvae

In the complete larval development of *Parapagurodes constans*, there were four zoeal stages and one megalopal stage (Fig. 1). Of the 40 individually reared zoeal larvae, 22 zoeae

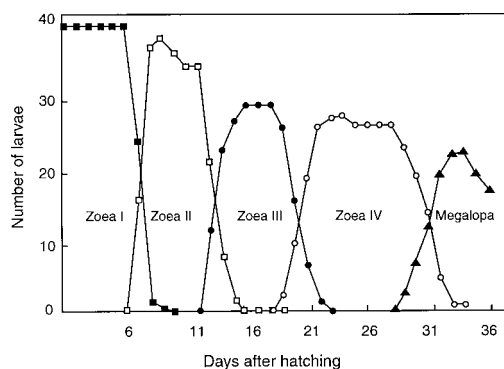


Fig. 1. *Parapagurodes constans* (Stimpson). Survival and duration by stage of larvae reared under laboratory conditions of $15^{\circ} \pm 2^{\circ}\text{C}$ and $34\text{‰} \pm 2\text{‰}$.

molted to megalopae. Although not indicated in Fig. 1, 10 megalopae molted to the first crab stage after 10 days.

Descriptions

First Zoea

Fig. 2

Size.—CL = 0.9–1.1 mm (mean 1.0 mm); TL = 2.5 mm (mean 2.5 mm).

Duration.—7–9 days.

Carapace (Fig. 2A, B).—Rostrum slightly longer than or approximately equal to length of antennae; posterolateral carapace spines small; eyes sessile.

Abdomen (Fig. 2A, B, K).—Five somites and telson; last somite fused with telson; posterodorsal margins of somites as follows: first somite naked, with 2 pairs of very small spines, second through fifth somites each with pair of middorsal setae on posterior margin and 2 pairs of spines, outermost pair frequently smaller, spine pairs progressively increasing in size posteriorly; posterolateral margins of somites 2–4 each with small spine; fifth somite with pair of strong, elongate posterolateral spines.

Telson (Fig. 2K).—Fan-shaped posteriorly; posterior margin with shallow median cleft and 7+7 processes, outermost an immovable naked spine, second an anomuran hair, third through seventh articulated, plumodenticulate

processes, of which fourth is longest; very short marginal setae between processes and on median cleft; anal spine present.

Antennule (Fig. 2C).—Subcylindrical, indistinctly bilobed, more than one-half length of antenna; exopod fused to protopod, with 5 aesthetascs; rudimentary endopodal bud with 1 long plumose terminal seta.

Antenna (Fig. 2D).—Scaphocerite with elongate distal spine; inner margin with 6 plumose setae; endopod shorter than scaphocerite, naked; protopod with strong spine armed with tiny denticles at base of endopodal junction.

Mandible (Fig. 2E).—Asymmetrically dentate; incisor process with strong teeth and few smaller teeth; molar process with few strong teeth and few acute small teeth; no palp bud.

Maxillule (Fig. 2F).—Endopod 3-segmented; setal formula progressing distally 2,1,3; coxal endite with 1 simple and 4 plumodenticulate setae marginally and 2 short simple setae submarginally; basal endite with 2 strong, elongate spinelike teeth armed with 2–6 small denticles and 2 short simple setae submarginally.

Maxilla (Fig. 2G).—Endopod weakly bilobed, with 3 marginal plumose setae on proximal lobe and 3 marginal and 1 submarginal plumose setae on distal lobe; coxal and basal endites distinctly bilobed; coxal endite with 1 submarginal and 6 marginal plumose setae on proximal lobe, 3 marginal and 1 submarginal plumose setae on distal lobe; basal endite with 4 marginal and 1 submarginal plumose setae on proximal lobe, 1 submarginal and 3 marginal plumose setae on distal lobe; scaphognathite posteriorly fused to protopod, distal lobe with 5 short, marginal plumose setae.

First Maxilliped (Fig. 2H).—Coxopod usually with 1 simple marginal seta; basipod with setal formula progressing distally 2,1,1,3,3; endopod 5-segmented, segmental setation proximal to distal 3,2,1,2,4+1 and additional fine setae on lateral margins of segments 1–3; exopod incompletely 2-segmented, with 4 terminal natatory setae.

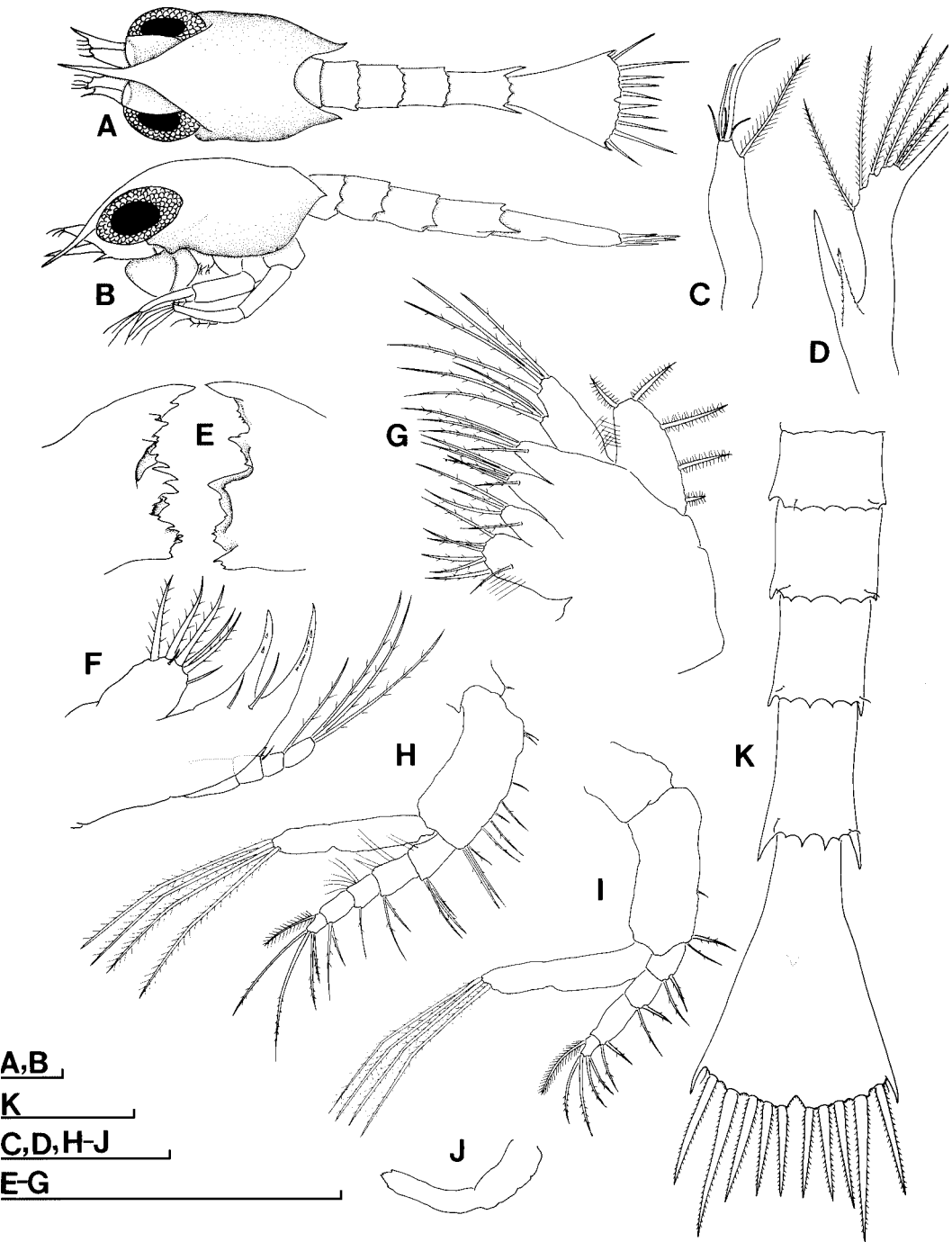


Fig. 2. *Parapagurodes constans* (Stimpson). First zoea. A, Dorsal view; B, Lateral view; C, Antennule; D, Antenna; E, Mandible; F, Maxillule; G, Maxilla; H, First maxilliped; I, Second maxilliped; J, Third maxilliped; K, Abdomen and telson. Scale bars = 0.4 mm.

Second Maxilliped (Fig. 2I).—Coxopod without setae; basipod with 1 simple marginal seta in distal half, 1 strong spinose process armed with marginal spinules, 1 plumose seta at distal angle; endopod 4-segmented, segments 1–3 each with 1 strong spinose process armed with marginal spinules and 1 plumose seta, distal segment with 4+1 plumose setae; exopod incompletely 2-segmented, with 4 terminal natatory setae.

Third Maxilliped (Fig. 2J).—Exopod unsegmented, simple or weakly bifurcated terminally.

Color.—Zoea transparent overall; red chromatophores on cephalothrax, above maxillipeds, at bases of mandibles and antennules, between fifth somite and fused sixth somite/telson, third somite of abdomen; yellow chromatophores on lateral carapace; corneas black.

Second Zoea Fig. 3

Size.—CL = 1.3–1.5 mm (mean 1.4 mm); TL = 2.7–3.1 mm (mean 2.9 mm).

Duration.—5–27 days.

Carapace (Fig. 3A, B).—Larger, but generally unchanged from stage I; rostrum slightly longer or equaling length of antenna; eyes stalked.

Abdomen (Fig. 3A, B).—Posterodorsal spines no longer apparent on somite 1, reduced on somites 2, 3; posterolateral angles with some increase in strength of spines; second through fifth somites each with pair of lateral setae.

Telson (Fig. 3K).—Posterior margin with 8+8 processes, with additional short median pair of spines; median cleft obsolescent or absent; anal spine absent.

Antennule (Fig. 3C).—Still weakly bilobed; endopod with 1 terminal plumose seta; exopod with 1 large and 4 small aesthetascs.

Antenna (Fig. 3D).—Spine of scaphocerite still very prominent, overreaching endopod, inner margin with 7 plumose setae; naked endopod still fused to protopod; protopod still with strong denticulate spine at endopodal junction.

Mandible (Fig. 3E).—Larger, but generally unchanged from stage I.

Maxillule (Fig. 3F).—Endopod unchanged from stage I; coxal endite now with 1 simple and 4 plumose setae marginally and 2 short simple setae submarginally; basal endite with 4 strong teeth each armed with 2–4 small denticles and 2 simple submarginal setae.

Maxilla (Fig. 3G).—Endopod and endites unchanged from stage I; scaphognathite now with 7 short marginal plumose setae.

First maxilliped (Fig. 3H).—Coxopod and basipod setation unchanged from stage I; endopod setal formula now 3+1,2+1,1+1,2,4+1; exopod now with 7 terminal natatory setae.

Second Maxilliped (Fig. 3I).—Coxopod and basipod setation unchanged from previous stage; endopod setal formula now 2,2+1,2+1,4+1; exopod now with 7 terminal natatory setae.

Third Maxilliped (Fig. 3J).—Protopod naked; exopod still incompletely 2-segmented, with 6 terminal natatory setae; endopod bud with 2 terminal simple setae.

Pereopods.—Distinct buds present.

Third Zoea Fig. 4

Size.—CL = 1.4–1.7 mm (mean 1.6 mm); TL = 3.1–3.7 mm (mean 3.4 mm).

Duration.—6–9 days.

Carapace (Fig. 4A, B).—Larger, but generally unchanged from stage II; rostrum now shorter than antennae.

Abdomen (Fig. 4A, B).—Posterodorsal spines very much reduced or absent on somites 2–4, reduced on somite 5; sixth somite now delineated, posterior margin unarmed; incompletely biramous uropods present, inner margins of exopods each with 5 plumodenticulate setae, endopodal bud naked.

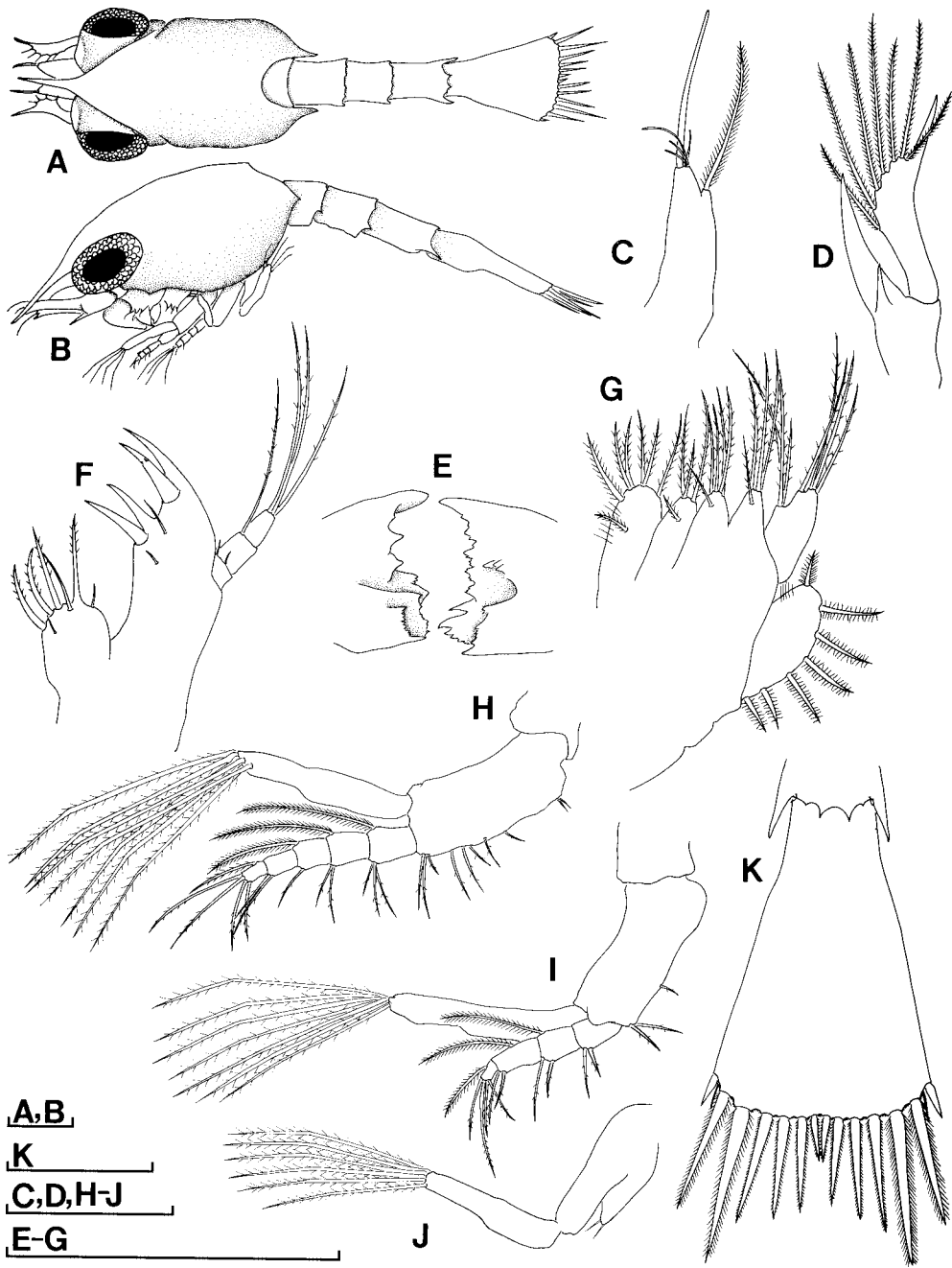


Fig. 3. *Parapagurodes constans* (Stimpson). Second zoea. A, Dorsal view; B, Lateral view; C, Antennule; D, Antenna; E, Mandible; F, Maxillule; G, Maxilla; H, First maxilliped; I, Second maxilliped; J, Third maxilliped; K, Telson. Scale bars = 0.4 mm.

Telson (Fig. 4K).—Armature of terminal margin unchanged from stage II, fourth process clearly articulated and much larger than other processes.

Antennule (Fig. 4C).—Exopod with 3 large and 3 small aesthetascs marginally, 2 aesthetascs submarginally; endopod with 1 terminal plumose seta; protopod with 1 plumose seta at

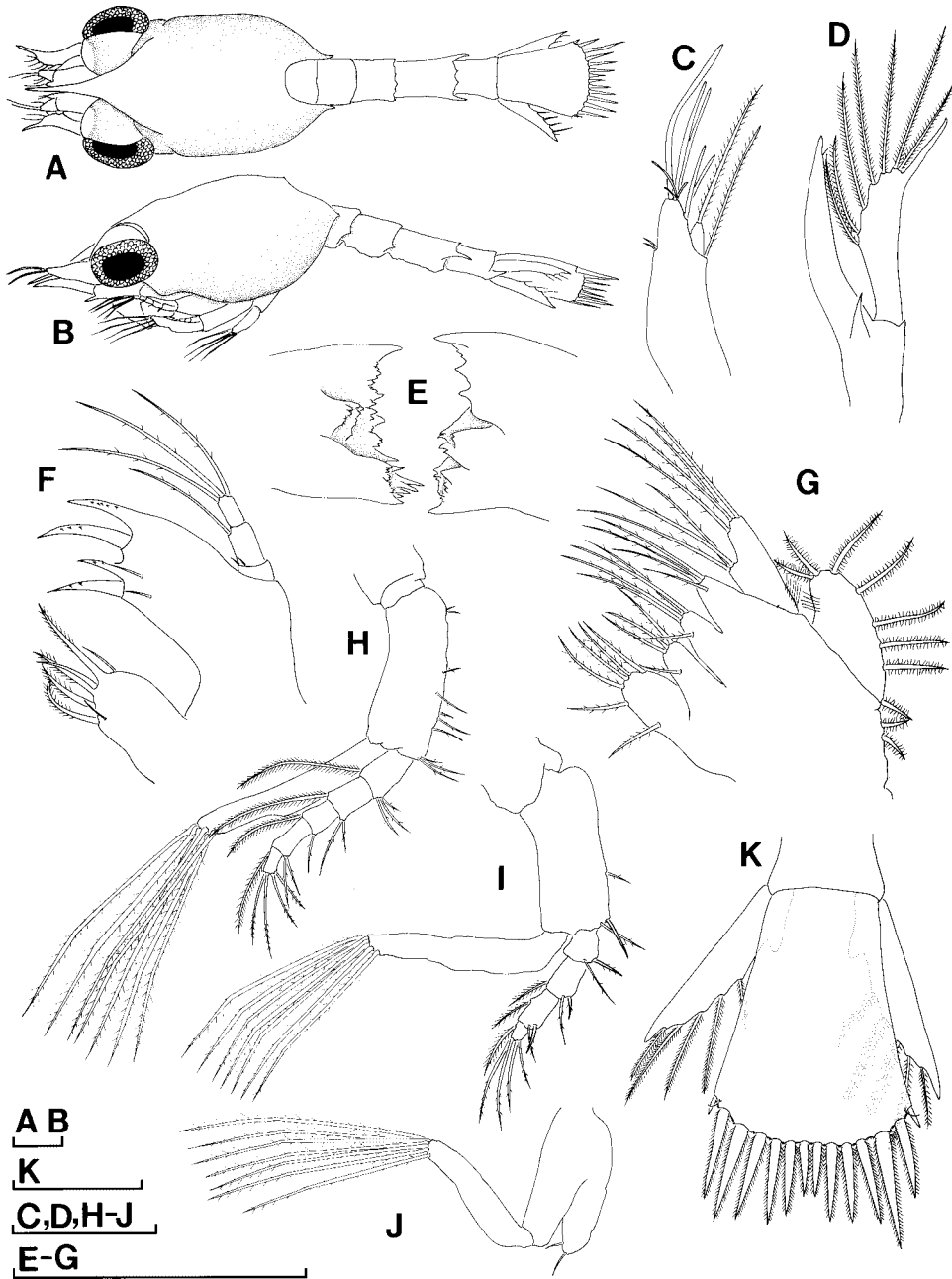


Fig. 4. *Parapagurodes constans* (Stimpson). Third zoea. A, Dorsal view; B, Lateral view; C, Antennule; D, Antenna; E, Mandible; F, Maxillule; G, Maxilla; H, First maxilliped; I, Second maxilliped; J, Third maxilliped; K, Telson. Scale bars = 0.4 mm.

endopodal junction and 2 short simple or weakly plumose setae at exopodal margin.

Antenna (Fig. 4D).—Margin of scaphocerite unchanged from stage II, inner margin with 7

plumose setae; endopod approximately equaling length of scaphocerite, inner margin with 1 subterminal seta; protopodal junction still with strong denticulate spine at endopodal junction and now additional small unarmed spine at base of scaphocerite.

Mandible (Fig. 4E).—Larger and with more acute teeth and denticles, but otherwise unchanged from stage II.

Maxillule (Fig. 4F).—Unchanged from stage II.

Maxilla (Fig. 4G).—Setation of endopod and endites unchanged from stage II; scaphognathite now with 10 or 11 short marginal plumose setae.

First Maxilliped (Fig. 4H).—Unchanged from stage II.

Second Maxilliped (Fig. 4I).—Unchanged from stage II.

Third Maxilliped (Fig. 4J).—Exopod now with 7 terminal natatory setae; endopod enlarged but still with 2 simple setae.

Pereopods.—Cheliped bud with dactyl distinguishable; gill buds absent.

Fourth Zoea Fig. 5

Size.—CL = 1.8–2.0 mm (mean 1.9 mm); TL = 4.0–4.3 mm (mean 4.1 mm).

Duration.—10–12 days.

Carapace (Fig. 5A, B).—Larger but essentially unchanged from stage III.

Abdomen (Fig. 5A, B).—Somites 2–5 with pleopod buds present. Uropodal exopods now separated from protopods, inner margins each with 6 plumodenticulate setae, terminating in strong spine; endopod buds fused to protopods, naked.

Telson (Fig. 5L).—Unchanged from stage III.

Antennule (Fig. 5C).—Endopod bud approximately two-thirds length of exopod, naked but with acute tip; aesthetascs of exopod progressing distally 2,3,3 large and 2 terminal; protopod still with 1 long plumose seta at endopodal junction and 2 short simple or weakly plumose setae at exopodal margin.

Antenna (Fig. 5D).—Margin of scaphocerite unchanged from stage III, inner margin with 6 or 7 plumose setae; endopod elongate and 2-segmented.

Mandible (Fig. 5E).—Enlarged; palp bud present.

Maxillule (Fig. 5F).—Endopod unchanged from stage III; coxal endite now with 1 simple and 5 plumodenticulate setae marginally and 2 short simple setae submarginally; basal endite with 6 strong teeth, most armed with several small denticles, and with 2 submarginal setae.

Maxilla (Fig. 5G).—Endopod with 2 marginal plumose setae on proximal lobe and 3 marginal and 1 submarginal plumose setae on distal lobe; setation of endites unchanged from stage III; scaphognathite with 12 marginal plumose setae on distal lobe; proximal lobe distinct, elongate, naked.

First Maxilliped (Fig. 5H).—Basipod and endopod unchanged from stage III; exopod usually with 8 natatory setae.

Second Maxilliped (Fig. 5I).—Basipod and endopod unchanged from stage III; exopod with 8 terminal natatory setae.

Third Maxilliped (Fig. 5J).—Endopod with 1 terminal and 2 subterminal plumose setae; exopod incompletely 2-segmented, with 8 natatory setae.

Pereopods.—Cheliped with chela enlarged, dactyl distinct; ambulatory legs moderately elongate.

Gills (Fig. 5K).—Pereopods 1–4 each with pair of arthrobranch buds, fourth also with 1 pleurobranch bud.

Megalopa Figs. 6, 7

Size.—SL = 0.9–1.0 mm (mean 0.9); TL = 2.7–2.8 mm (mean 2.8 mm).

Carapace (Fig. 6A, B).—Shield approximately two-thirds total carapace length, usually slightly longer than broad; rostrum moderately slender, subacute, and occasionally with small acute tip,

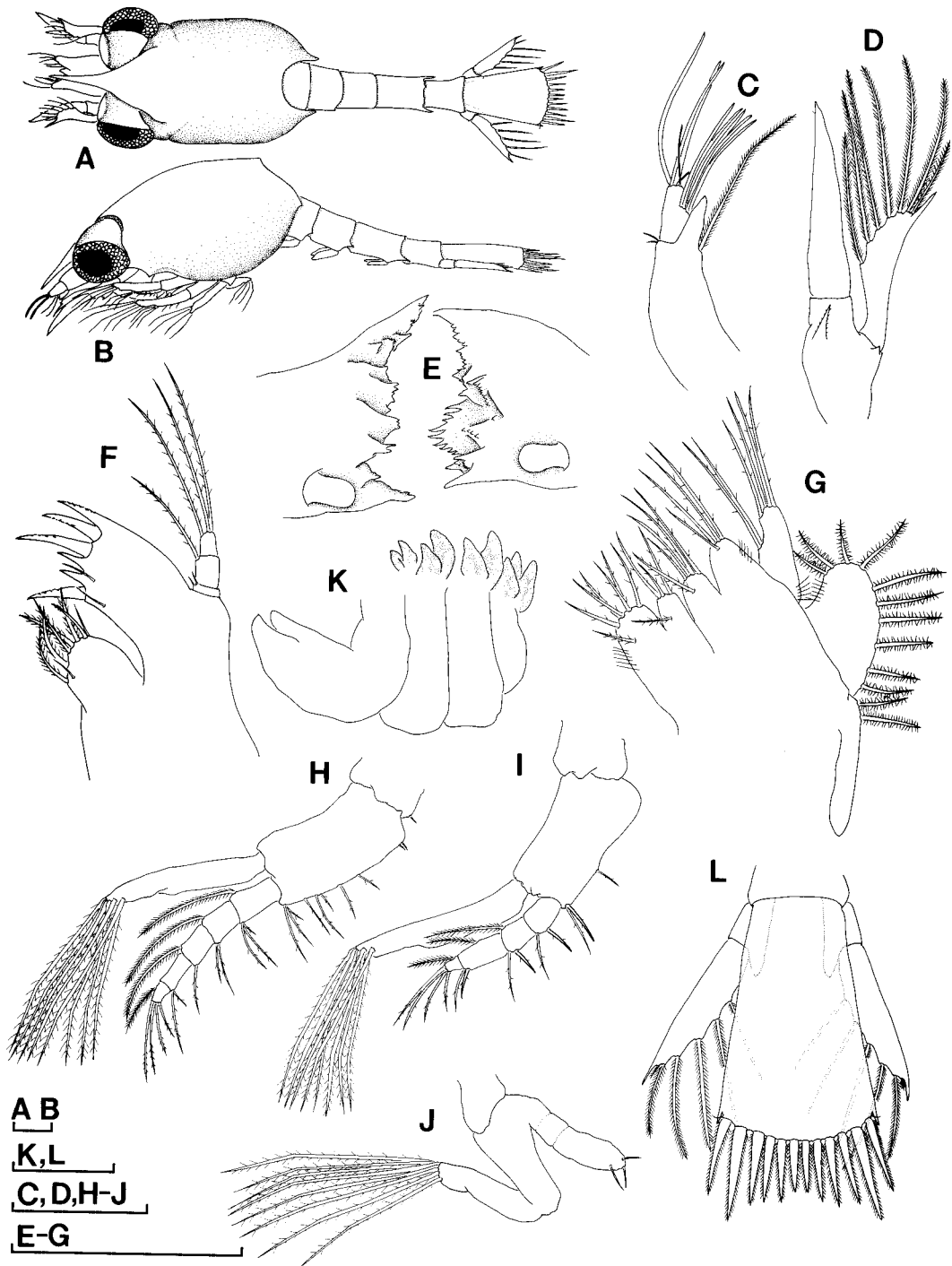


Fig. 5. *Parapagurodes constans* (Stimpson). Fourth zoea. A, Dorsal view; B, Lateral view; C, Antennule; D, Antenna; E, Mandible; F, Maxillule; G, Maxilla; H, First maxilliped; I, Second maxilliped; J, Third maxilliped; K, Pereopods and gills; L, Telson. Scale bars = 0.4 mm.

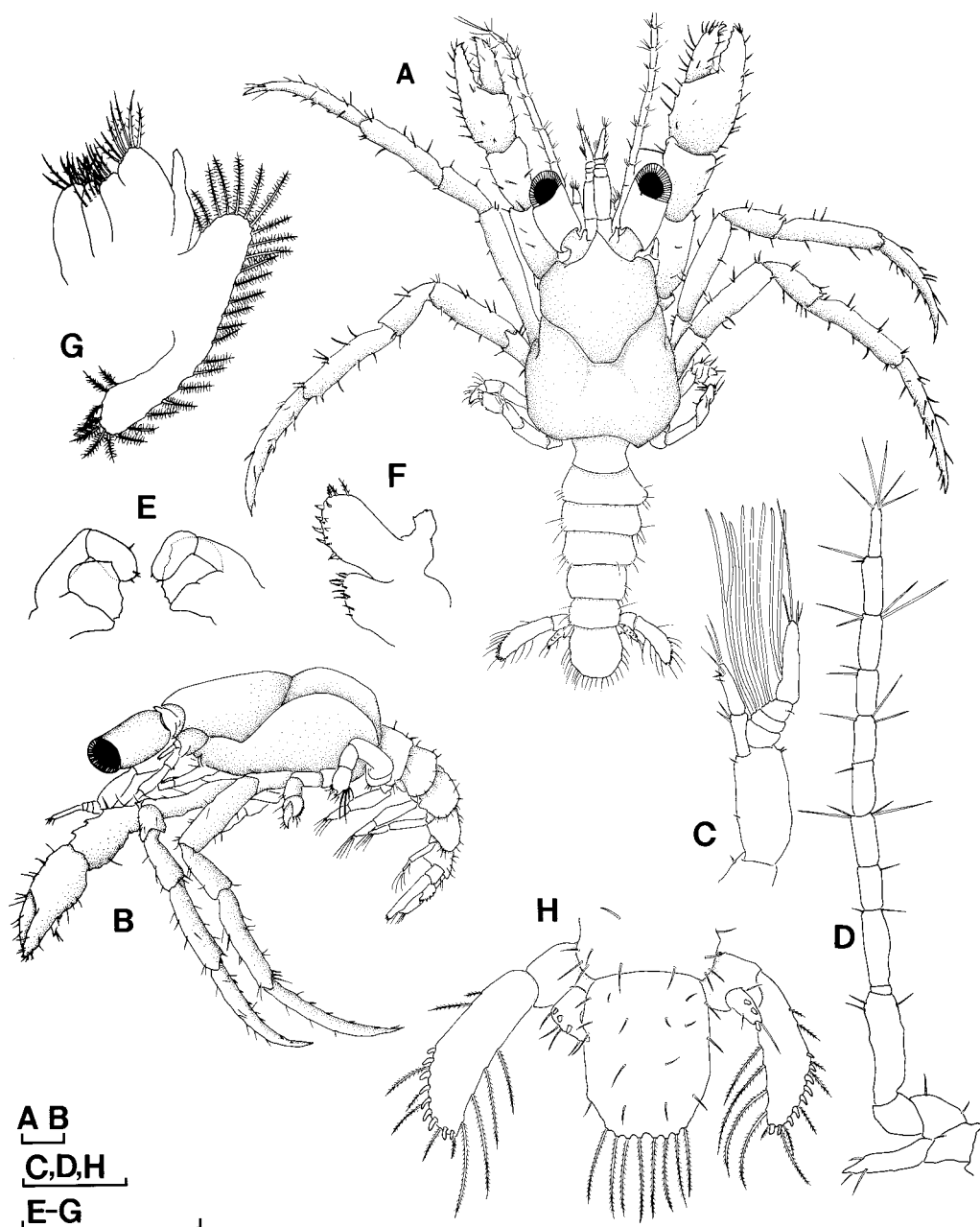


Fig. 6. *Parapagurodes constans* (Stimpson). Megalopa. A, Dorsal view; B, Lateral view; C, Antennule; D, Antenna; E, Mandible; F, Maxillule; G, Maxilla; H, Telson. Scale bars = 0.4 mm.

not overreaching moderately developed ocular acicles. Ocular peduncles moderately short, corneas slightly dilated.

Abdomen (Fig. 6A, B).—With six somites, all unarmed but with scattered short setae on dorsal and lateral surfaces; symmetrical biramous

pleopods (Fig. 7K) on somites 2–5; exopods well developed, each with 8–9 marginal, plumose setae; endopods each with appendix interna consisting of 2 apical hooks.

Tail Fan (Fig. 6H).—Telson with numerous scattered setae on dorsal surface; posterior

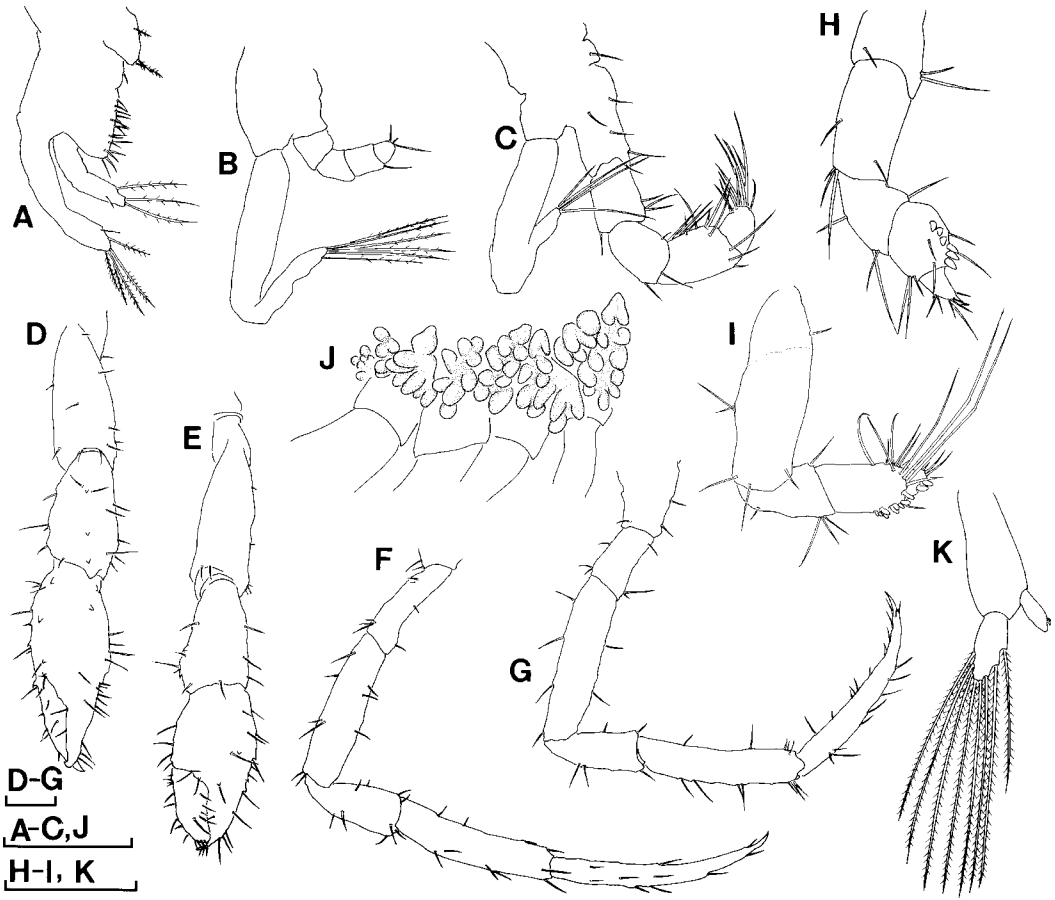


Fig. 7. *Parapagurodes constans* (Stimpson). Megalopa. A, First maxilliped; B, Second maxilliped; C, Third maxilliped; D, Right cheliped; E, Left cheliped; F, Second pereopod; G, Third pereopod; H, Fourth pereopod; I, Fifth pereopod; J, Gills; K, Pleopod. Scale bars = 0.4 mm.

margin straight or slightly convex, setal formula 4+4; uropods symmetrical, biramous, protopods naked; exopods with 9 scalelike processes posterolaterally and 11 or 12 long setae; endopods with 3 scalelike processes and 3 or 4 short setae.

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

Antenna (Fig. 6D).—With supernumerary segment apparent; acicle terminating acutely, often with several scattered short setae; flagellum usually with 10 articles, setal formula variable.

Mandible (Fig. 6E).—Reduced and simplified, incisor and molar processes indicated only by pairs of small protuberances; palp incompletely 2-segmented, terminal segment with 2–4 small marginal setae.

Maxillule (Fig. 6F).—Endopod unsegmented, naked; coxal endite with 10 setae; basal endite with 11 or 12 teeth in 2 or 3 rows and 3 short plumose setae.

Maxilla (Fig. 6G).—Endopod unsegmented and naked; coxal and basal endites still bilobed,

Table 1. Comparison of morphological characters of larval stages of *Parapagurodes constans*, *Parapagurodes hartae*, and *Pagurus ochotensis*.

Characters	<i>Parapagurodes constans</i> (present study)	<i>Parapagurodes hartae</i> (McLaughlin and Jensen, 1996)	<i>Pagurus ochotensis</i> (Quintana and Iwata, 1987)	<i>Pagurus ochotensis</i> (McLaughlin et al., 1992)
Middorsal setae on abdomen	present on somites 2–5	absent	present on somites 4 and 5	absent
Carapace length of Zoea I	1.0 mm	0.92–1.00 mm	1.78 mm	1.52–1.67 mm
Anal spine of Zoea I	present	present	present	present
Lateral spines on somite 5	long	long	long	long
First telson process of Zoea I	fused	articulated	articulated	articulated
Fourth telson process	long	long	long	long
Morphology of the antennal endopod of Zoea I	simple	bifid	simple	simple
Number of antennal endopod setae	6 or 7	9	7 or 8	6 or 7
Number of maxillular endopodite	2+1+3	2+1+3	2+1+3	1+1+3
Mandibular palp of Zoea IV	present	–	present	present
Number of uropod endopod setae	0	–	0	0
Pleopod number of Zoea IV	4	–	4	4
Length of the A2 of Megalopa	long	–	long	long

–: presently unknown.

coxal endite with 5 and 4 marginal plumose setae on proximal and distal lobes, respectively; basal endite with 5 and 7 plumose marginal setae on proximal and distal lobes, respectively; scaphognathite with 28–30 moderately short marginal plumose setae.

First Maxilliped (Fig. 7A).—Exopod incompletely 2-segmented, distal segment with 6 plumose setae; endopod unsegmented, with 3 plumose setae marginally and 1 submarginal simple seta; coxal endite with 3 short plumose setae marginally or submarginally; basal endite broad, with 17 or 18 marginal plumose setae.

Second Maxilliped (Fig. 7B).—Endopod 4-segmented, basal and second segments naked, penultimate segment with 1 short simple seta, ultimate segment with 3 terminal simple setae; exopod 2-segmented, distal segment with 6 plumose setae.

Third Maxilliped (Fig. 7C).—Endopod 5-segmented, all segments with numerous setae, those of ultimate and penultimate segments often serrated or barbed; exopod incompletely 2-segmented, distal segment with 4 terminal plumose setae.

Pereopods (Fig. 7D–I).—Chelipeds unequal, right somewhat larger. Cutting edges of dactyl and fixed finger of right cheliped with few small teeth; chela with 4 small spines on dorsomesial

margin, 4 slightly smaller spines on dorsolateral margin; carpus with 3 spines on dorsomesial margin; merus unarmed; all segments with scattered setae. Cutting edges of dactyl and fixed finger of left cheliped with few small teeth; chela with 2 small spines on dorsomesial margin and occasionally with scattered low protuberances on dorsal surface; carpus with 2 or 3 spines on dorsolateral margin; merus unarmed; all segments with scattered setae (Fig. 7D, E). Ambulatory legs moderately long; dactyls each with row of small spinules on ventral margin, all segments with scattered setae (Fig. 7F, G). Fourth pereopod with several large scales on propodal margin (Fig. 7H). Fifth pereopod with several corneous scales on propodus and scattered setae (Fig. 7I).

Gills (Fig. 7J).—Arthrobranchs of chelipeds slightly larger than in stage IV; arthrobranchs of second to fourth and pleurobranch of fourth becoming lobular.

DISCUSSION

According to the generic diagnosis of McLaughlin and Haig (1973) that has been emended by Komai (1999), adults of *Parapagurodes* are distinguished from those of *Pagurus* species primarily by gill structure and sexual tube development on the coxa of the fifth pereopod. *Parapagurodes* have eleven pairs of biserial gills, but gill lamellae sometimes with a shallow median indentation, cleft,

or concavity. Males of *Parapagurodes* have a short to very short sexual tube developed on the coxa of the right fifth pereopod, left usually lacking, but occasionally with short sexual tube. Komai (1999) redescribed the adult morphology of *Pagurus constans* from Boso Peninsula, central Japan, and reported that the generic diagnosis of adult *Pagurus constans* are similar to those of *Parapagurodes*. Based on his works, Komai (1999) transferred *Pagurus constans* to the genus *Parapagurodes*.

The first zoea of *P. constans* in the present study differs from those of *P. makarovi*, *P. laurentae*, and *P. hartae* in several points. The most remarkable difference is found in the shape of the first telson process: in *P. constans*, it is a fused spine, whereas in *P. makarovi*, *P. laurentae*, and *P. hartae*, it is an articulated spine. *Parapagurodes constans* is also distinguished from *P. hartae* in the antennal endopod form, carapace shape, and abdominal armature. *Parapagurodes constans* has a simple antennal endopod, whereas *P. hartae* has a bifid antennal endopod (Table 1).

It is noted that the larvae of *Parapagurodes constans* differ from those of both other *Parapagurodes* or *Pagurus* in having a pair of middorsal setae on abdominal somites 2–5 in all zoeal stages. These middorsal setae have not been commonly reported in the larvae of pagurids. Of the previously known pagurid larvae, those of *Pagurus ochotensis* Brandt, 1851, described by Quintana and Iwata (1987) have such middorsal setae, whereas those of *P. ochotensis* described by McLaughlin *et al.* (1992) do not have such setae on the abdomen. The middorsal setae are also found in the larvae of *Phimochirus holthuisi*, described by Gore and Scotto (1983). In addition to the middorsal setae on the abdomen, the zoeal morphology of *Pagurus ochotensis* is rather similar to that of *Parapagurodes constans* in several points except for the shape of the first telson process of the first zoeal stage (Table 1). *Parapagurodes constans* has a fused first telson process, whereas *Pagurus ochotensis* has an articulated one.

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